

ECOLOGICAL STUDY OF SAN ANTONIO BAY

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Biological Study of San Antonio Bay

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EXECUTIVE SUMMARY

The purpose of this project was to compile, evaluate and present information on several features of the ecology of San Antonio Bay, as the first phase of a projected study of the causal relations between external forcing, notably but not exclusively freshwater inflow, and measures of the quality of the bay ecosystem. Properties of San Antonio Bay that would facilitate exposing estuary responses to freshwater inflow include:

- (1) Almost all of the freshwater input to the system, i.e. the confluence of the Guadalupe and San Antonio rivers, enters at the head of the estuary (in contrast to multiple entry points characteristic of most of the Texas bays).
- (2) Development around the periphery of the bay is relatively minor.
- (3) The bay is not transected by a deep-draft ship channel (which in other bays is responsible for increasing salinity of the estuary).
- (4) Because of its geographic location, San Antonio Bay is alternately exposed to drought and wet hydroclimatology on a time scale of years.
- (5) Because of its relatively slow exchange with the sea, because of the absence of a direct inlet, the effects of wet and dry conditions tend to be sustained in San Antonio Bay.

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.

This report addresses the characteristics of freshwater inflow to San Antonio Bay, including the relative contributions of various sources of freshwater, the status and evolution of the closest inlet to the sea, namely Cedar Bayou, and the attributes of time-space distribution of a selected organism, the blue crab (*Callinectes sapidus* Rathbun) in San Antonio Bay.

The main contributors of inflow to San Antonio Bay are runoff from the land surface, and human diversions and return flows. Most of this inflow is carried into the bay in stream channels, the

most important of which are the Guadalupe River and the San Antonio River, which conflow about 6 km (4 mis) upstream from the bay. Based upon analysis of the 1942-2009 period of record, some 94% of the watershed is gauged, representing about 89% of the total inflow. The remainder derives from the ungauged portions of the watershed, which are generally on the coastal prairie (including the peripheral drainage around the bay).

Averaged over the period analyzed, approximately 69% enters from the Guadalupe watershed, 33% from the San Antonio watershed, 4% from the bay periphery and -5% from net returns over diversions. The human component, i.e., the net of returns over diversions, is minor, generally within the uncertainty of measurement of the gauged inflows. During wet conditions, especially floods, this is negligible compared to runoff and river flow. However, during drought conditions, the proportionate influence of human water use becomes a much greater factor in the water budget. The components of inflow are quantified and presented in the report in both tabular and graphical formats.

Seasonally, the annual pattern of inflows to the bay is bimodal, with high inflows in the spring and fall. There has been a substantial increasing trend in inflow to the bay over the 1942-2009 period. The annual inflows to the bay have increased about 80% over this period. The time variability in inflow has changed as well, with increasing high-flow surges separated by more intense drought periods. Over the 1942-2009 record, the magnitude of these surges has increased by about a factor of two. Over this period, there appears to be little association of wet versus dry conditions with El Niño - La Niña conditions in the Equatorial Pacific.

Ten droughts exceeding one-year duration occurred in the 1942-2009 record, representing 40.5 of the 68-year period, i.e., the bay inflows are in drought conditions about 60% of the time. A distinction is made between the severity and the intensity of a drought (based upon a drought-analysis methodology with some novelty). The most *severe* drought on record is the Drought of the Fifties. The three most *intense* droughts on record have occurred in the last two decades. Most intense was the drought of 2008-09.*

* This work was completed before the drought of 2010-11, which will probably exceed the others in intensity.

Inflows dilute marine waters in an estuary thereby reducing salinity. This would suggest there should be a direct relation between inflow and salinity, but this is corrupted by responses of salinity to external factors other than inflow, such as internal circulations and evaporation. Salinity responses to freshwater inflow in the lower segment of the bay (where the main salinity gradient is generally located) were studied by a sigmoid regression, which was found to explain nearly 75% of the variance in the measurements.

Exchanges with the sea are an important feature of the hydrography of an estuary. For San Antonio Bay, the principal exchanges occur through the Pass Cavallo complex (including the Matagorda Entrance Channel) and through Aransas Pass. The closest inlet to the bay, however, is Cedar Bayou. When open, Cedar Bayou is an effective passage for migratory organisms, so analysis of long-term organism abundance data requires knowledge of the state of the pass.

This project constructed a chronology for Cedar Bayou for 1900-2009. Cedar Bayou has tended to diminish in size from the surveys of the early twentieth century to the aerial photography of the twenty-first century. It has been chronically closed, or just marginally open, during the past three decades, despite two dredging projects. The mechanisms that scour and maintain tidal inlets seem to be operating at roughly the same intensity and frequency over this period, except perhaps for freshwater inflow, which is trending upward. The largest recorded cross sections of Cedar Bayou (in the 1900-2009 period) were attained in the late 1960's to early 1970's (during which Texas Parks and Wildlife performed an intensive study of migratory organisms using the inlet).

The blue crab (*Callinectes sapidus* Rathbun) is a ubiquitous crustacean in San Antonio Bay. 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. A substantial literature survey of the biology and life stages of the blue crab was carried out in this project, with particular emphasis upon the Texas environment. 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 from that on the

Atlantic. The survey was undertaken to better qualify literature results for their applicability to the Texas environment. In general, 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 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. For example, in Delaware Bay and Chesapeake Bay, the females hatch their brood in the mouths of the estuaries. In San Antonio Bay, they migrate into the Gulf before hatching.

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, 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 is capable of carrying the larval patches many tens of kilometers down the coast. At the same time, cross-shelf transport mixes the patches across the shelf potentially several tens of kilometers. During late summer, on both coasts, the longshore currents reverse, setting to the northeast. This would transport the larvae back up the coast. The net effect is to disperse the larvae and postlarvae along the coast and make the postlarvae available to 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 megalop 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 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 this 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 with this variable 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 the sudden reduction of salinity 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), which will be undertaken in the next phase of work on this project.

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 other 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.

Researchers in Louisiana have found the decline to be associated with a large-scale climatological change, namely the Atlantic multidecadal oscillation (AMO). Prior to 1995, conditions were wet with high runoff, and associated high catches of blue crab. After 1995, conditions became drier and the blue crab catches dropped. These researchers noted also the pre-1995 cold-AMO period was also associated with strong onshore (south) winds, in contrast to the 1997-2005 period. That such a drop in crab abundance occurred 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, and, if anything, are higher, not lower, during the later period. The fact that the pre-1995 conditions were also correlated with stronger onshore wind would suggest that the difference in abundance may be keyed to megalop supply, rather than hydrology.

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1. INTRODUCTION

This report presents the results of first phase of a projected two-phase study addressing several aspects of the ecology of San Antonio Bay on the south Texas coast. 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. (2010).

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. The project strategy is founded on these premises.

The first phase of this project was primarily one of data compilation and information gathering, to support the more technical second phase of the project. This report addresses the characteristics of freshwater inflow to San Antonio Bay, including the relative contributions of



Figure 1-1 - San Antonio Bay

various sources of freshwater, the status and evolution of the closest inlet to the sea, namely Cedar Bayou, and the attributes of time-space distribution of a selected organism, the blue crab (*Callinectes sapidus* Rathbun) in San Antonio Bay. Although parts of the report require some technical background in hydromechanics, statistics, or data processing, the report has been written to be largely accessible to the nonspecialist.

A word of explanation is needed about units of measurement. 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. The preference observed in this report is 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. INFLOWS AND SALINITY IN SAN ANTONIO BAY

2.1 Inflows to San Antonio Bay

The watershed of San Antonio Bay is comprised of the basins of the Guadalupe and San Antonio Rivers, which conflow some 4 miles upstream from the estuary proper, and a relatively small peripheral area which drains directly into the bay. This overall drainage area, totaling 10,230 sq mis, is shown in Figure 2-1, including the principal watercourses and some geographic features. The fact that the river inflows enter the estuary through a single channel at the head of the

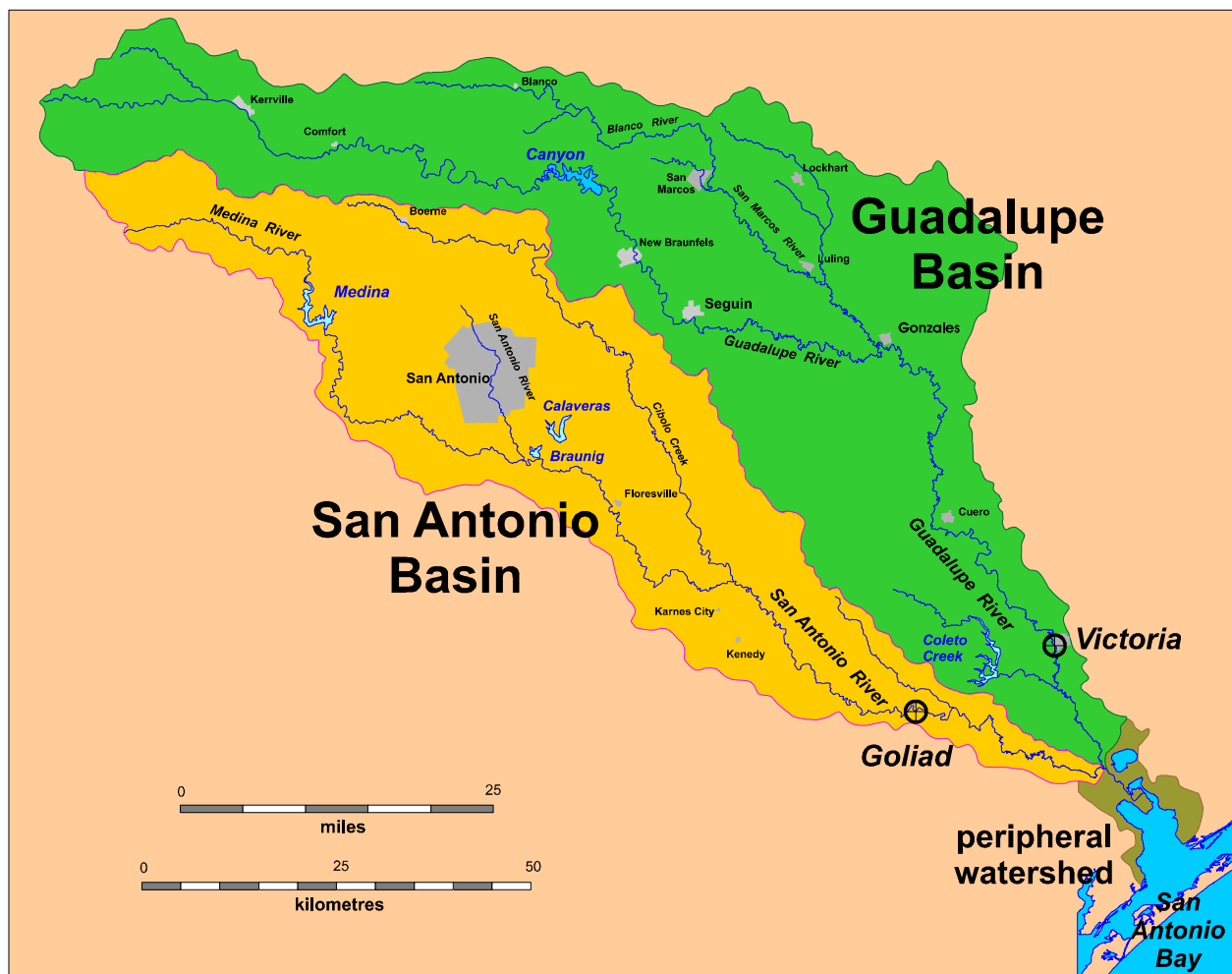


Figure 2-1 - Watershed of San Antonio Bay showing principal tributaries

estuary is unique to San Antonio Bay of all of the Texas estuaries. In many respects, this fact greatly simplifies the analysis of the response of the estuary, both hydrographically and ecologically, to freshwater inflow. In the river channel between the river confluence and the head of the estuary is located an inflatable dam, which serves as a salt barrier under low-flow conditions. Apart from preventing upstream migration of some species, this dam has little effect on the estuary, but it is a convenient location to differentiate the inflows from the river basins upstream, and runoff from the estuary periphery downstream.

The purpose of this chapter is to present a summary of the general hydrological features of San Antonio Bay, in particular to delineate the historical variation of inflows, their organization into periods of surfeit and deficit flows, notably drought, and to quantify the relative contributions from each of the river basins, peripheral runoff, and withdrawals and return flows. The emphasis is upon the longer term time variability of inflow, based upon measurements or estimates of the flows of water at a monthly resolution, utilizing a data base of nearly seven decades, from 1942-2009. It is intended that this report serve as an introduction to a more detailed study of the bay hydrology in which the short-term runoff events are isolated and quantified, and coupled with analyses of salinity response. In addition, it is hoped that, given the current interest in San Antonio Bay, the activities of the National Estuarine Research Reserve, and the present focus of the Senate Bill 3 process to formulate environmental flow standards for the Guadalupe-San Antonio basin, this report may find utility as a convenient reference.

2.1.1 Data sources

2.1.1.1 Streamflow

The lowest U.S. Geological Survey (USGS) gauges in the watershed are summarized in Table 2-1. (There is an additional recently installed gauge on the Guadalupe near Bloomington, but this presently reports only stage.) Gauges with appreciable records are those on the Guadalupe at Victoria, on Coleta Creek at two locations, and on the San Antonio at Goliad. The data from

Table 2-1
 Drainage areas (d/a) and periods of record (POR)
 of lowest gauges on the principal rivers

	<i>Guadalupe basin</i>			<i>San Antonio basin</i>		<i>salt barrier</i>
	Guadalupe Victoria	Coleta Crk Victoria Schroeder		San Antonio Goliad	San Antonio McFaddin	Guadalupe Tivoli
Number	8176500	8177500	8177000	8188500	8188570	8188800
d/a (mi ²)	5198	500	369	3921	4134	10128
POR	12/34-pres	7/39 - pres	1/30-10/79	7/24-pres	12/2005-pres	8/2000-pres
Missing		10/54-6/78	1/34 - 9/52	4/29-2/39		

these gauges provide measurements of flows from 94% of the watershed of the estuary (Table 2-1) for over six decades.

The remainder of the watershed below these locations is ungauged. While the flow originating from this drainage is generally a minority of that entering the bay, it is nonnegligible, and a complete accounting of the sources and variation of inflows must include this contribution. The Texas Water Development Board (TWDB) has developed a model that computes runoff flows from a small watershed, given the input of rainfall on the watershed and some key hydrological parameters of the surface and soil layers. This model, TxRR, is an adaptation of the SCS curve-number method, which is essentially statistical. This method was published as part of the SCS *National Engineering Handbook* based upon data from "small watersheds" collected by ARS in the 1950's and early 1960's (Mockus, 1972, see also the review in Ward and Benaman, 1999). TxRR has been under development for many years, and presently has the capability to accept daily rainfall data and produce modeled runoff flows on a daily resolution. The watershed identification scheme of TWDB, for the watersheds modeled by TxRR and used by TWDB in its water budgeting of San Antonio Bay, is summarized in Table 2-2, and depicted in the stem diagram of Figure 2-2 (cf. Fig. 2-1). TxRR model output is the source for the ungauged

Table 2-2
Texas Water Development Board TxRR model watersheds

<i>Guadalupe Basin</i>					
<i>ID no</i>	<i>d/a (mi²)</i>	<i>comments</i>			
18012	215.27	below Victoria, including Coleta Crk downstream from Victoria gauge, to point above confluence of Linn Bayou			
18014	141.70	between Schroeder gauge and Victoria gauge on Coleta Creek			
18020	43.90	from a point above confluence of Linn Bayou to the salt barrier			
<i>San Antonio Basin</i>					
<i>ID no</i>	<i>d/a (mi²)</i>	<i>comments</i>			
19011	101.53	Manahuilla Creek watershed			
19012	166.80	from Goliad gauge to confluence with Guadalupe			
<i>San Antonio Bay Periphery</i>			<i>Espiritu Santo (north shore)</i>		
<i>ID no</i>	<i>d/a (mi²)</i>	<i>ID no</i>	<i>d/a (mi²)</i>	<i>ID no</i>	<i>d/a (mi²)</i>
24601	22.90	24605	11.69	24608	47.11
24602	42.38	24606	6.83		
24603	7.02	24607	22.45		
24604	10.93				

watershed inflows used in the present study; however, we prefer to exclude the flow contribution to Espiritu Santo from the inflows to San Antonio Bay because this is regarded as a distinct estuarine system. (This leads to minor numerical differences in some of the monthly inflow values between these results and those of the TWDB.)

There are two complications in using the TxRR data for San Antonio Bay. The first arises from the two gauges on Coleta Creek. As indicated in Table 2-1, Schroeder (8177000) operated for about five years starting in 1930. Victoria (8177500) was installed in 1939 and operated until 1954. Meanwhile, Schroeder was re-activated in 1952, and operated until 1979 when it was inundated by Coleta Creek reservoir. Victoria was re-activated prior to the reservoir construction, and is now the operating gauge on the stream. Apart from minor periods of overlap, the operating gauge on Coleta Creek was Victoria from 1939 through the early 1950's,

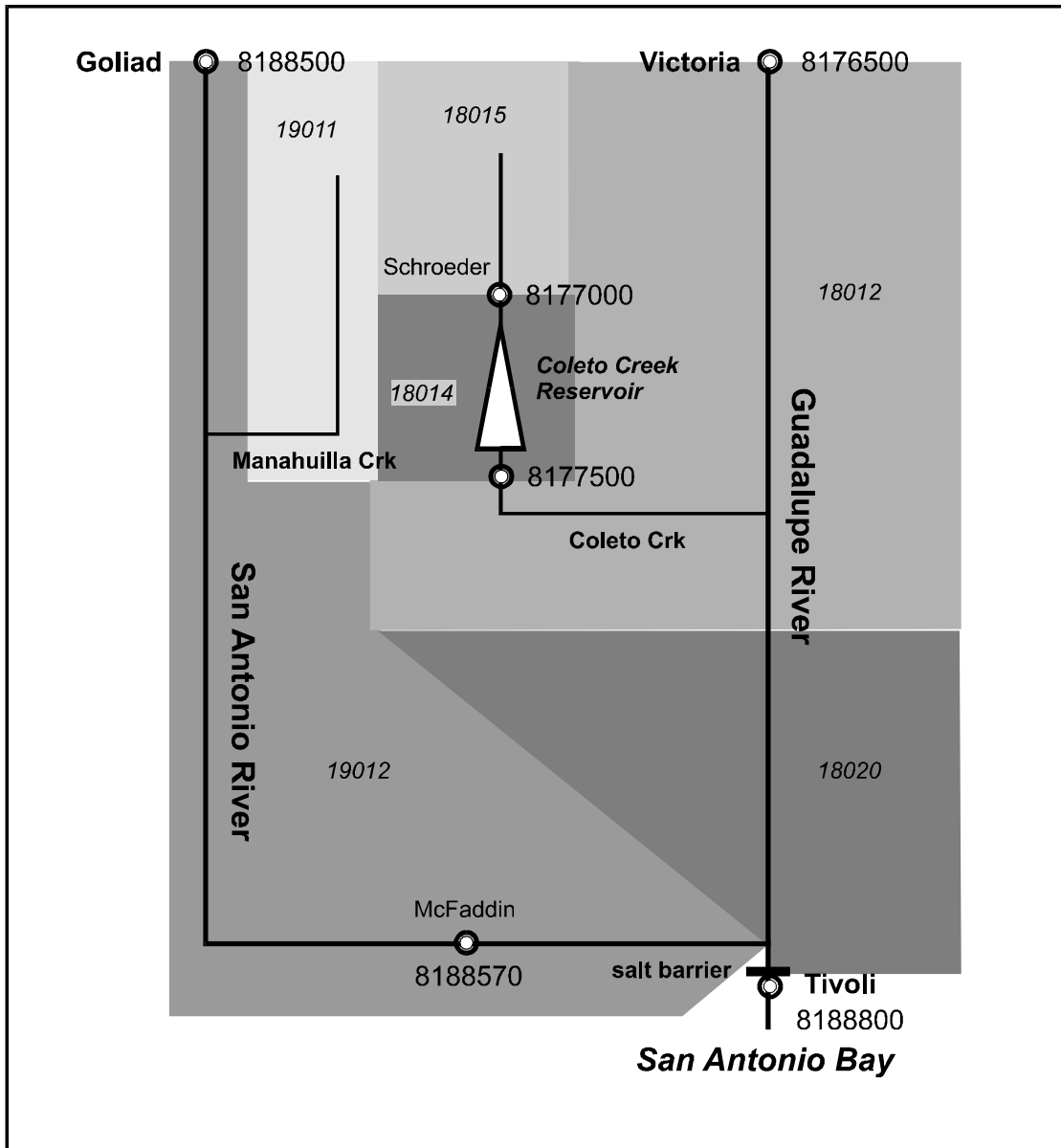


Figure 2-2 - Stem diagram of San Antonio Bay watershed downstream from principal gauges

Schroeder from the early 1950's through the beginning of impoundment in Coleta Creek Reservoir in 1979, and Victoria thereafter. For the period of record in which Schroeder was the functional gauge on Coleta Creek, TWDB operated TxRR for the watershed 18014 between the two gauges (Fig. 2-2).

The second complication derives from the history of computing water budgets in the Bays and Estuaries program at TWDB. The early development of a methodology for relating inflows to productivity in the 1960's and 70's culminated in the LP-series of reports for each major estuary of Texas, notably TDWR (1980) for San Antonio Bay, based upon the 1941-76 period of data. While the TxRR simulation must have been carried out for each of the watersheds of Table 2-2, and may have included daily resolution output (though it appears that TxRR was validated only for monthly runoff flows, see TDWR, 1980), the only results to have survived are the *monthly total ungauged* inflows for the bay. Apparently, the Thiessen-polygon-averaged rainfall input data have not survived either, making a re-run of TxRR for this period impractical. The later work at TWDB during the 1980's and 90's led to the formulation of the State Methodology presented in Longley (1994). This extended the period of hydrological data to include 1977-1986. Subsequent to the Longley (1994) report, TxRR runs were carried out through 2008, and in the past summer (of 2010) runs were extended through 2009. For the period 1977-2009, therefore, we have available *daily* TxRR model values of runoff flows for each of the watersheds of Table 2-2, except that 18014 results are only for the 1977-79 period (when the Schroeder gauge was operative).

The present objective is to use this data to construct a history of inflows into San Antonio Bay from 1942 – 2009 at a monthly resolution, to quantify the relative importance of contributors to the total flow, and to exhibit their long-term variation over time. This requires being able to separate the component inflows. For those TxRR data prior to 1977, this cannot be done, because we have only the *total* ungauged flow into the bay. Moreover, the “ungauged” data include watershed 18014 for 1954-76, but not for 1942-54. (Nor is it certain that TWDB began the 18014 simulation in 1954, but that is likely, as there exist gauge data from the Victoria station on Coleta Creek through September.)

This problem was approached by a synthetic separation of TxRR total ungauged inflow into its components. First, statistical relations between monthly rainfall on the watershed and the TxRR monthly runoff flows were established for each of the watersheds: (1) ungauged Guadalupe (w/s 18012 + 18020, plus the runoff from w/s 18014 whenever the Victoria gauge on Coleta Creek is unavailable), (2) ungauged San Antonio (w/s 19011 + 19012), (3) bay periphery (w/s 24601-07),

and (4) Espiritu Santo watershed (24608). To determine these relations, the 1977-2008 TxRR runoff values* for the watersheds in Table 2-2 were used together with corresponding rainfall data from the optimal combination of National Climatic Data Center (NCDC) data from Victoria, Goliad, Port O'Connor, and Aransas National Wildlife Refuge (ANWR) + Austwell (ANWR and Austwell being nearly the same location). A least-squares fit to a quadratic function of runoff flow versus precipitation was used, with respective explained variances of 0.57, 0.52, 0.84, and 0.70. This is an attempt to depict the TxRR predicted flows as a rather simple function of rainfall. TxRR in fact exhibits a complex lagged relation between rainfall and runoff, because of the variation of rate of infiltration as soil water increases, so the relation is not one-to-one, and is further corrupted by the parsing of the two variables, rainfall and runoff, at the break between months. For smaller watersheds (*viz.*, the bay periphery and 24608), the response is faster, and the statistical relation exhibits higher explained variance than for larger watersheds (*viz.*, the Guadalupe and San Antonio).

From these relations, the runoff flows for the period 1942-76 for each of the four ungauged watersheds can be estimated from the NCDC records of monthly rainfall. Since we have the TxRR total for each month, one of these four runoff flow values is redundant, as it can be obtained by subtracting the sum of the other three from the known total. An optimum process was pursued in which the three flow values to be used were selected to minimize the error in total inflow compared to the TxRR value, an average error that turned out to be about 8% over the 1942-76 period. The gruesome details are relegated to Appendix A. A complete tabulation of the monthly component flows and the bay total flows is provided in Appendix C.

2.1.1.2 Diversions and return flows

The final set of data necessary to quantify inflow to the bay is the net of return flows over diversions. Since the net return-diversion flows above a streamflow gauge are implicit in the

* At the time this work was done, the TxRR 2009 model results were not yet available from TWDB.

gauged record, only those returns and diversions below the primary gauges on the Guadalupe River, Coletto Creek, and San Antonio River are needed for this work. These return flows are mainly municipal and industrial wastewater discharges, and the diversions are for municipal, industrial and agricultural purposes. As these activities require permits with (monthly) reporting requirements, in principle monthly data should exist in the files of the Texas Commission on Environmental Quality (TCEQ) dating back to the first half of the last century. Unfortunately, in the 1980's, the predecessor agency (Texas Natural Resources Conservation Commission, TNRCC) embarked on a program of "records management" (a.k.a. "information destruction") in which these data and other information central to the history of water management in Texas were summarily destroyed. For several years, HDR, Inc., has sought to restore this information for the Guadalupe-San Antonio basin based upon the best sources extant, including records from Guadalupe-Blanco River Authority (GBRA), Victoria, DuPont/INVISTA, Dow/UCC, TCEQ, the South Texas Watermaster, and the Environmental Protection Agency (Brian Perkins and Sam Vaugh, HDR, pers. comm.). This data was kindly provided by HDR for use in the present study.

A chronological summary of the returns and diversions data is as follows:

1942-1966: No reliable independent data for all of the individual major dischargers have been found. From files of HDR (pre-1962 from TCEQ, 1963-66 from GBRA), the earlier diversion and returns of DuPont (now INVISTA) have been found. No data on the Victoria return flows exist, so these were estimated by HDR based upon population. Also, GBRA has provided monthly irrigation diversion records from the operation of the canal before it was taken over by GBRA in 1967, but these numbers are suspiciously constant from month to month, and are not considered trustworthy. From earlier basin modeling work of HDR with data provided by TCEQ's predecessor agencies, monthly values of total diversions (including *net* diversion for DuPont) have survived, although these cannot be tracked back to the original reported flows nor separated into components. These appear to be the best record of the historical diversions and have been used here, together with the estimated Victoria return flows.

1967 – 1989: The GBRA diversion data are considered reliable, as are the returns and diversions of DuPont, mainly found in the files of GBRA and INVISTA, though some data used in earlier water-basin modeling of HDR were obtained from TCEQ (née TNRCC, née Texas Water Commission, TWC). No information has survived on the Dow discharge into the Victoria Barge Canal. Victoria discharge records for 1973-1991 were obtained from HDR records for the earlier modeling work, obtained at the time from TWC/TNRCC. Victoria discharge records for 1967-1972 were estimated by HDR from population data.

1990 – 2009: Reported returns for Dow/Union Carbide Corporation (UCC) have been provided to HDR by Dow/UCC starting in 1990. DuPont returns and diversions were obtained from GBRA files through 1994, with supplemental information from TCEQ, and data for a few missing months have been estimated by HDR. Reported values provided by INVISTA start in 1995. Reported Victoria return flows from GBRA files start in 1992.

2.1.2 Historical inflows to San Antonio Bay

2.1.2.1 Historical annual flows

The general behavior of inflows to the San Antonio Bay over the nearly seven-decade period of 1942-2009 is exhibited by the calendar-year annual values of the above data sources, presented in Table 2-3. (The bold line after year 1976 in this table is a reminder that the TxRR component flows before this point in time have been estimated from the TxRR San Antonio Bay monthly totals, as summarized in Section 2.1.1.1 and detailed in Appendix A.)

The total annual flow into the bay over this period is plotted in Figure 2-3. Over this period there has been an upward trend in inflow, as indicated by the least-squares regression line in Fig. 2-3. This trend is substantial, approximately an 80% increase in flow over the 68-year period. While there is statistical uncertainty about the precise magnitude of the trend line (see Section 2.1.2.2,

Table 2-3
Annual flows (calendar year) into San Antonio Bay in thousands of acre feet (Taf)

year	gauged flows			ungauged flows		returns - diversions u/s of salt barrier	flow at salt barrier	ungauged from bay periphery	total flow into bay
	Guadalupe 8176500	Coleta Cr 8177500	San Antonio 8188500	Guad TWDB	San Ant TxRR				
1942	1525.2	76.3	903.4	131.4	260.9	-0.7	2888.0	91.1	2979.1
1943	685.7	20.3	301.3	85.9	85.0	0.1	1156.5	41.4	1197.9
1944	1332.6	55.6	374.2	114.1	297.4	0.3	2169.3	80.5	2249.8
1945	1382.1	18.4	349.6	63.0	143.8	-1.3	1950.9	105.3	2056.2
1946	1740.4	179.6	1034.7	91.8	294.8	-1.3	3326.2	84.8	3410.9
1947	1102.9	41.0	317.4	85.0	86.3	-84.4	1517.8	73.7	1591.5
1948	470.4	9.3	219.1	62.7	106.1	-98.0	747.3	62.4	809.8
1949	1072.8	34.5	481.4	104.1	202.7	-48.1	1821.3	92.1	1913.5
1950	556.1	3.1	169.2	38.1	12.1	-57.2	694.7	25.6	720.3
1951	377.6	25.7	225.3	86.1	59.4	-111.5	646.8	71.4	718.2
1952	757.4	75.3	341.4	76.6	109.7	-115.2	1228.1	42.3	1270.4
1953	759.9	47.8	253.2	57.4	98.7	-125.2	1081.8	82.8	1164.6
1954	232.0	2.3	89.0	34.4	2.4	-114.4	215.6	41.2	256.8
1955	260.3	9.3	117.8	58.8	29.6	-80.4	359.9	42.8	402.6
1956	115.3	7.9	110.5	39.5	9.0	-35.2	216.2	30.8	247.0
1957	2246.5	111.0	779.9	149.0	554.4	-20.7	3807.3	75.4	3882.7
1958	2038.2	120.6	780.1	147.3	412.2	-27.3	3467.4	82.2	3549.6
1959	1108.2	42.1	312.7	89.4	299.2	-38.1	1810.4	91.4	1901.8
1960	2211.8	96.7	543.7	198.4	631.4	-39.4	3640.2	131.7	3771.9
1961	1825.0	34.0	503.9	103.3	332.2	-21.1	2767.8	89.7	2857.4
1962	534.3	15.8	214.6	64.9	52.3	-31.7	830.7	53.2	883.9
1963	367.1	5.4	148.7	51.8	4.8	-73.5	460.6	28.3	489.0
1964	465.2	14.9	225.5	89.5	78.7	-69.3	791.0	40.1	831.1
1965	1527.5	70.5	514.7	79.0	240.7	-74.7	2341.6	47.5	2389.1
1966	898.5	20.8	221.7	81.6	420.1	-33.2	1608.9	58.9	1667.9
1967	1093.9	361.0	956.2	123.6	943.2	-65.5	3410.0	150.1	3560.1
1968	2029.3	110.7	756.5	152.8	427.5	-60.2	3397.6	136.6	3534.2
1969	1332.3	102.2	375.8	132.2	256.4	-73.3	2081.6	68.9	2150.5
1970	1201.3	23.1	348.0	106.3	319.5	-53.4	1903.1	88.6	1991.7
1971	771.6	61.6	404.6	122.8	490.2	-76.5	1745.6	109.8	1855.4
1972	1610.6	66.4	622.0	138.2	279.2	-72.7	2553.3	74.9	2628.2
1973	2752.3	240.5	1590.2	153.7	259.7	-73.9	4830.0	103.6	4933.6
1974	1617.7	38.8	562.7	121.1	297.3	-92.8	2501.9	149.7	2651.5
1975	2198.7	30.7	764.7	110.2	340.3	-94.4	3293.4	50.8	3344.2
1976	2364.3	114.5	893.8	127.6	483.1	-68.1	3858.0	100.6	3958.6
1977	2088.3	68.6	987.4	232.6	99.8	-74.3	3402.4	94.5	3496.9
1978	1119.7	50.7	585.1	161.9	38.3	-77.8	1877.8	41.1	1918.9
1979	2394.1	117.9	924.4	227.2	106.5	-75.8	3694.2	195.4	3889.6
1980	740.4	15.6	392.5	74.3	40.8	-86.5	1177.3	30.6	1207.9
1981	2533.9	174.0	909.9	184.2	187.1	-65.1	3923.9	148.8	4072.7
1982	952.6	79.7	368.2	94.2	37.7	-54.6	1478.0	51.2	1529.2
1983	802.3	64.0	318.0	105.0	31.5	-47.2	1273.5	61.6	1335.1
1984	351.4	25.8	265.6	37.8	9.3	-58.6	631.2	35.1	666.3
1985	1534.8	53.0	515.1	134.0	35.6	-44.9	2227.6	45.7	2273.3
1986	1451.3	32.8	591.2	76.0	24.2	-55.8	2119.7	68.7	2188.4

(continued)

Table 2-3
(Continued)

year	gauged flows			ungauged flows		returns - diversions u/s of salt barrier	flow at salt barrier	ungauged from bay periphery	total flow into bay
	Guadalupe 8176500	Coletto Cr 8177500	San Antonio 8188500	Guad TWDB	San Ant TxRR				
1987	3502.1	98.1	1635.7	144.6	41.1	-62.5	5359.2	53.7	5412.9
1988	586.5	3.0	271.6	8.4	4.5	-97.2	776.8	7.5	784.3
1989	407.7	1.7	218.5	36.5	13.6	-82.1	595.9	49.1	644.9
1990	536.7	29.8	355.1	103.3	97.7	-63.5	1059.0	70.7	1142.2
1991	1798.3	81.0	705.5	223.4	67.3	-46.6	2829.0	127.7	2970.5
1992	4663.6	168.2	2229.1	374.8	118.4	-37.8	7516.2	138.1	7669.0
1993	1628.9	164.2	781.7	283.8	61.7	-43.4	2876.8	129.9	3018.8
1994	1099.8	92.9	505.9	134.8	55.9	-60.2	1829.0	40.5	1880.7
1995	996.2	12.7	323.5	84.9	29.8	-50.0	1397.2	58.6	1465.7
1996	407.8	1.4	194.2	57.2	5.9	-58.9	607.6	12.5	629.6
1997	2423.9	259.7	606.3	74.6	77.0	-36.2	3405.3	159.2	3575.6
1998	3741.0	224.2	952.2	14.8	91.0	-54.3	4968.9	85.4	5064.2
1999	844.0	9.1	351.7	53.5	31.6	-61.8	1228.1	7.9	1244.7
2000	861.7	6.7	452.7	75.0	42.2	-47.9	1390.4	110.4	1509.6
2001	1944.9	145.9	919.3	126.0	96.4	-47.5	3184.9	53.0	3248.9
2002	3510.7	102.6	2061.7	172.4	116.9	-46.9	5917.3	161.9	6089.9
2003	1479.4	52.3	672.0	62.8	32.7	-41.4	2257.7	104.4	2371.7
2004	3292.6	179.9	1406.8	398.1	67.3	-34.8	5310.0	124.6	5445.2
2005	1559.2	75.3	594.7	78.8	28.6	-46.7	2289.8	37.7	2336.2
2006	411.6	3.6	226.0	164.7	58.5	-42.9	821.4	109.3	940.8
2007	3017.6	149.1	1613.3	219.3	104.2	-24.8	5078.6	180.8	5271.3
2008	507.5	2.9	305.5	18.8	9.1	-49.5	794.3	29.2	829.2
2009	839.0	26.7	398.8	29.9	26.8	-50.8	1270.3	41.6	1317.9
mean	1429.2	72.1	597.7	115.1	160.9	-56.9	2304.8	79.5	2387.2

below), it is about 96% probable that its slope is positive. The variability of this annual flow as well as the month-to-month fluctuations are responses to hydroclimatology, and are explored in the following section.

2.1.2.2 Historical flows according to source

Table 2-3, above, presents the annual component flows from the various sources, as well as the total flows into San Antonio Bay. There are two ways of viewing these component flows, each

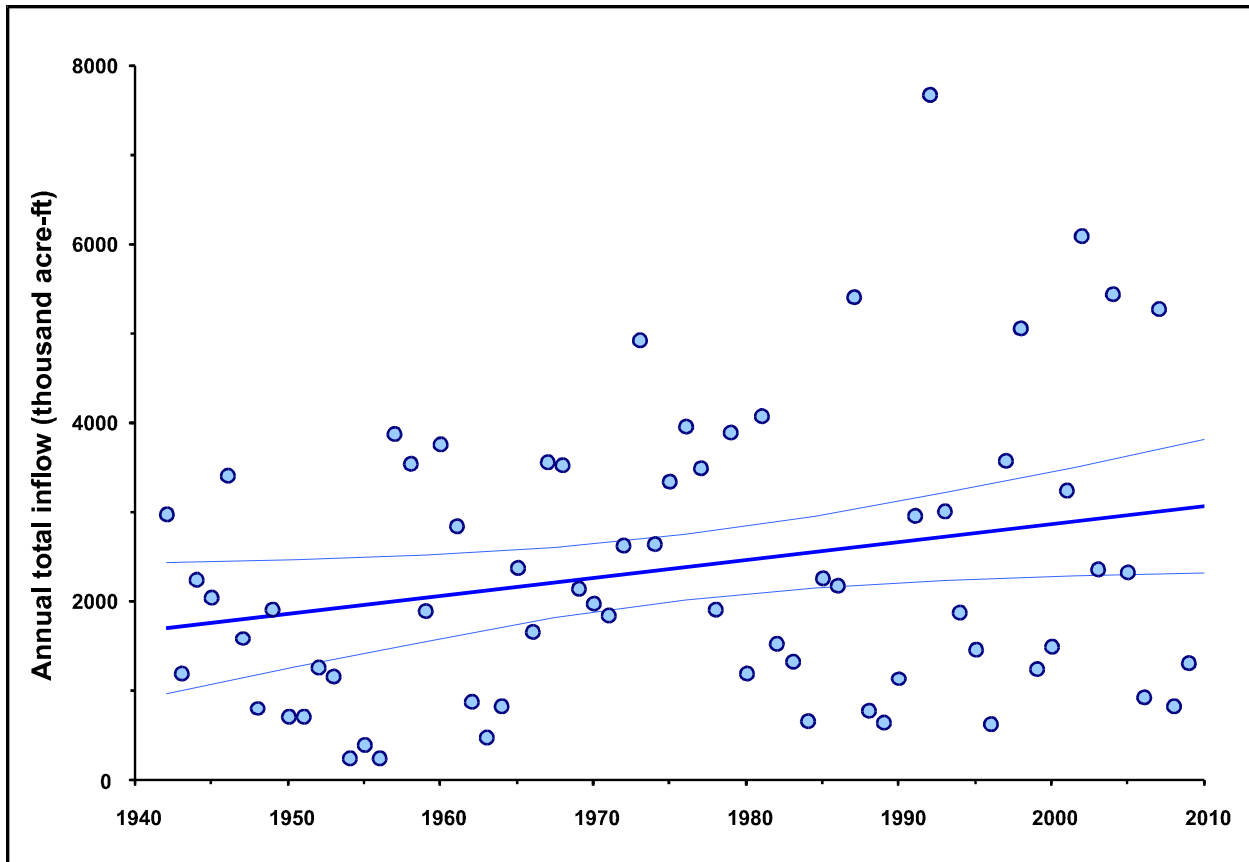


Figure 2-3 - Annual inflows into San Antonio Bay, 1942-2009.
Straight line is least-squares trend with 95% confidence bounds.

of which has its utility, *viz.* by data source, i.e., measured by streamflow gauging versus modeled runoff based on rainfall, in this case the TxRR model; and by physical source, i.e., the component watersheds of the Guadalupe, the San Antonio, and the coastal periphery draining directly into San Antonio Bay. The data-source viewpoint also admits a physical interpretation, in that the positions of the primary gauges on the Guadalupe River, Coletto Creek, and San Antonio River are approximately along the inland boundary of the Coastal Prairie. One can therefore regard the gauged data as the contribution from the upland regions of the basin (i.e. the Interior Coastal Plain and the Edwards Plateau), and the ungauged (and modeled) data as the contribution from the Coastal Prairie.

In Table 2-4, the annual component flows of Table 2-3 are organized by data source, and displayed as the fraction of the total inflow to the bay each component represents for the given

year. (Algebraic signs are preserved in this depiction, hence the returns net of diversions are negative.) On average, 89% of the inflows into the bay are gauged, versus 16% ungauged (which do not sum to zero because of the negative contribution of net return flows). Therefore, inaccuracy in modeling, rather than measuring, flows arising from the drainage area below the primary gauges and surrounding the bay does not contribute a major error in the water budget. Of course, the truth of this statement varies with year. Especially during drought conditions, the ungauged contribution can make up one third of the flow into the bay. In comparison, the net returns are smaller yet, typically 5% of the total flow, though these become more substantive during droughts. In 1954, during the infamous Drought of the Fifties, net returns represented a diversion (i.e., negative net return) of almost 45% of the bay's inflow. As a standard of uncertainty, the nominal error in a streamflow measurement is on the order of 10% (e.g., Pelletier, 1988, Sauer and Meyer, 1992).^{*} This relative uncertainty increases as flows diminish, and does not include the uncertainty of discharge measurements about the gauge rating relation. Nominally, therefore, the net returns are generally less than the uncertainty in the gauged inflows, but may approach this uncertainty under low flow conditions.

The annual component flows are organized by physical source in Table 2-5, again expressed as a (signed) fraction of total inflow to San Antonio Bay for that year. On average, the Guadalupe basin contributes about twice as much inflow to the bay as the San Antonio, about 69% from the Guadalupe compared to about 33% from the San Antonio. The contribution from the coastal drainage peripheral to the bay is only about 4%. Even under drought conditions, this peripheral contribution rarely exceeds 10%. The same information is displayed graphically in Figure 2-4.

While the inflows into San Antonio Bay exhibited an increasing trend over the 1942-2009 period, this was not uniformly reflected in the component flows. The least-squares trend-line analyses for each component flow are summarized in Table 2-6. The increasing trend is seen to be driven by the river basins, mainly above the primary gauges. Over this period each river more-or-less doubled its flow. Below the gauges, the Guadalupe trended upward, but the San Antonio trended downward substantially enough to diminish the net increase for its basin. (We

^{*} A more precise statement is that it is 95% probable that the estimated flow will lie in a range $\pm 5\%$ about the correct value.

Table 2-4
Proportions (%) of contributions to annual inflows to San Antonio Bay by data source

	gauged			ungauged		rets-divs		gauged			ungauged		rets-divs
	Guadalupe	Coleto Cr	San Antonio	u/s of salt barrier	d/s of salt barrier	u/s of salt barrier		Guadalupe	Coleto Cr	San Antonio	u/s of salt barrier	d/s of salt barrier	u/s of salt barrier
1942	51.2	2.6	30.3	12.9	3.1	0.0	1977	59.7	2.0	28.2	9.5	2.7	-2.1
1943	57.2	1.7	25.1	12.5	3.5	0.0	1978	58.4	2.6	30.5	10.4	2.1	-4.1
1944	59.2	2.5	16.6	18.1	3.6	0.0	1979	61.6	3.0	23.8	8.6	5.0	-1.9
1945	67.2	0.9	17.0	9.8	5.1	-0.1	1980	61.3	1.3	32.5	9.5	2.5	-7.2
1946	51.0	5.3	30.3	10.9	2.5	0.0	1981	62.2	4.3	22.3	9.1	3.7	-1.6
1947	69.3	2.6	19.9	8.9	4.6	-5.3	1982	62.3	5.2	24.1	8.6	3.3	-3.6
1948	58.1	1.2	27.1	18.1	7.7	-12.1	1983	60.1	4.8	23.8	10.2	4.6	-3.5
1949	56.1	1.8	25.2	14.7	4.8	-2.5	1984	52.7	3.9	39.9	7.1	5.3	-8.8
1950	77.2	0.4	23.5	3.3	3.6	-7.9	1985	67.5	2.3	22.7	7.5	2.0	-2.0
1951	52.6	3.6	31.4	18.0	9.9	-15.5	1986	66.3	1.5	27.0	4.6	3.1	-2.6
1952	59.6	5.9	26.9	13.3	3.3	-9.1	1987	64.7	1.8	30.2	3.4	1.0	-1.2
1953	65.2	4.1	21.7	12.6	7.1	-10.8	1988	74.8	0.4	34.6	1.6	1.0	-12.4
1954	90.4	0.9	34.7	2.6	16.0	-44.6	1989	63.2	0.3	33.9	7.8	7.6	-12.7
1955	64.6	2.3	29.3	13.1	10.6	-20.0	1990	47.0	2.6	31.1	17.6	6.2	-5.6
1956	46.7	3.2	44.7	7.2	12.5	-14.2	1991	60.5	2.7	23.7	9.8	4.3	-1.6
1957	57.9	2.9	20.1	17.8	1.9	-0.5	1992	60.8	2.2	29.1	6.4	1.8	-0.5
1958	57.4	3.4	22.0	15.7	2.3	-0.8	1993	54.0	5.4	25.9	11.4	4.3	-1.4
1959	58.3	2.2	16.4	20.3	4.8	-2.0	1994	58.5	4.9	26.9	10.1	2.2	-3.2
1960	58.6	2.6	14.4	21.9	3.5	-1.0	1995	68.0	0.9	22.1	7.8	4.0	-3.4
1961	63.9	1.2	17.6	14.9	3.1	-0.7	1996	64.8	0.2	30.8	10.0	2.0	-9.4
1962	60.5	1.8	24.3	11.1	6.0	-3.6	1997	67.8	7.3	17.0	4.2	4.5	-1.0
1963	75.1	1.1	30.4	2.6	5.8	-15.0	1998	73.9	4.4	18.8	2.1	1.7	-1.1
1964	56.0	1.8	27.1	18.6	4.8	-8.3	1999	67.8	0.7	28.3	6.8	0.6	-5.0
1965	63.9	3.0	21.5	12.7	2.0	-3.1	2000	57.1	0.4	30.0	7.8	7.3	-3.2
1966	53.9	1.2	13.3	30.0	3.5	-2.0	2001	59.9	4.5	28.3	6.8	1.6	-1.5
1967	30.7	10.1	26.9	29.9	4.2	-1.8	2002	57.6	1.7	33.9	4.8	2.7	-0.8
1968	57.4	3.1	21.4	15.9	3.9	-1.7	2003	62.4	2.2	28.3	4.0	4.4	-1.7
1969	62.0	4.8	17.5	16.0	3.2	-3.4	2004	60.5	3.3	25.8	8.5	2.3	-0.6
1970	60.3	1.2	17.5	19.3	4.4	-2.7	2005	66.7	3.2	25.5	4.6	1.6	-2.0
1971	41.6	3.3	21.8	31.5	5.9	-4.1	2006	43.8	0.4	24.0	23.7	11.6	-4.6
1972	61.3	2.5	23.7	12.4	2.9	-2.8	2007	57.2	2.8	30.6	6.1	3.4	-0.5
1973	55.8	4.9	32.2	6.5	2.1	-1.5	2008	61.2	0.4	36.8	3.4	3.5	-6.0
1974	61.0	1.5	21.2	14.2	5.6	-3.5	2009	63.7	2.0	30.3	4.3	3.2	-3.9
1975	65.7	0.9	22.9	11.8	1.5	-2.8							
1976	59.7	2.9	22.6	14.0	2.5	-1.7	mean	60.5	2.7	25.8	11.4	4.3	-4.8

Table 2-5
Proportions (%) of contributions to annual inflows to San Antonio Bay by physical source

	Guadalupe		San Antonio		rets-divs u/s of salt barrier	periphery of bay		Guadalupe		San Antonio		rets-divs u/s of salt barrier	periphery of bay
	Victoria	d/s Victoria	Goliad	d/s Goliad				Victoria	d/s Victoria	Goliad	d/s Goliad		
1942	51.2	7.0	30.3	8.8	0.0	3.1	1977	59.7	8.6	28.2	2.9	-2.1	2.7
1943	57.2	8.9	25.1	7.1	0.0	3.5	1978	58.4	11.1	30.5	2.0	-4.1	2.1
1944	59.2	7.5	16.6	13.2	0.0	3.6	1979	61.6	8.9	23.8	2.7	-1.9	5.0
1945	67.2	4.0	17.0	7.0	-0.1	5.1	1980	61.3	7.4	32.5	3.4	-7.2	2.5
1946	51.0	8.0	30.3	8.6	0.0	2.5	1981	62.2	8.8	22.3	4.6	-1.6	3.7
1947	69.3	7.9	19.9	5.4	-5.3	4.6	1982	62.3	11.4	24.1	2.5	-3.6	3.3
1948	58.1	8.9	27.1	13.1	-12.1	7.7	1983	60.1	12.7	23.8	2.4	-3.5	4.6
1949	56.1	7.2	25.2	10.6	-2.5	4.8	1984	52.7	9.5	39.9	1.4	-8.8	5.3
1950	77.2	5.7	23.5	1.7	-7.9	3.6	1985	67.5	8.2	22.7	1.6	-2.0	2.0
1951	52.6	15.6	31.4	8.3	-15.5	9.9	1986	66.3	5.0	27.0	1.1	-2.6	3.1
1952	59.6	12.0	26.9	8.6	-9.1	3.3	1987	64.7	4.5	30.2	0.8	-1.2	1.0
1953	65.2	9.0	21.7	8.5	-10.8	7.1	1988	74.8	1.5	34.6	0.6	-12.4	1.0
1954	90.4	14.3	34.7	0.9	-44.6	16.0	1989	63.2	5.9	33.9	2.1	-12.7	7.6
1955	64.6	16.9	29.3	7.4	-20.0	10.6	1990	47.0	11.6	31.1	8.6	-5.6	6.2
1956	46.7	19.2	44.7	3.7	-14.2	12.5	1991	60.5	10.2	23.7	2.3	-1.6	4.3
1957	57.9	6.7	20.1	14.3	-0.5	1.9	1992	60.8	7.1	29.1	1.5	-0.5	1.8
1958	57.4	7.5	22.0	11.6	-0.8	2.3	1993	54.0	14.8	25.9	2.0	-1.4	4.3
1959	58.3	6.9	16.4	15.7	-2.0	4.8	1994	58.5	12.1	26.9	3.0	-3.2	2.2
1960	58.6	7.8	14.4	16.7	-1.0	3.5	1995	68.0	6.7	22.1	2.0	-3.4	4.0
1961	63.9	4.8	17.6	11.6	-0.7	3.1	1996	64.8	9.3	30.8	0.9	-9.4	2.0
1962	60.5	9.1	24.3	5.9	-3.6	6.0	1997	67.8	9.4	17.0	2.2	-1.0	4.5
1963	75.1	11.7	30.4	1.0	-15.0	5.8	1998	73.9	4.7	18.8	1.8	-1.1	1.7
1964	56.0	12.6	27.1	9.5	-8.3	4.8	1999	67.8	5.0	28.3	2.5	-5.0	0.6
1965	63.9	6.3	21.5	10.1	-3.1	2.0	2000	57.1	5.4	30.0	2.8	-3.2	7.3
1966	53.9	6.1	13.3	25.2	-2.0	3.5	2001	59.9	8.4	28.3	3.0	-1.5	1.6
1967	30.7	13.6	26.9	26.5	-1.8	4.2	2002	57.6	4.5	33.9	1.9	-0.8	2.7
1968	57.4	7.5	21.4	12.1	-1.7	3.9	2003	62.4	4.9	28.3	1.4	-1.7	4.4
1969	62.0	10.9	17.5	11.9	-3.4	3.2	2004	60.5	10.6	25.8	1.2	-0.6	2.3
1970	60.3	6.5	17.5	16.0	-2.7	4.4	2005	66.7	6.6	25.5	1.2	-2.0	1.6
1971	41.6	9.9	21.8	26.4	-4.1	5.9	2006	43.8	17.9	24.0	6.2	-4.6	11.6
1972	61.3	7.8	23.7	10.6	-2.8	2.9	2007	57.2	7.0	30.6	2.0	-0.5	3.4
1973	55.8	8.0	32.2	5.3	-1.5	2.1	2008	61.2	2.6	36.8	1.1	-6.0	3.5
1974	61.0	6.0	21.2	11.2	-3.5	5.6	2009	63.7	4.3	30.3	2.0	-3.9	3.2
1975	65.7	4.2	22.9	10.2	-2.8	1.5							
1976	59.7	6.1	22.6	12.2	-1.7	2.5	mean	60.5	8.6	25.8	6.8	-4.8	4.3

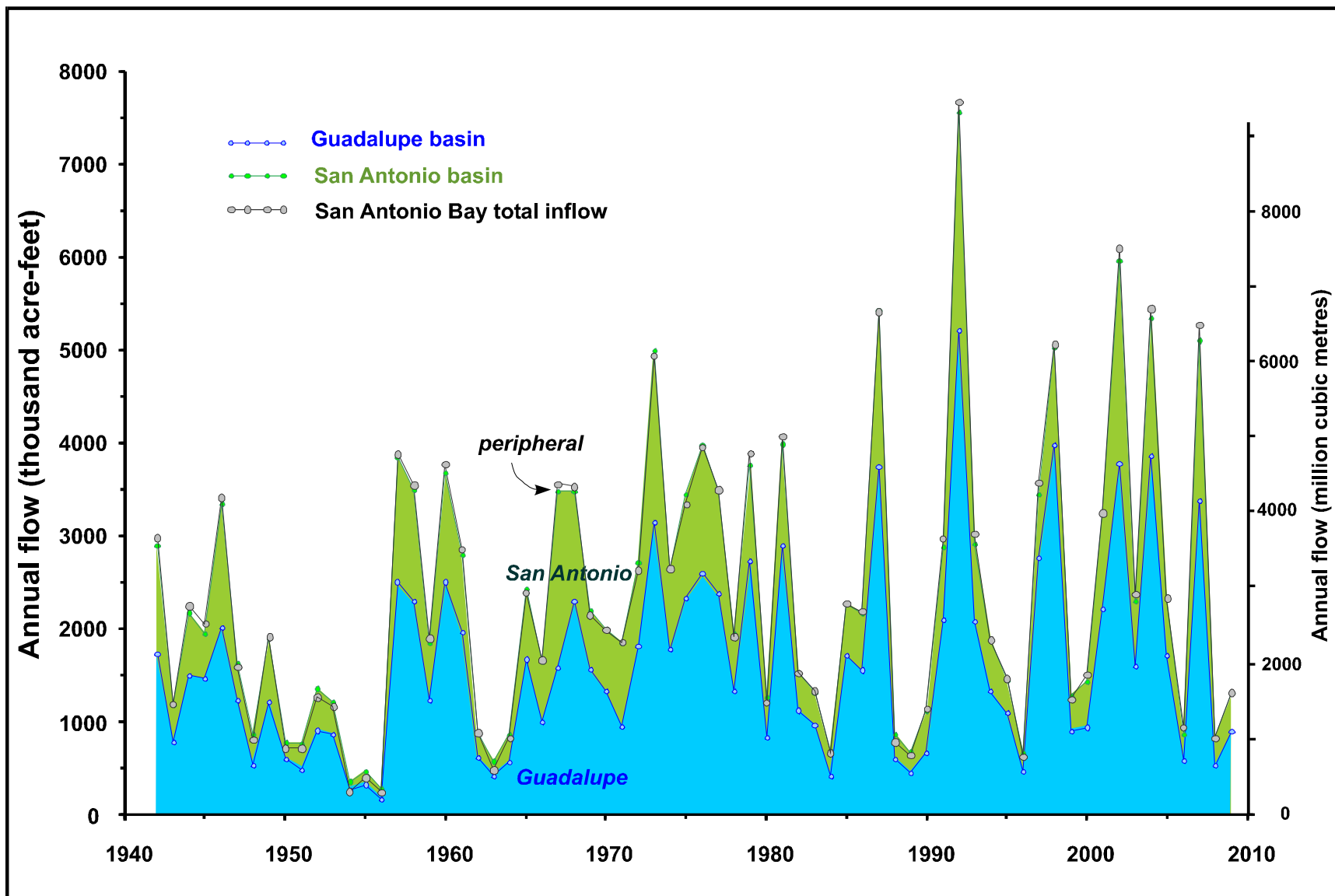


Figure 2-4 - Total inflow into San Antonio Bay and Guadalupe and San Antonio component flows

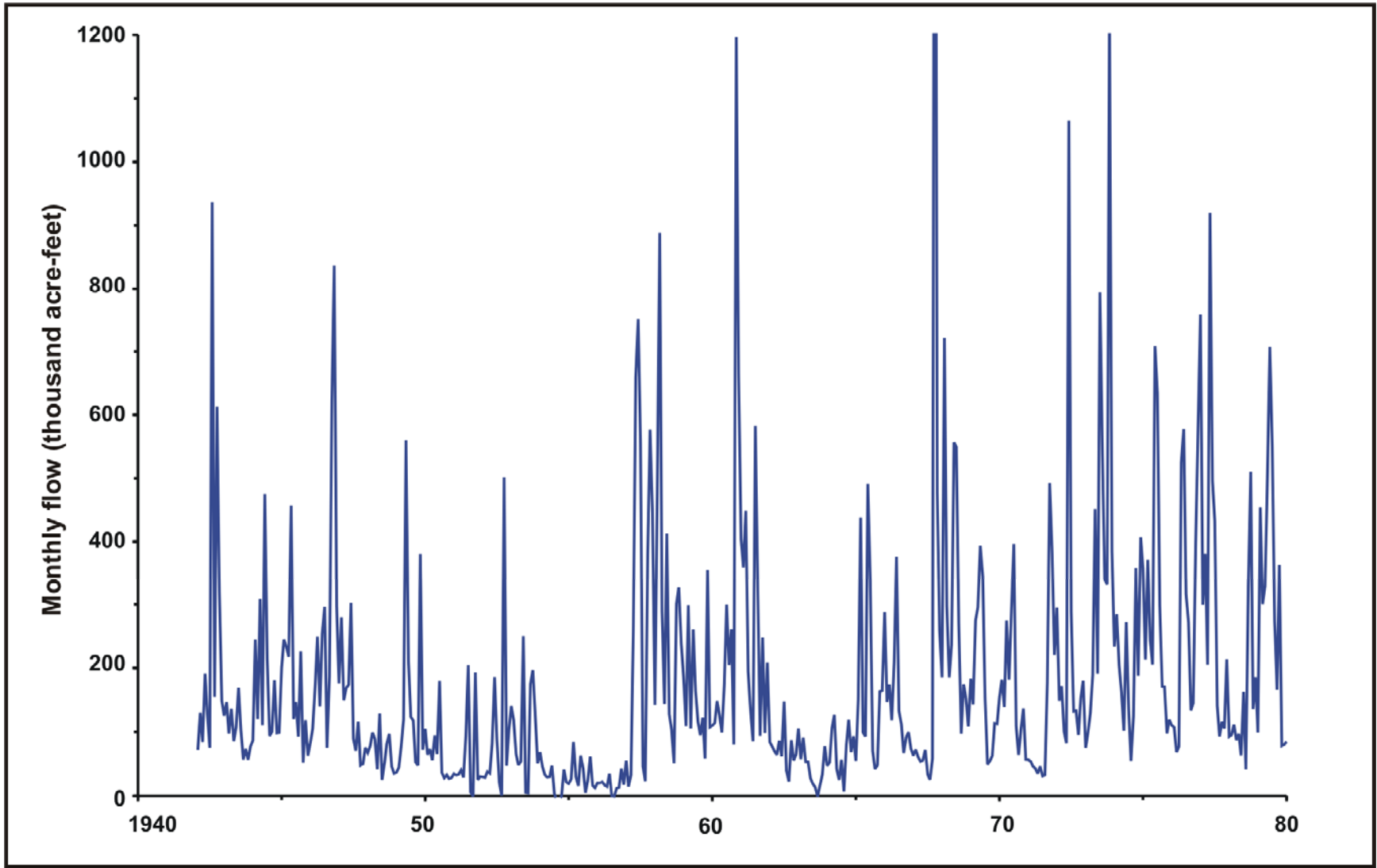


Figure 2-5a - Monthly total inflow into San Antonio Bay, 1942-80

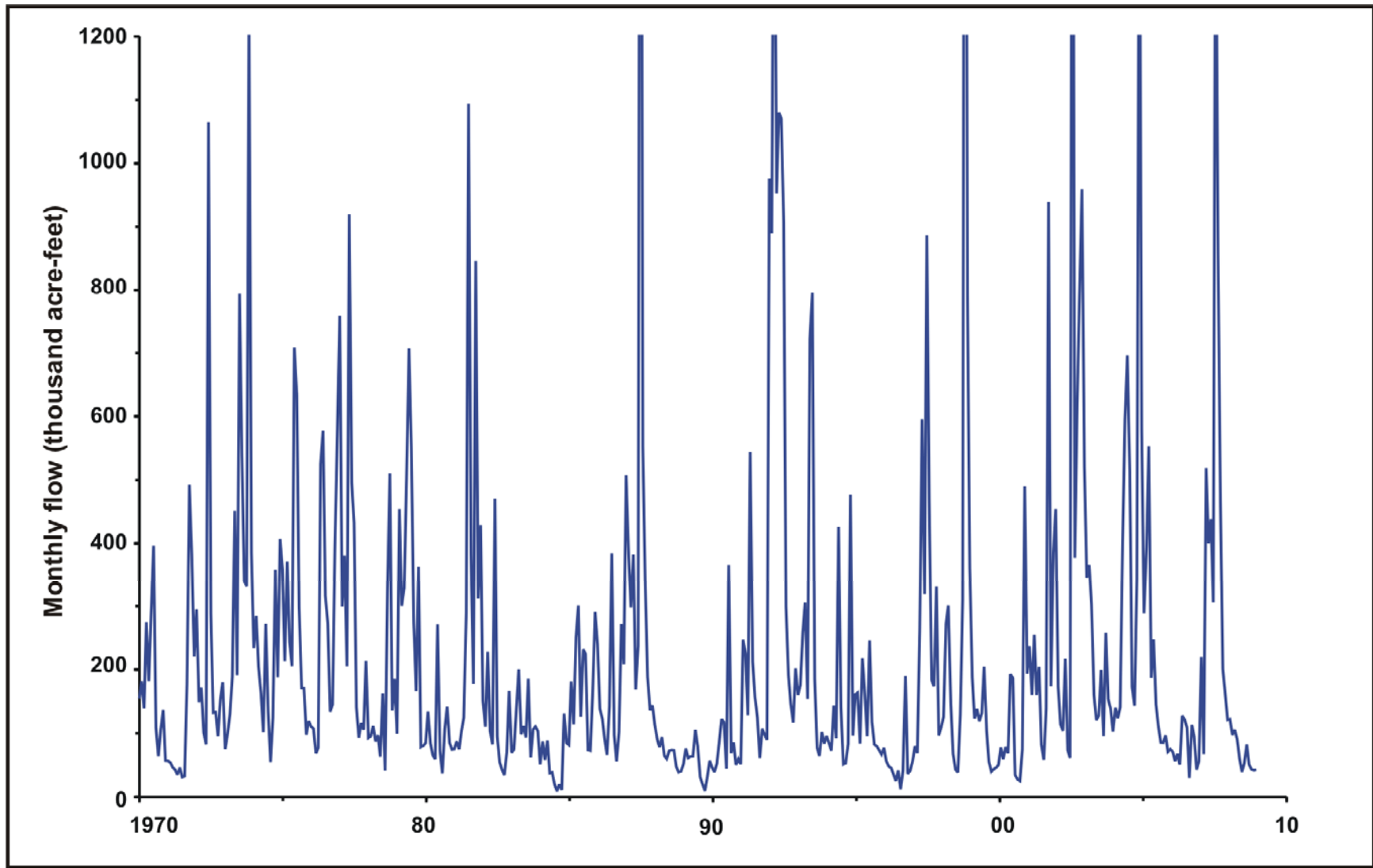


Figure 2-5b - Monthly total inflow into San Antonio Bay, 1970-2009

Table 2-6
Time trends (least-squares regression) in component flows into San Antonio Bay, 1942-2009

	<i>Trend line</i>			<i>Trend projection</i>			
	<i>slope</i> (Taf/yr)	± 0.95 <i>conf bnds</i> (Taf/yr)	(Taf/yr)	1942 (Taf)	2009 (Taf)	<i>increase</i> (Taf)	(%)
<i>Gauged flows</i>							
<i>Guadalupe at Victoria</i>	13.9	0.7	27.0	956	1885	928	97
<i>Coletto Creek</i>	0.6	-0.4	1.6	52	91	39	74
<i>San Antonio at Goliad</i>	7.2	1.2	13.3	352	838	485	138
<i>Ungauged flows</i>							
<i>Guadalupe</i>	0.8	-0.3	1.8	88	140	52	59
<i>San Antonio</i>	-3.2	-5.6	-0.8	267	51	-216	-81
<i>Rets - divs w/s of salt barrier</i>	0.0	-0.4	0.4	-57	-56	1	-2
<i>Flow at salt barrier</i>	19.6	-1.7	41.0	1631	2948	1316	81
<i>Bay peripheral drainage</i>	0.3	-0.4	0.9	70	88	17	25
<i>Total flow into bay</i>	20.1	-1.6	41.8	1699	3044	1346	79

note that these are TxRR-modeled flows driven by data on precipitation.) Statistically, the return flows net of diversions showed no trend, and the increasing trend of peripheral flows was modest.

2.1.3 Historical hydroclimatology

In this section, the natural variability in the inflows to San Antonio Bay is addressed. This requires a finer time resolution than the annual time step of the previous chapter, namely data at monthly intervals. Compilations of monthly component inflows, as surveyed in Section 2.1.1, comprise the basic data for the present analyses. (Analysis of data at the even finer time resolution of daily is addressed in a separate report.) The 1942-2009 time history of total monthly inflow into San Antonio Bay is displayed in Figure 2-5, subdivided into two time series with 10-year overlap for clarity. (These data are tabulated in Appendix C for reference.) Even at a relatively coarse time resolution of one month, it is apparent that there is considerable

fluctuation. In order to expose general features of the several contributions to inflow and their variability over time, additional processing of the data time series must be employed.

2.1.3.1 *Interannual inflow variation*

The largest scale of variability, annual to decadal, is exhibited by a smoothed time series. Figure 2-6 shows the monthly time series of the inflow components of the two river basins and the total inflow to the bay (which differs from the total of the two river basins by the algebraic sum of peripheral runoff and net returns), after being subjected to a running centered 12-month mean. (Like Fig. 2-5, this figure is presented in two sections with a 10-year overlap to facilitate reading.) The resolution of the time traces of this figure is one-month, but the running 12-month mean in effect acts as a low-pass filter, removing much of the short-period (month-to-month) variation. There is much similarity between this figure and the plot of annual flows of Fig. 2-4: apart from the different flow units, Fig. 2-4 in effect plots a sample of Fig. 2-6 taken every 12 months. The same general increasing trend of inflows is apparent (as we would expect). The periods of relative inflow surfeits and deficits are now better revealed, especially sustained drought periods. There is also an apparent increase in range (or, in time-signal terminology, amplitude) of the excursions in inflow with passage of time.

A more revealing display of drought occurrence is provided by an analysis of the so-called residual mass curve (Rippl, 1883, McMahon and Mein, 1986, see also Ward and Proesmans, 1996), given by the cumulative sum:

$$\sum (Q - \bar{Q})$$

where \bar{Q} is the period-of-record mean (in this case, 1942-2009). This is shown in Figure 2-7. For present purposes, a drought is considered to be a period of at least one (1) year whose mean flow is less than 60% of the 1942-2009 average flow \bar{Q} . A period of below-average flow is

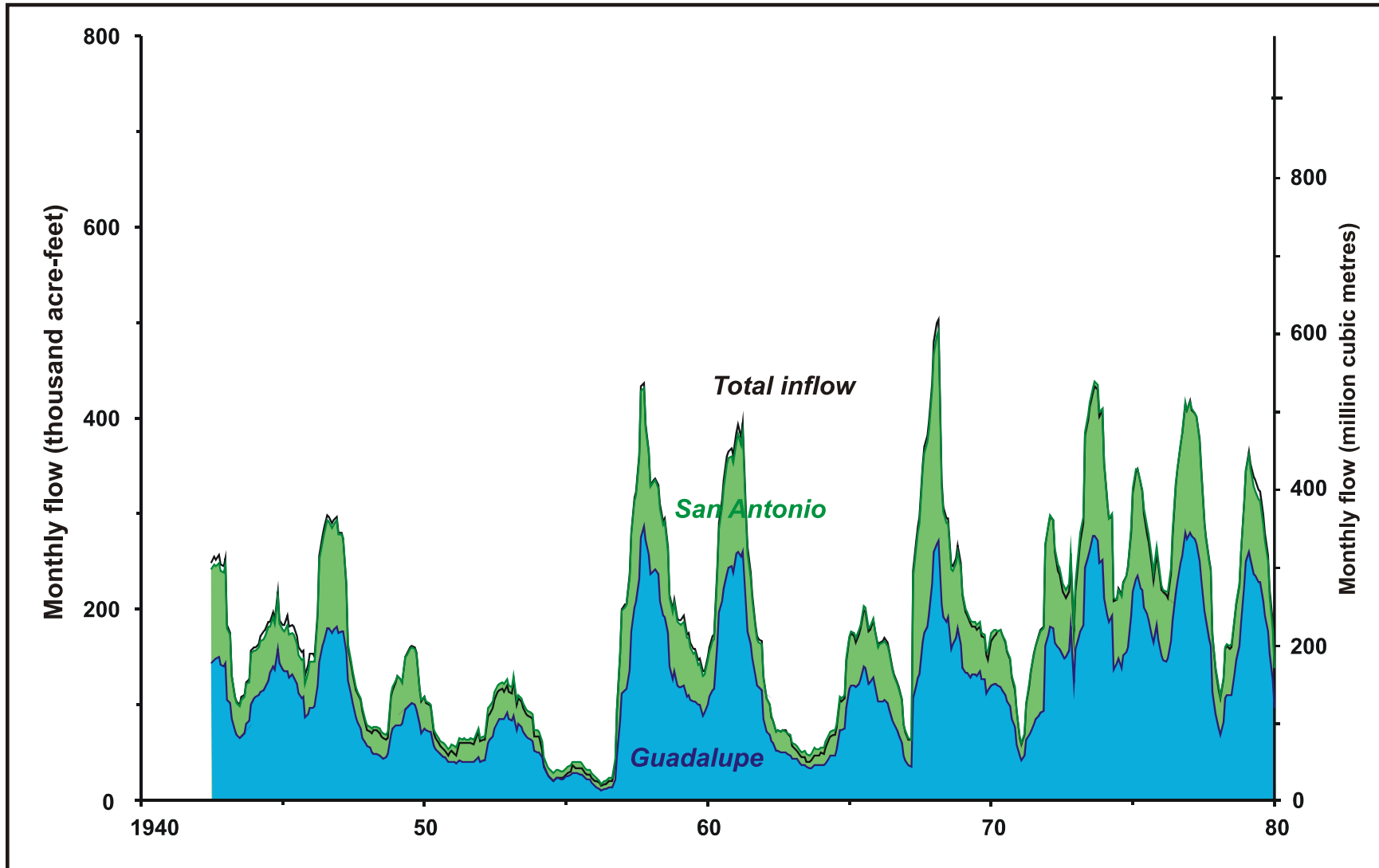


Figure 2-6a - Monthly total inflow into San Antonio Bay, with Guadalupe and San Antonio component flows, after running 12-month mean, 1942-80

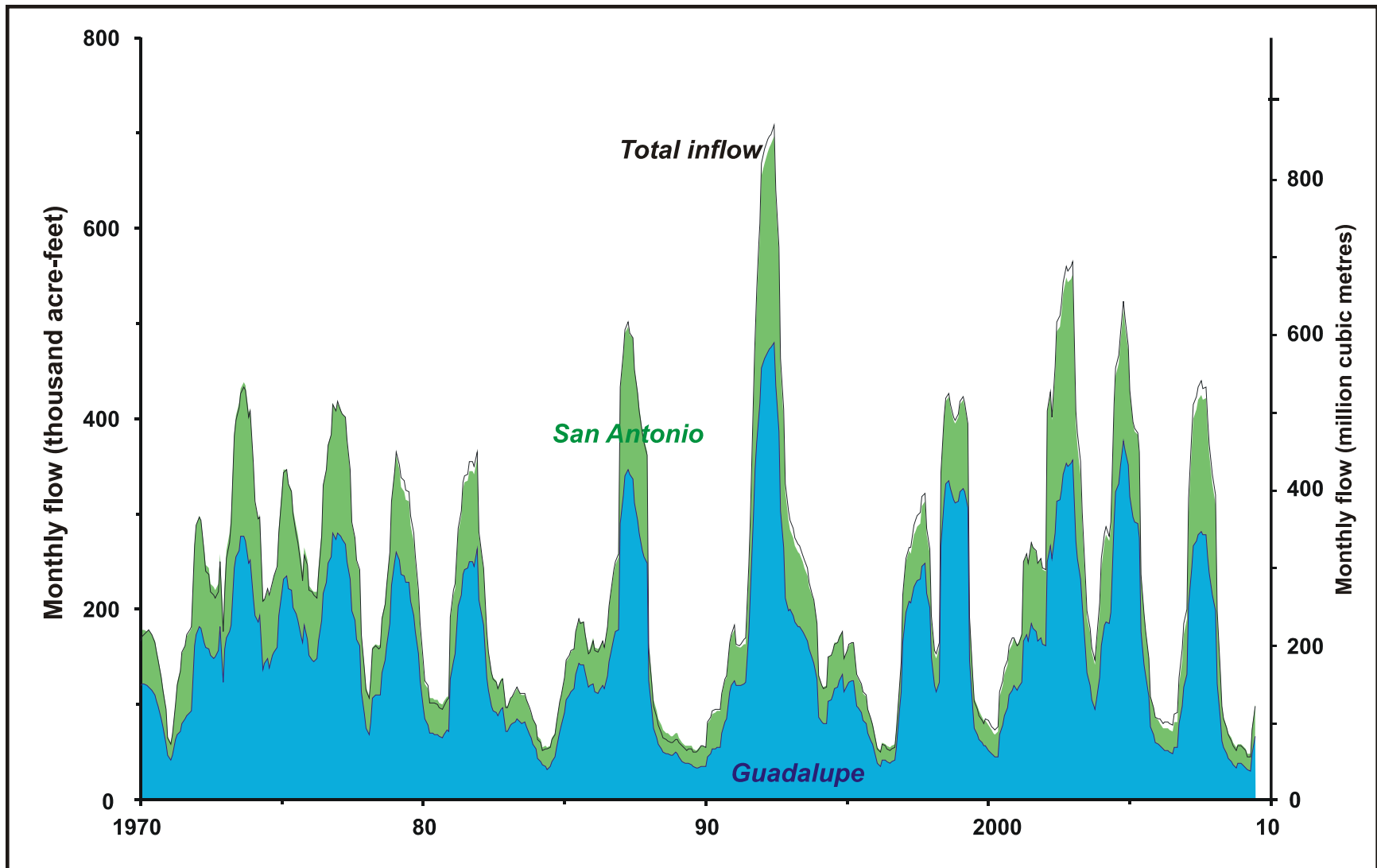


Figure 2-6b - Monthly total inflow into San Antonio Bay, with Guadalupe and San Antonio component flows, after running 12-month mean, 1970-2009

exhibited in the cumulative-residual-flow diagram of Fig. 2-7 as a decline in the curve. Droughts by the present definition are diagnosed when the general downward segment of the curve is steeper than the straight line

$$y(t) = \sum(Q_o - \bar{Q}) - (1 - f) \bar{Q} (t - t_o) \quad (1)$$

where $(t_o, \sum(Q_o - \bar{Q}))$ is the first point of the declining segment and $f = 0.6$.*

Historical droughts so diagnosed are listed in Table 2-7 and indicated in Figure 2-7. For each drought, two lines are shown, the diagnostic line with slope $0.6\bar{Q}$, and the regression line through the drought period (see Appendix B for mathematical details). The duration of a drought is defined by the beginning of the period of decline and the intersection of the $0.6\bar{Q}$ -slope line with the rising limb of the residual curve. Mass residual curves for the two primary basins are also plotted on Fig. 2-7, though drought periods are not explicitly identified.

Two aspects of quantifying a drought are its intensity and its severity. Intensity is the degree by which the flow (or any other water-budget parameter) falls below a diagnostic criterion (typically long-term average, but in the present analysis, $0.6\bar{Q}$.) Severity, in contradistinction to intensity, is the total cumulative stress on the surface water resource, and is affected by both intensity and duration. The intensity of the drought is measured by the (negative) slope of the regression line. The steeper the slope of the regression line, the more intense the drought in terms of average flow deficit. These slopes are given in Table 2-7 (as “best-fit slope”). The severity of the drought is measured by the maximum deficit below the criterion line (1). Those familiar with the use of the residual mass-curve methods for reservoir capacity estimation will recognize this

* Definition of droughts is complex and would take this brief survey too far afield to explore. The definition adopted here is pragmatic: the 60% average flow criterion successfully identifies the historical droughts that have impacted the San Antonio Bay watershed. Many hydroclimatological studies adopt the more expansive definition of a drought as a period of below-average flows. It is interesting to observe that with this definition, inflows to San Antonio Bay would be considered to be in drought conditions from 1947 until 2004, because this long was required to recover the mathematical deficit of the Drought of the Fifties. Clearly, this does not accord with the conventional view of San Antonio basin hydroclimatology.

deficit volume as the capacity necessary for a theoretical reservoir to provide a firm yield of the criterion slope, in this case, 60% of the period of record mean flow.

Several observations about the time series of monthly inflows relevant to drought are immediate from inspection of Fig. 2-7 and Table 2-7:

- (1) The time series behavior of the two major river basins and the total flow to the bay are, at this scale of resolution, quite coherent.
- (2) Over the seven-decade period of record, there have been ten droughts with durations exceeding one year, a frequency of roughly one every seven (7) years.
- (3) Of the 68 years analyzed, 40.5 years were in drought conditions.
- (4) By far, the drought with the longest duration and greatest severity is the Drought of the Fifties, for each of the two basins and for the total flow to the bay.
- (5) The most intense droughts in the record are those of the early 1990's and 2008-09.

The coherence of the mass curves for the two basins indicates that drought events are correlated between the basins, and therefore the drought conditions generally occur regionally over both basins. While the average frequency of droughts during this period is about one per seven years, the distribution is much more irregular than this statistic would indicate. The first two droughts in the period together represent a total of over 19 years. The subsequent droughts average 2.7 years in duration. While there seems to be a tendency for shorter drought durations since the 1950's, there is also a tendency for increased drought intensities, the three most intense droughts having occurred in the last two decades.

The irregular spacing of drought occurrence and the variability in drought duration are, of course, intimately related to the distribution and magnitudes of high-flow sequences in the record. It was noted above that there has been an apparent increase in magnitude (i.e., amplitude) of flow excursions from low-flow conditions to high-flow conditions in recent years. But there is more to it than that, as can be assessed by the time-honored method of eyeballing. An inspection of Figs. 2-5 and 2-6 reveals that the behavior of the time series as indicated by the

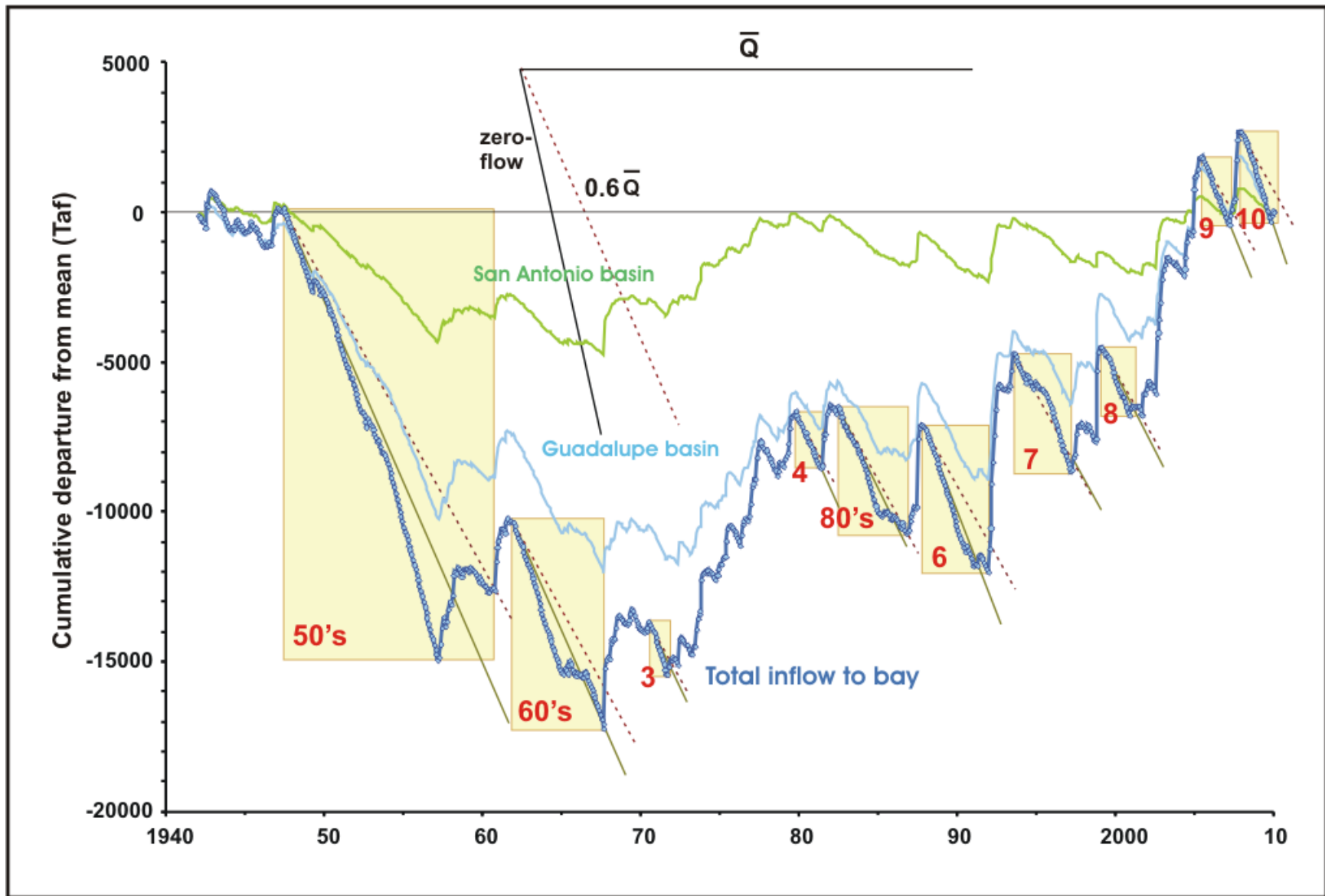


Figure 2-7 - Residual mass curve of monthly flow time series, prominent droughts indicated by constant-flow ($0.6\bar{Q}$) criterion lines & regression lines.

Table 2-7
Droughts during 1942-09 period, based upon mean flow $< 0.6 \bar{Q}$ (see text)

<i>Drought ID</i>	<i>drought period*</i>		<i>best-fit slope (Taf/yr)</i>	<i>max depletion</i>		<i>mean SOI†</i>
	<i>start (year)</i>	<i>end (year)</i>		<i>volume (Taf)</i>	<i>date (year)</i>	
50's	47.50	60.75	-1209	5777	57.17	0.26
60's	62.00	68.00	-1182	2065	65.00	0.21
3	70.58	72.17	-1089	716	71.58	1.63
4	79.83	81.42	-1173	378	81.25	-0.55
80's	82.50	86.92	-1100	1117	85.00	-1.42
6	88.00	92.00	-1374	1697	91.00	0.40
7	93.67	97.25	-933	509	97.17	-0.66
8	99.25	01.62	-1025	632	00.83	1.15
9	05.58	07.33	-1280	661	07.00	-0.33
10	08.00	10.00	-1508	1240	09.75	1.17

* Dates are given as years after 31 Dec 1900 omitting the hundreds unit. 05.58 is therefore 0.58 of a year into 2005, i.e. day 0.58 X 365 of 2005.

† Southern Oscillation Index

height and number of “surges” or “humps” in the graph is different for three subdivisions of the data, roughly 1942-65, 1965-85, and 1985-2009. In the first period, 1942-65 (23 years), there are seven (7) surge peaks, averaging one every 3.3 years, of average range about 190. In the second period, 1965-85 (20 years), there are nine (9) averaging one every 2.2 years, of average range about 230. In the third period, 1985-2009 (24 years), there are seven (7) averaging one every 3.4 years, of average range about 380. The precise numerical values depend upon one’s generosity in identifying a “hump” and where one places its “base” for estimating its height, but two qualitative facts emerge. The average recurrence is about the same in the first and third periods, say 3.5 years or so, but is much shorter (i.e., the surges are more frequent), about every 2 years or so, in the middle period. The average height of these surges increases over the period of record, with the last period about double the first.

Those readers not interested in Fourier analysis, and/or not prone to masochism, are advised to skip the next paragraph and Figure 2-8.

This can be explored more precisely by examining the change in the frequency spectrum of monthly inflows, which were shown in Fig. 2-5. Figure 2-8 displays the spectrum, as determined by the Fast Fourier Transform, for three different time segments of the record, January 1942 – May 1963, January 1965 – May 1986, and September 1988 – December 2009.* The most dramatic feature of these spectra is the pronounced increase in power, about a factor of 2, at lower frequencies (longer periods) from the earlier to the later time segments. The higher frequencies are influenced by the month-to-month noise in the data, and are not of particular significance, so are grayed out in the figure. In terms of dominant frequencies, the earlier and later segments are more similar, the earlier evidencing a spectral peak around 3.5 years, and the later around 5.5 years. Even during the Drought of the Fifties, this interannual variation of 4-5 year periodicity was occurring, but the amplitude of the excursion did not rise to a sufficient level to break the drought. It is the increase in power of this variation, i.e., the excursion amplitude, that is the difference between the two periods. In the later period, the flood-prone (“wet”) years evidence higher flows, and the drought (“dry”) years more intense drought. The central time segment about 1965-85 seems more irregular, perhaps transitional, exhibiting higher frequency variation with a prominent 2-year periodicity.

It has recently become fashionable in some quarters to ascribe the vacillations between drought (dry) and flood-prone (wet) periods to El Niño and La Niña conditions, respectively, in the tropical Pacific. It is therefore worthwhile to examine the correlation between San Antonio Bay hydroclimatology and the tropical Pacific, to establish whether the El Niño-Southern Oscillation (ENSO) is a viable predictor for average inflows to the bay. The intensity of ENSO is measured by the Southern Oscillation Index (SOI), defined as the atmospheric pressure difference between Tahiti and Darwin, which is anticorrelated with El Niño. To examine their correspondence, we examine the association between the monthly SOI and the monthly inflow to San Antonio Bay in excess of the 1942-2009 mean ($Q - \bar{Q}$), as a measure of wet (positive) versus dry (negative) conditions. Like the monthly inflows to San Antonio Bay, the monthly SOI is a noisy time

*Each period encompasses 256 months. The FFT can only accommodate a number of data points equal to a power of 2 without the artifice of padding. This also accounts for the resolution in frequency in Fig. 2-8 of 1/256 cycles per month.

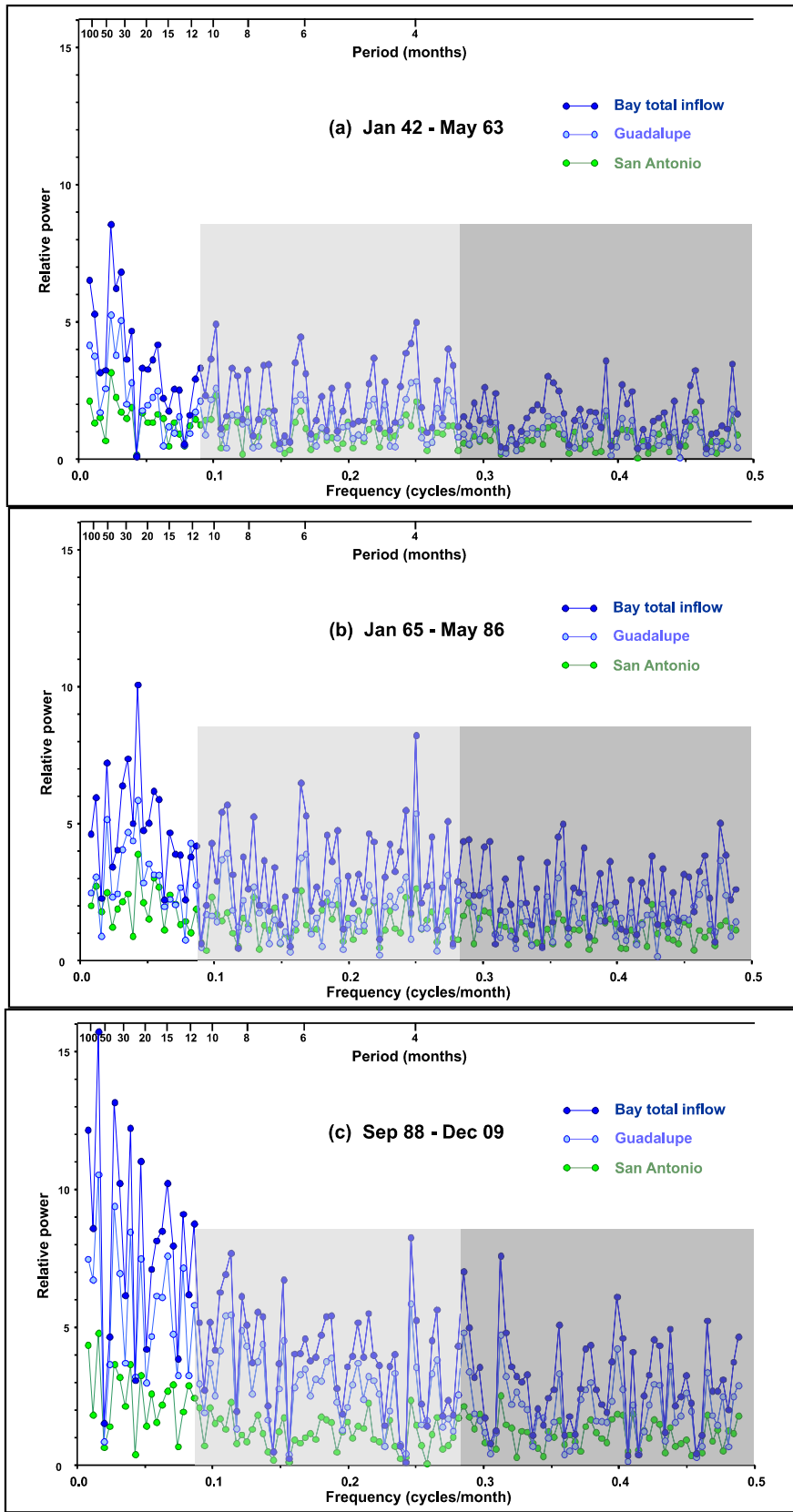


Figure 2-8 - Frequency spectra (Fast Fourier Transform) of subperiods of inflow time series

series. Both were smoothed with a running, centered 12-month mean, and plotted to exhibit time correlations in Figure 2-9. The atmospheric measure in this figure is actually the negative of the SOI, i.e., the pressure difference Darwin – Tahiti. This is because negative values of the SOI are associated with El Niño conditions, and the hypothetical relation is that El Niño produces stormy conditions, hence high runoff in the San Antonio Bay watershed. By plotting $-SOI$, we would expect to see its positive values correlated with above-average inflows, thereby facilitating a visual comparison.

While there appears to be some general correlation in the post-2000 period in Fig. 2-9, over the longer term of seven decades there is little. This is better exhibited by isolating those periods of larger departure of inflows from the mean, either runs of wet or dry conditions, by excluding the central third (33%) of the data (which turns out to be those 12-month mean monthly flows within ± 62 taf about the mean), and computing the average flow for positive and negative runs of the remaining data, along with the same average of the corresponding (smoothed) monthly SOI values. The resulting data points are shown in Figure 2-10. The hypothesized association between ENSO and wet-or-dry climatology would result in the data points lying in the upper left or lower right segments. This is clearly not the case.

An important but secondary supply of moisture originates in the tropical Pacific off Central America, so it is not unreasonable to expect a physical coupling between El Niño and Texas hydroclimatology. The lack of correlation in Fig. 2-10 is due to the influence of other factors, not correlated with El Niño, such as vapor influx from the Gulf of Mexico (which is by far the more important source of moisture to the state), position of the long-waves in the westerlies, especially an omega block over the western U.S., and the frequency and characteristics of frontal passages.*

* California is far more sensitive to the ENSO cycle than Texas due to its proximity to the eastern equatorial Pacific. One need look no further for an exemplar of the maxim that large-scale atmospheric circulations trump ENSO than fall of 2010, where despite La Niña conditions, California is plagued by phenomenal rainfall, flooding and mudslides.

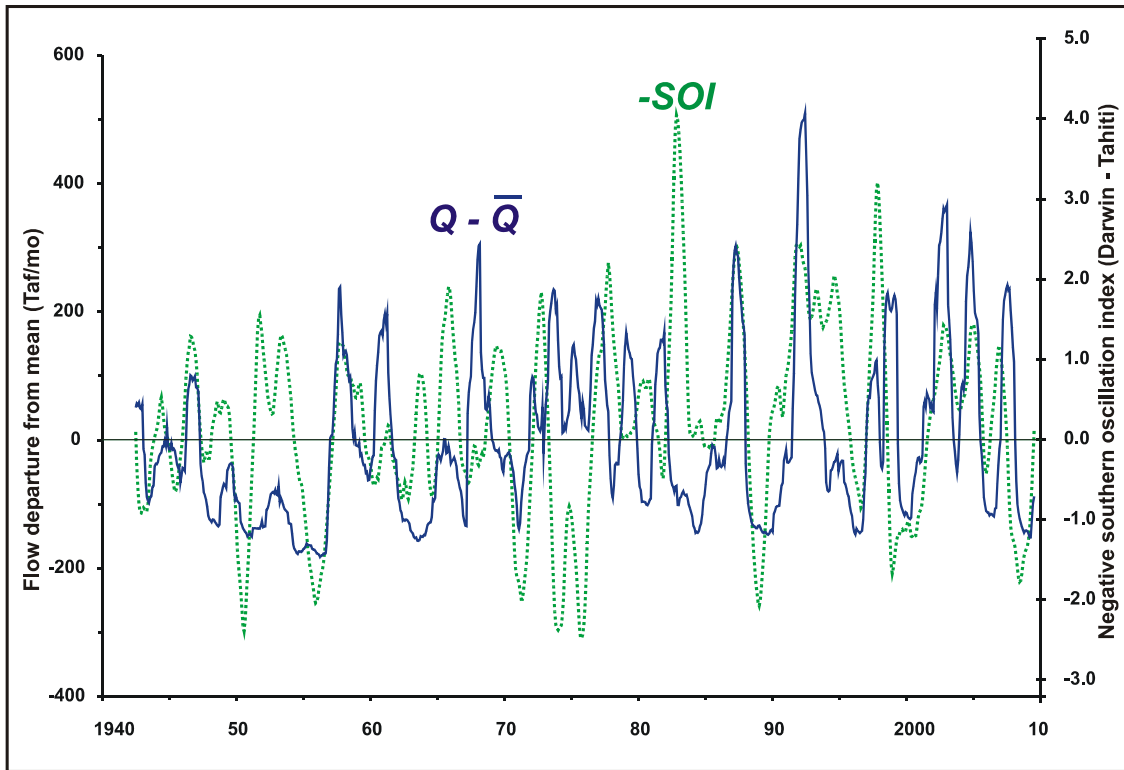


Figure 2-9 - Twelve-month running average of total inflow into San Antonio Bay in excess of mean, and negative Southern Oscillation Index (SOI), for 1942-2009 period. Positive values of $-SOI$ correspond to El Niño.

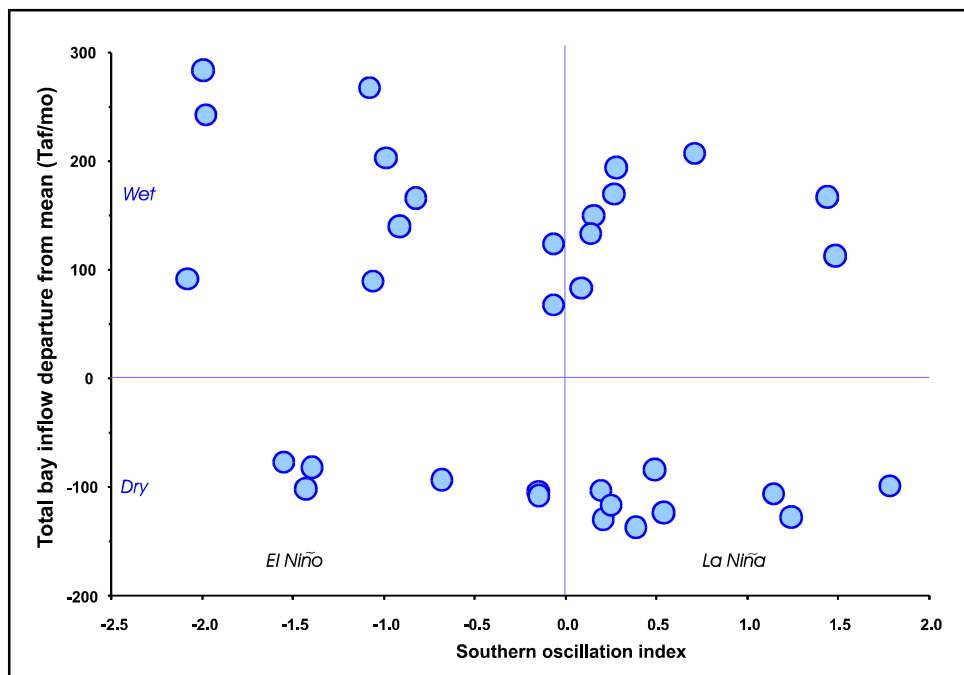


Figure 2-10 - Association of runs of high departure of flows from the mean, averaged over the run versus the averaged SOI over the same period.

2.1.3.2 Seasonal inflow variation

Figure 2-11a displays the variation in the cumulative frequency distribution (or ogive) of monthly flows into San Antonio Bay by month over the course of the year, the statistics being based on the period 1942-2009. The flows corresponding to occurrence frequencies of the quartiles (50% of course corresponding to the median) and highest and lowest deciles (i.e., 10% and 90%) are plotted versus month of the year. The mean monthly flows for each month are shown also (and differ from the medians when the monthly data are skewed). Figures 2-11b through 2-11d plot exactly the same information on the same ordinate scale (to facilitate comparison) but are each limited to the periods 1942-65, 1966-1985, and 1986-2009, resp., which correspond roughly to the time segments of the previous section. Figures 2-12 and 2-13 are exactly the same display except for the individual river basins of the Guadalupe and San Antonio (and have the same ordinate scale, though different from Fig. 2-11). These figures confirm the common knowledge that the intra-annual variation of flows into San Antonio Bay tends to be bimodal, with peak flows in the spring and fall. (This bimodal behavior is responsible for another important feature of the spectra of Fig. 2-8, namely the power peaks at periodicities of approximately six months.)

It is immediately apparent that, while the annual variation is indeed bimodal, the peaks are not equal, the spring peak being dominant, and are not equally distributed in the calendar. (This accounts for the additional spectral peaks at 4 and 12 months in Fig. 2-8.) Also, the bimodality is derived more from the occurrence of the higher flows and is not nearly so clearly exhibited in the lower flows (with occurrence frequency less than 50%). Indeed, the low flows occurring in the lowest quartile of the frequency distribution have little systematic seasonal variation. Flows at this occurrence frequency tend to be predominantly baseflow, rather than directly derived from storm events, hence seasonality would not be expected.

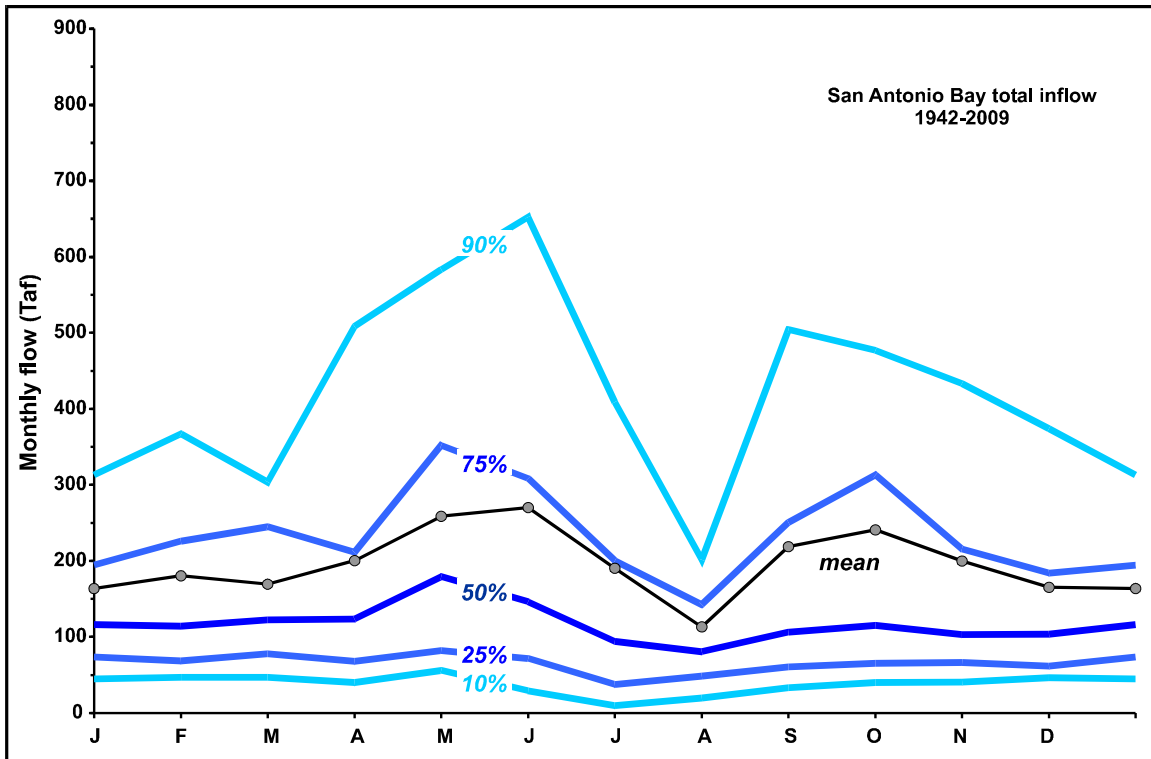


Figure 2-11a - Monthly total flows into San Antonio Bay at key frequencies of occurrence by month, and mean monthly flows, 1942 – 2009.

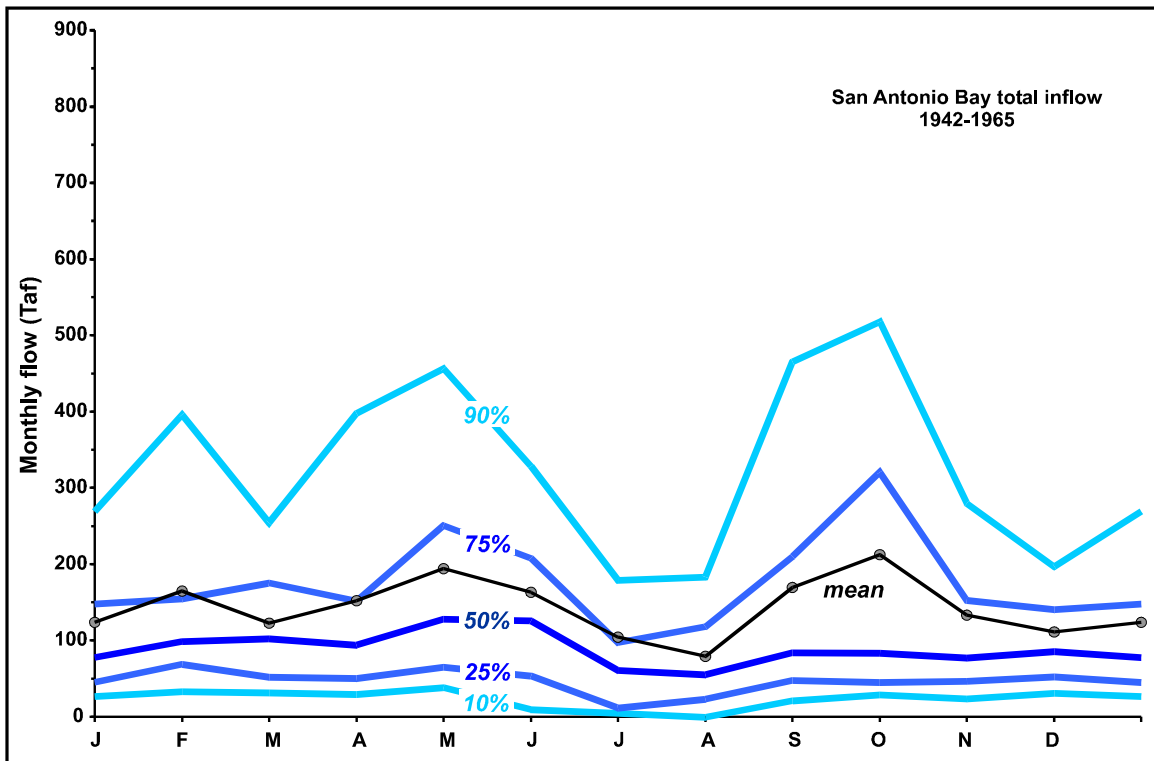


Figure 2-11b - As Fig. 2-11a, except only for the period 1942-1965 period

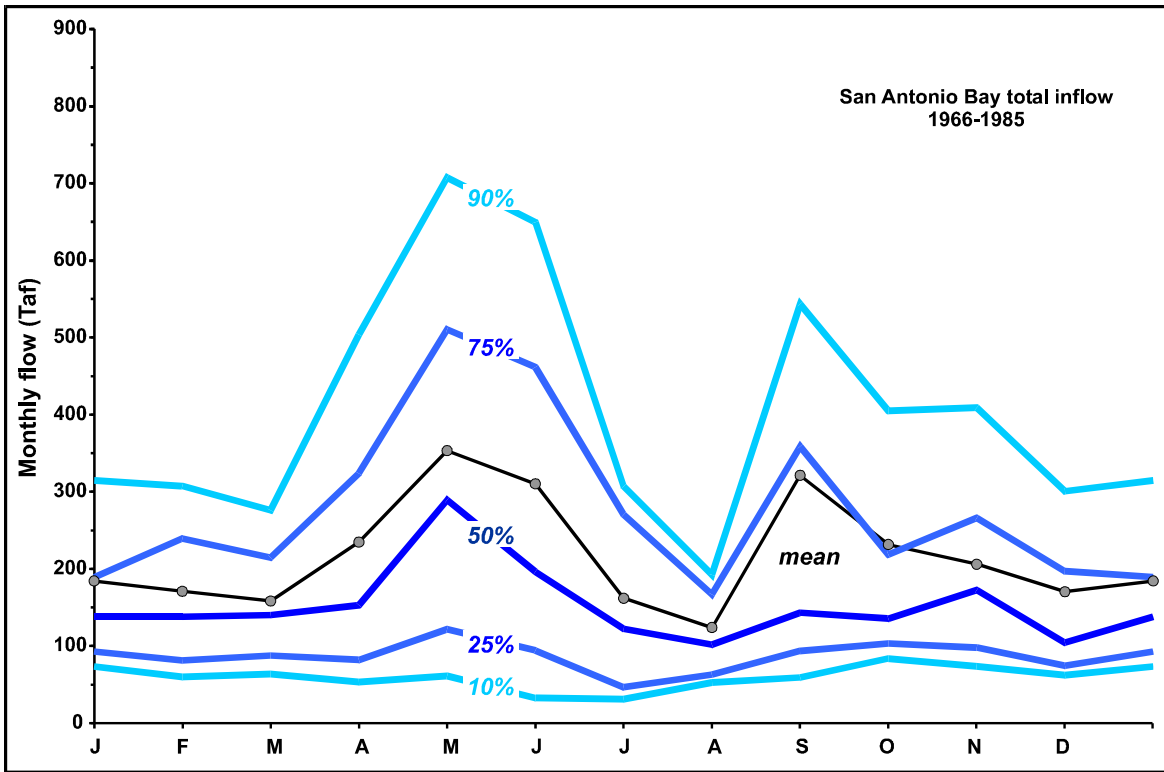


Figure 2-11c - As Fig. 2-11a, only for the period 1966 – 1985 period

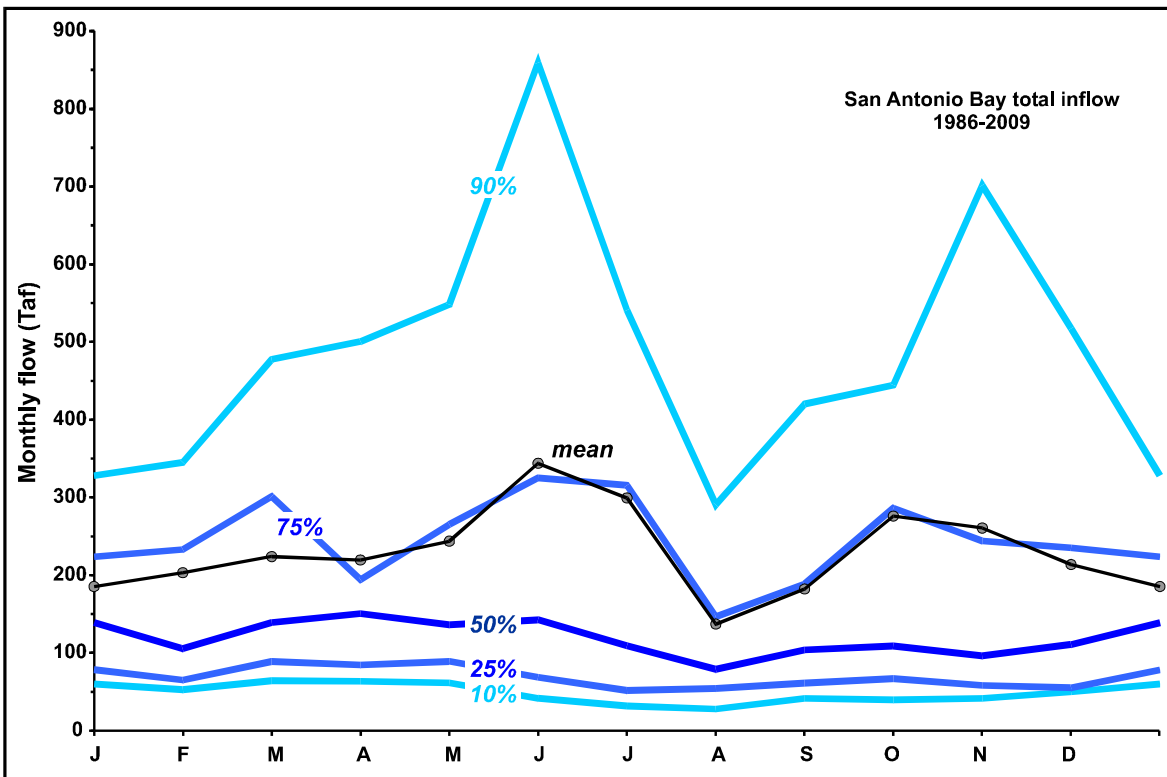


Figure 2-11d - As Fig. 2-11a, only for the period 1986 - 2009 period

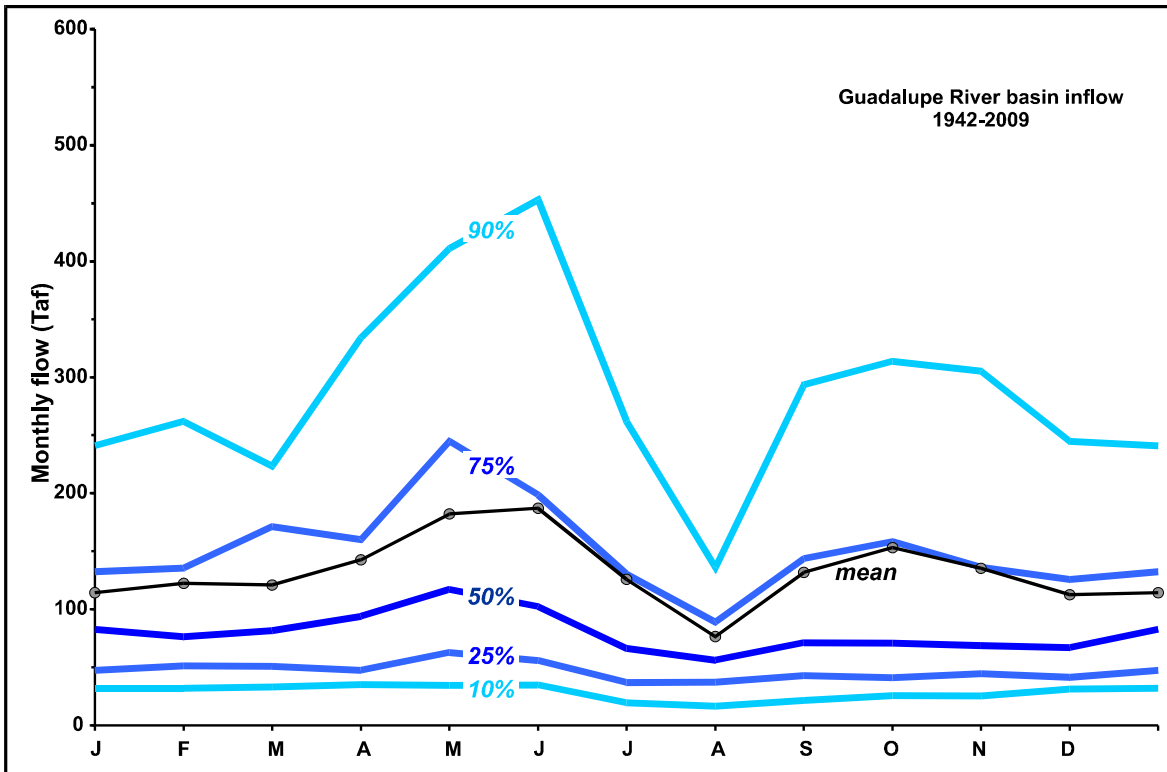


Figure 2-12a - As Fig. 2-11a, except for Guadalupe River basin only

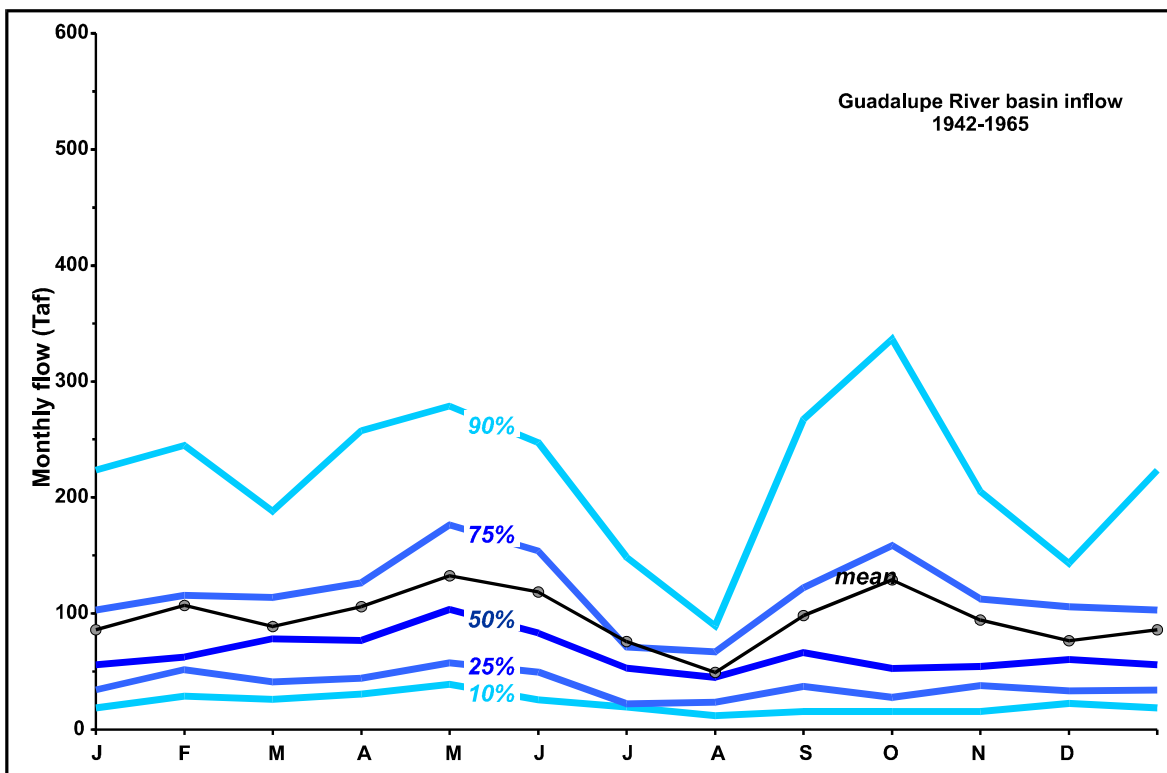


Figure 2-12b - As Fig. 2-11b, except for Guadalupe River basin only

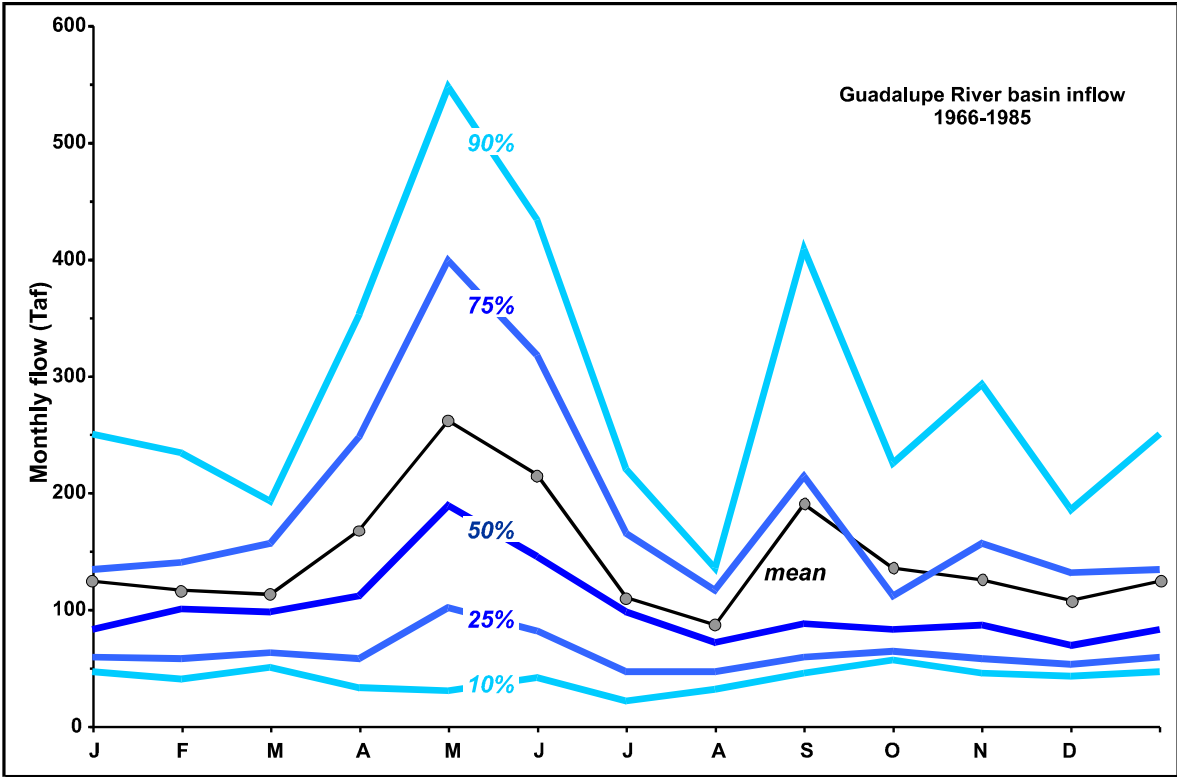


Figure 2-12c - As Fig. 2-11c, except for Guadalupe River basin only

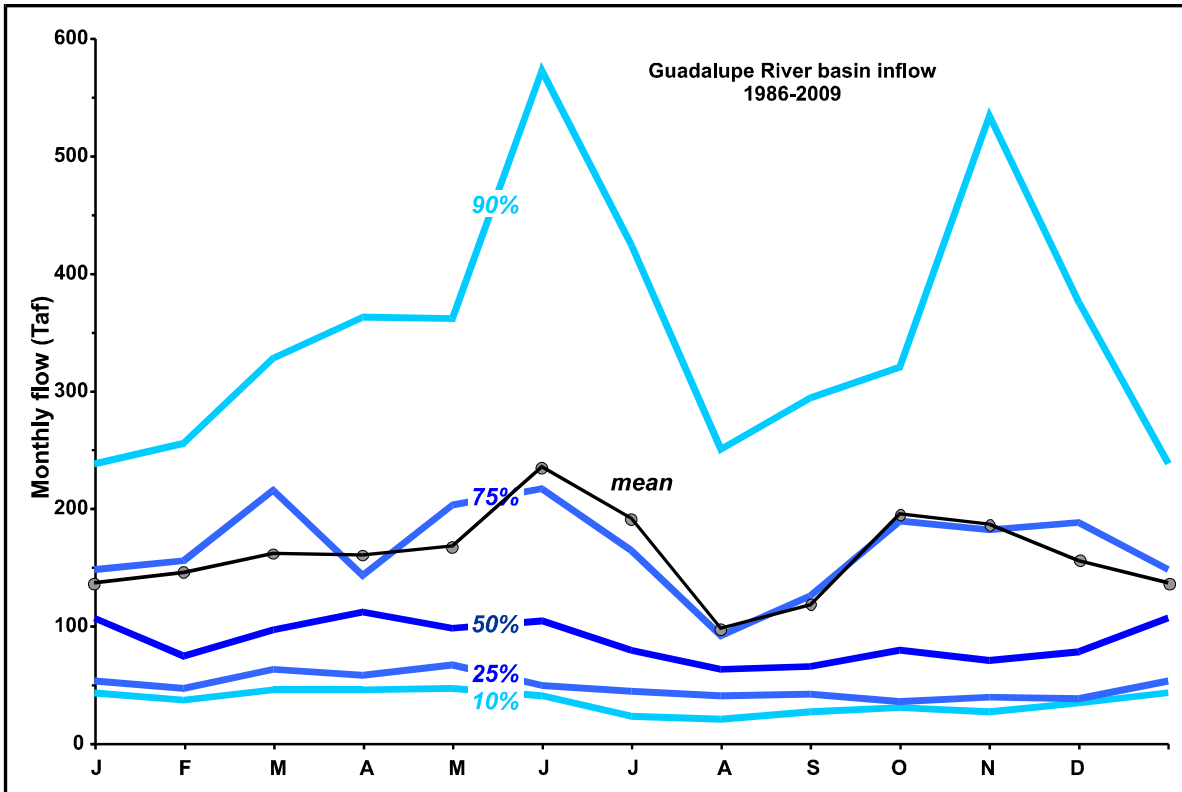


Figure 2-12d - As Fig. 2-11d, except for Guadalupe River basin only

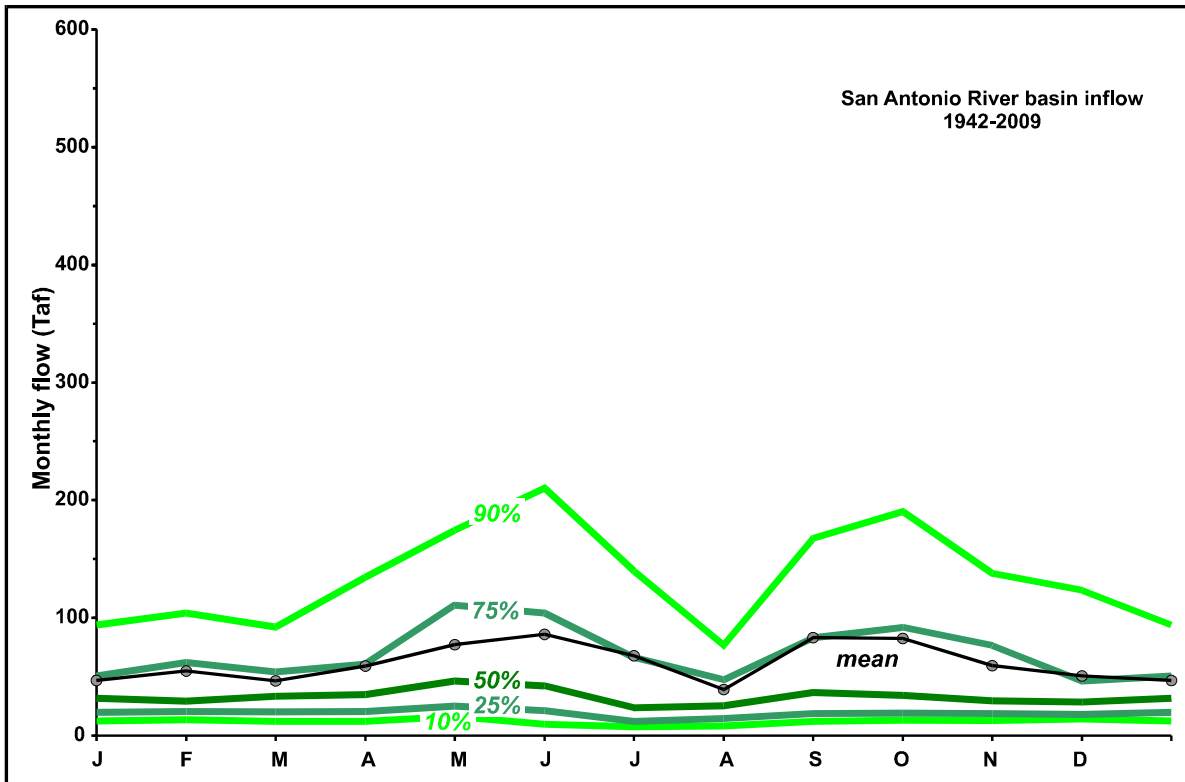


Figure 2-13a - As Fig. 2-11a, except for San Antonio River basin only

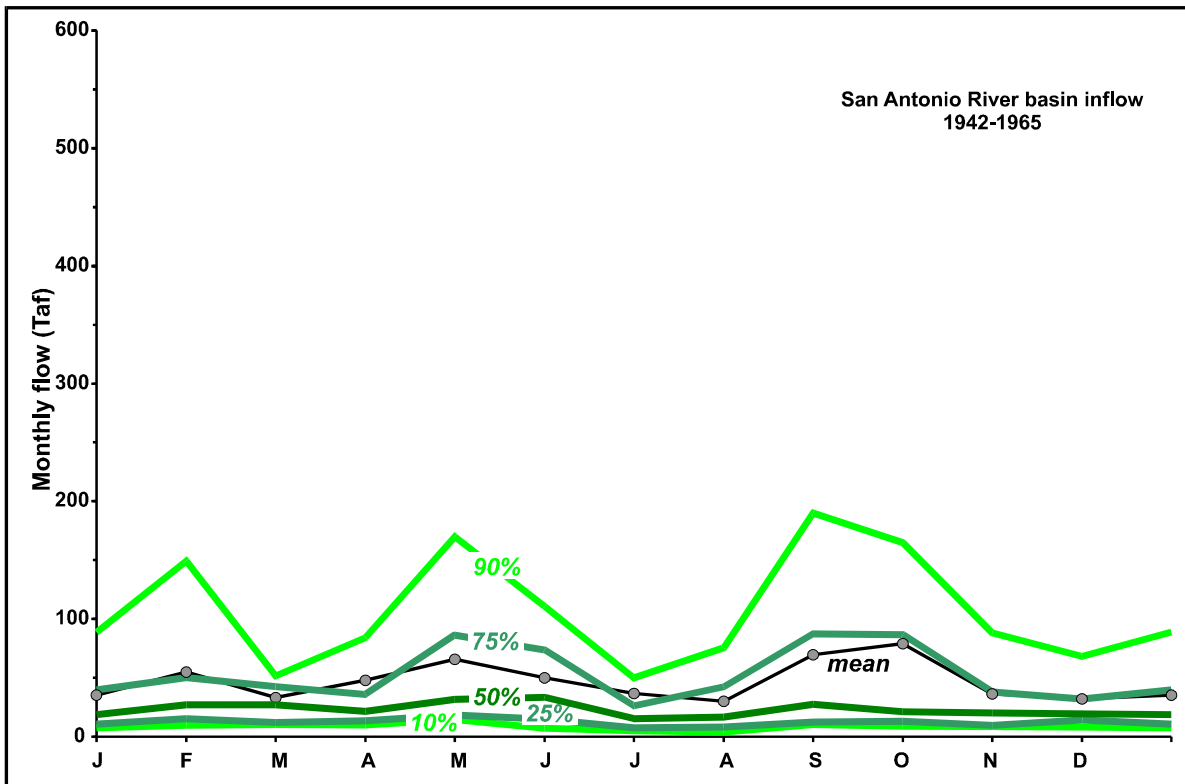


Figure 2-13b - As Fig. 2-11b, except for San Antonio River basin only

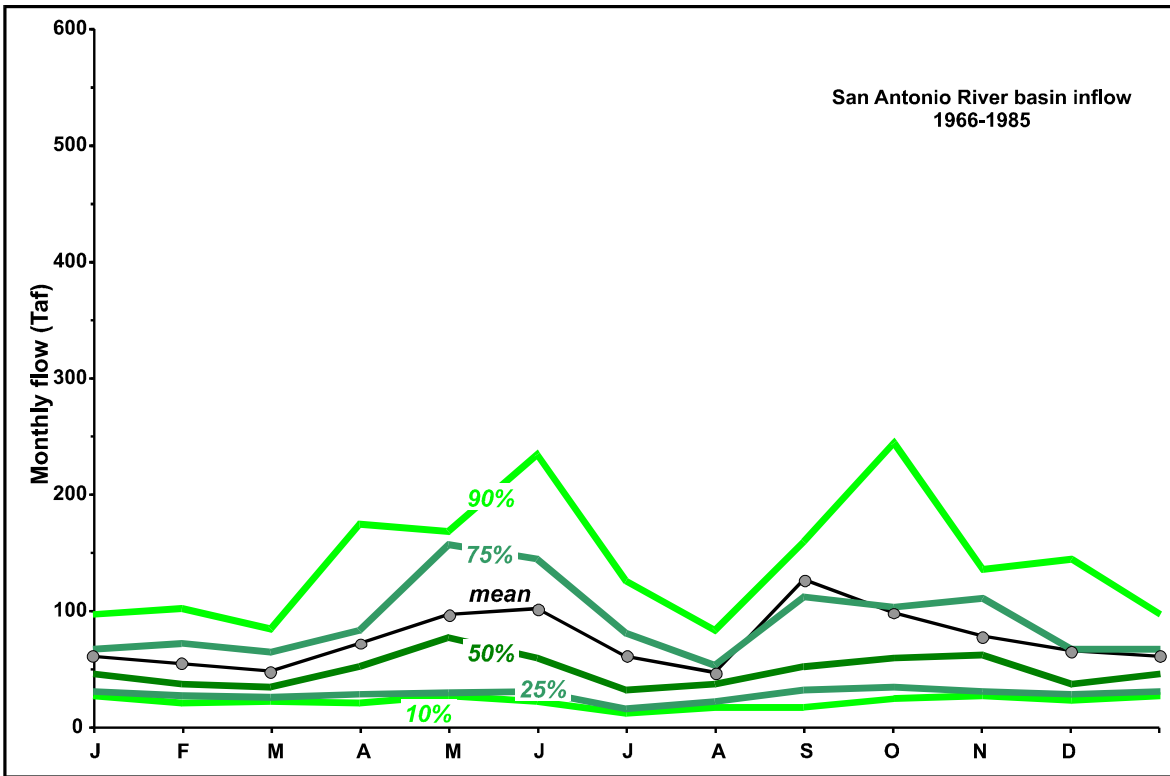


Figure 2-13c - As Fig. 2-11c, except for San Antonio River basin only

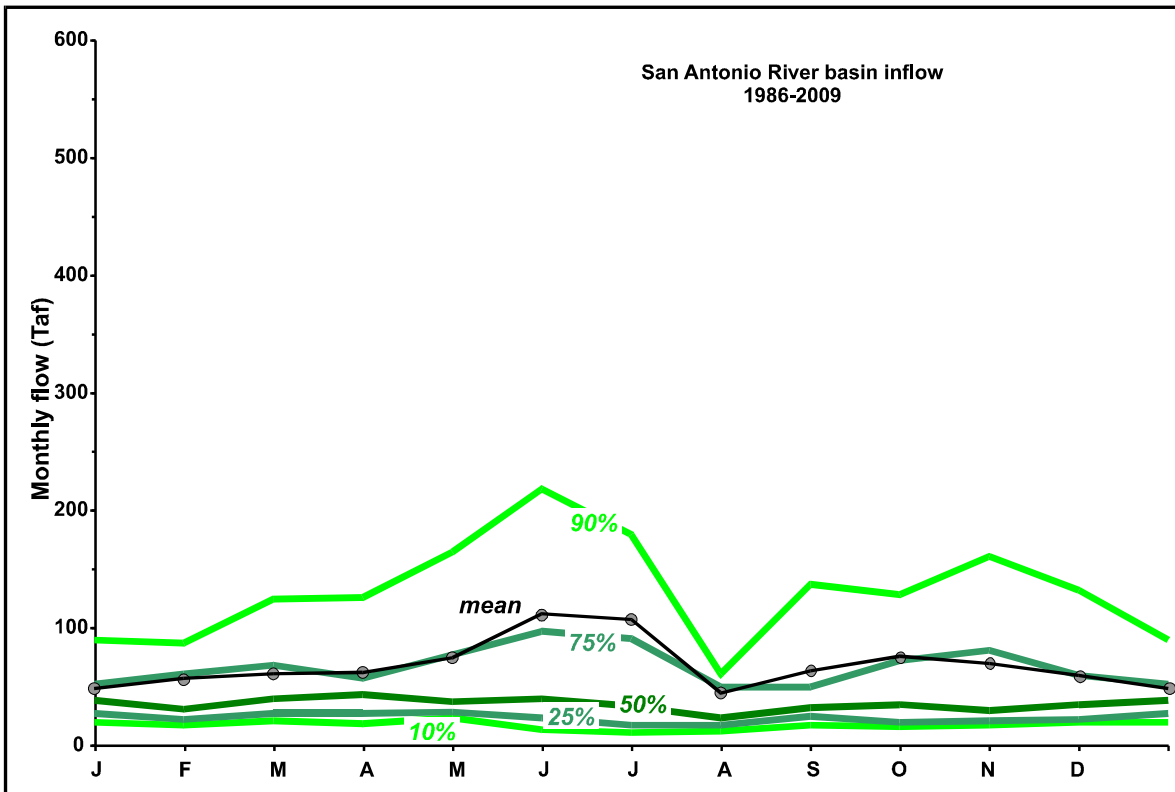


Figure 2-13d - As Fig. 2-11d, except for San Antonio River basin only

2.1.4. Summary

The principal observations and conclusions from the foregoing analyses may be summarized as follows:

1. The main contributors of inflow to San Antonio Bay are runoff from the land surface and human diversions and return flows in the stream channels. These are quantified by a combination of measured streamflow at gauging stations, modeled runoff based upon precipitation data, and measured or estimated diversions and discharges.

- 1.1 The lowest gauges on the drainageways of the San Antonio Bay watershed with sufficiently long records for hydroclimatological analysis are the San Antonio at Goliad, the Guadalupe at Victoria, and Coletto Creek near Victoria or Schroeder (a major tributary of the Guadalupe conflowing downstream from Victoria).

- 1.1.1 The total period of record utilized in the present analysis is 1942-2009.

- 1.1.2 The three gauge stations represent about 94% of the total watershed.

- 1.2 To estimate flows originating on the watershed below the gauges, results from the TWDB TxRR model were employed.

- 1.2.1 Starting in 1977, runoff data for individual subwatersheds (see Fig. 2-2) on a daily resolution are available.

- 1.2.2 For 1942-76, the only model results available are for the total ungauged watershed at a monthly resolution. These data were subjected to a statistical analysis to estimate the separate components of the Guadalupe, San Antonio, and bay periphery.

- 1.3 Diversions and return flows associated with human activities (irrigation, municipal and industrial operations) are available from several sources, and/or can be estimated. The extent and quality of information is variable and is generally poorer for the early period of record. The most comprehensive compilation has been carried out by HDR, who provided their data for this analysis.

2. By far, the majority of the inflow to San Antonio Bay is gauged, the ungauged inflows making up a small, but nonnegligible contribution, and human activities even less. Gauged and nongauged together, the Guadalupe contributes about two-thirds of the inflow to San Antonio Bay, and the San Antonio about one-third, with the bay periphery contributing less than 5%.
 - 2.1 By data source, approximately 89% of the inflow to San Antonio Bay is gauged, 16% is ungauged and -5% is the net returns over diversions. Due to the locations of the gauges, the ungauged watershed is roughly the contribution from the Coastal Prairie.
 - 2.2 By physical source, approximately 69% enters from the Guadalupe watershed, 33% from the San Antonio watershed, 4% from the bay periphery and -5% from net returns over diversions.
 - 2.3 The human component, i.e., the net of returns over diversions, is minor, generally within the uncertainty of measurement of the gauged inflows.
 - 2.4 While these proportions obtain on average over the period 1942-2009, there is considerable variability.
 - 2.4.1 At times the ungauged watershed contributes a greater proportion to the bay, when prolific rainfall on the coastal plain results from marine airmasses or tropical storms.
 - 2.4.2 During drought conditions, the proportionate influence of ungauged flows and human activities become much greater factors in the water budget.
3. There has been a substantial increasing trend in inflow to the bay over the 1942-2009 period. The time variability in inflow has changed as well, with increasing high-flow surges separated by more intense drought periods.

- 3.1 The annual inflows to the bay have increased about 80% over the nearly seven-decades of data.
- 3.2 Ten droughts exceeding one-year duration were identified in the 1942-2009 record, representing 40.5 of the 68-year period, i.e., the bay inflows are in drought conditions about 60% of the time. The most severe drought on record is the Drought of the Fifties.
- 3.3 Inflows to the bay exhibit surges separated by periods of low flow. These surges generally recur every four to five years, except during the middle two decades of the record when their frequency was about every two years. Over the 1942-2009 record, the magnitude of these surges has increased by about a factor of two.
- 3.4 Droughts separating the surges of inflow have tended to increase in intensity over time. The three most intense droughts on record have occurred in the last two decades. Most intense was the drought of 2008-09.
- 3.5 The play in the popular press notwithstanding, there appears to be little association of wet versus dry conditions, as measured by departures from normal of bay inflows, with El Niño versus La Niña in the Equatorial Pacific.
- 3.6 While the magnitudes and year-to-year variation of inflows have changed over the past seven decades, there has been little change in their seasonal distribution, the basic bimodal pattern being maintained, with high inflows in the spring and fall.
 - 3.6.1 The bimodal pattern is driven mainly by the higher flows, i.e. those exceeding the monthly medians.

2.2 Relations between inflow and salinity within San Antonio Bay

2.2.1 Salinity in estuaries

An estuary, by definition, is a coastal watercourse that is transitional between the terrestrial and marine environments. An estuary is therefore subject to external factors deriving from both the ocean and land, as well as some factors that are peculiar to the coastal zone. Among the oceanic influences are tides, waves, marine meteorology and seasonal water-level variation. Among the terrestrial influences are continental meteorology, drainage of runoff (freshwater inflow) and sediment transport from erosion of the surface. Among the factors specifically operating in the coastal zone are land-sea breeze circulations, nearshore sediment mobilization and transport, and circulations driven by the difference in density between sea water and fresh water. (See, e.g., Ward and Montague, 1996, for more detail on the estuarine environment.) One implication of the transitional nature of the estuary is that its waters exhibit a gradient zone in which salinity (the concentration of dissolved salts) increases from zero (0) at its inland freshwater limit to oceanic salinity, nominally 3.5% (or, in the more conventional units, 35‰, parts per thousand, see Section 1). Figure 2-14 shows a sketch of a simple estuary with schematic salinity contours (isohalines). Generally, for higher river flows, the salinity gradient zone is displaced farther down the estuary and oceanic salinities are acquired farther out in the nearshore zone of the sea. For lower river flows, in contrast, the salinity gradient retreats farther up the estuary. For very low flows, oceanic salinities may be found well within the estuary bounds.

Estuaries have salinities less than oceanic due to dilution by freshwater inflow. This would lead one to expect salinity at a point in an estuary to be a nicely behaved, monotonically decreasing function of inflow. Actual data from estuaries belie this expectation however, exhibiting considerable scatter on a graph of salinity plotted versus inflow. (“Buckshot” is an apt description.) This scatter is due largely to the complexity of the response of salinity to inflow. A relatively slow influx of freshwater can be mixed into the water in the estuary by natural turbulence. If this influx increases to a substantial flow, it begins to displace, rather than mix into, the water resident in the estuary. A flood hydrograph can replace much, sometimes all, of the volume of the estuary. As this freshwater displaces the estuary water, the salinity at an

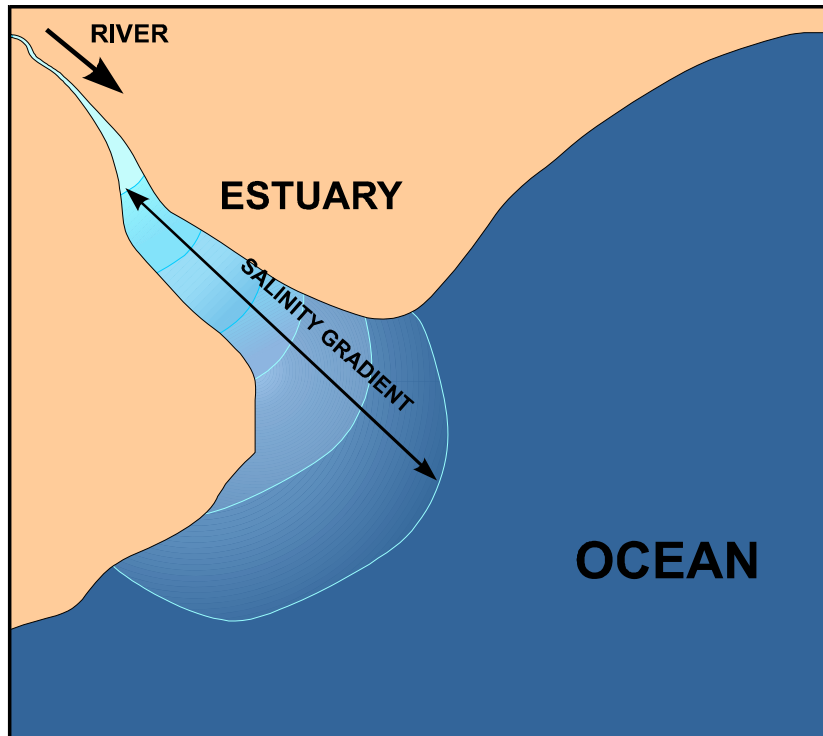


Figure 2-14 - Schematic of simple estuary, showing salinity gradient from fresh to oceanic

affected location in the estuary drops to much lower, perhaps near-zero values. Saltier water from the ocean then begins working back into the estuary, effected by tides, turbulent mixing, and the greater density of saltwater, so that salinity begins to rise. These processes are referred to collectively as salinity intrusion. The result of freshwater displacement followed by salinity intrusion means that the time behavior of salinity is different from that of the freshwater inflow. Technically, salinity exhibits a lagged, integrated response to the excitation of the inflow time function.

A schematic example is shown in Figure 2-15, which might typify the idealized estuary of Fig. 2-14. Salinity at a fixed location in the estuary begins to drop after the rising limb of the flow hydrograph (how soon after depending upon the measurement location in the estuary), and decreases down to a low value determined by the diminishing but still substantial rate of inflow. As flow continues to decline, salinity begins to slowly increase due to intrusion and mixing. For most of the values of flow, there are two occurrences on this graph, e.g., Q_0 and Q_1 , one on the

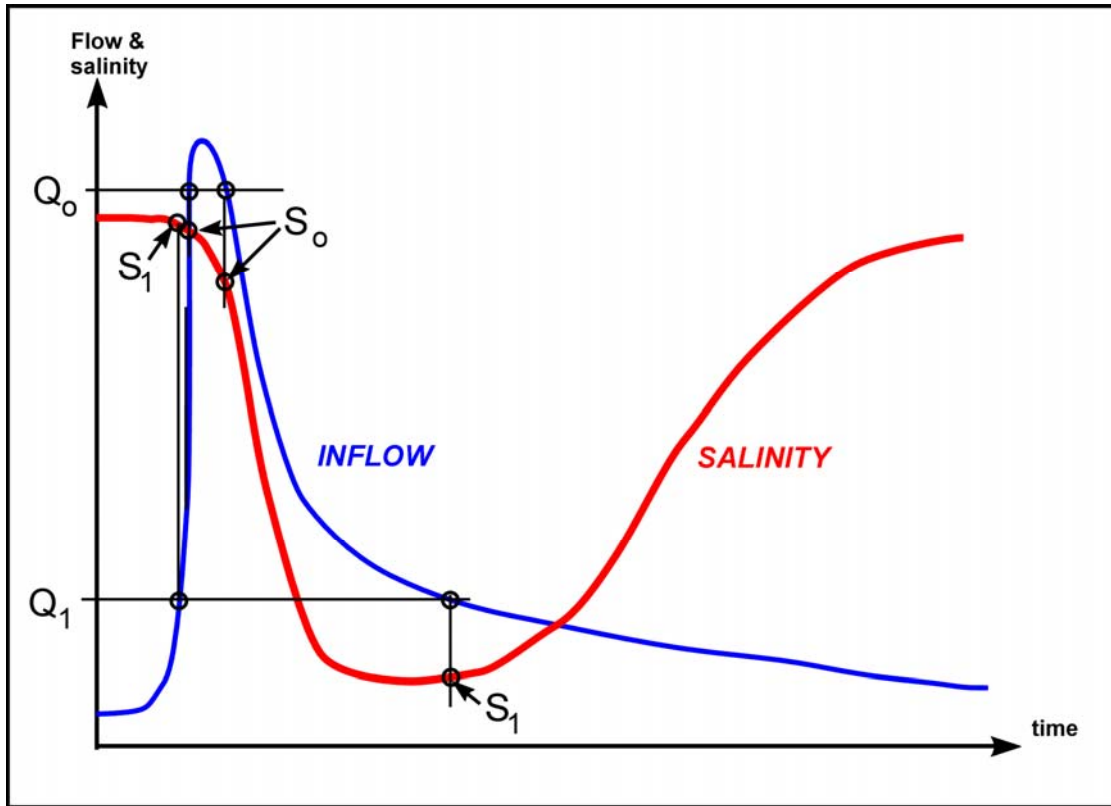


Figure 2-15 - Schematic of salinity response to a single flood hydrograph

rising limb and one on the falling limb. The two salinity values corresponding to these occurrences of the *same* flow value are generally different, exemplified by the two values of S_0 corresponding to Q_0 and two values of S_1 corresponding to Q_1 . These may differ widely, such as the example of S_1 in this diagram. If this time plot were sampled at intervals of time (as one would do if making routine measurements of salinity at a fixed location in the estuary) and the results plotted as salinity versus inflow, there would result considerable scatter because of the different salinity values for each value of inflow.

In the real world, neat isolated hydrographs like that of Fig. 2-15 rarely occur. Instead, there are multiple, superposed hydrographs forming a complex time series to which salinity exhibits an even more complex response, giving multiple values of salinity for a specific value of inflow. Moreover, salinity also responds to other processes that have no direct relation to inflow,



Figure 2-16 - A portion of the lower Texas coast showing the principal bays, including San Antonio

including internal circulations driven by wind and density currents, direct precipitation, evaporation, and emptying and filling of the estuary by tidal motions.

2.2.2 Salinity in San Antonio Bay

Most estuaries are much more complex than the idealization of Fig. 2-14. The physiography and bathymetry of the estuary may be highly varied, with deep channels and extensive shoals, there may be multiple points of freshwater flow entry, and the connection to the sea may be obstructed by reefs or islands. The bays of Texas are estuaries of a type known as lagoonal or bar-built



Figure 2-17 - San Antonio Bay

(Ward and Montague, 1996). These are broad, relatively shallow systems fronted by a barrier island, through which narrow tidal inlets effect exchange between estuary and the sea.

A portion of the coastal bend of Texas is shown in Figure 2-16, including the San Antonio Bay system, and San Antonio Bay is shown in more detail in Figure 2-17. From a large-scale viewpoint, Corpus Christi Bay, Aransas-Copano Bay, San Antonio Bay and Matagorda Bay can, together, be considered a single estuarine system, with multiple river inflows and with two primary inlets for exchange with the sea, *viz.* Aransas Pass on the south and Pass Cavallo/ Entrance Channel on the north. (Indeed, the Laguna Madre, which lies off the map of Fig. 2-16 to the south, could be argued to be a part of this “superestuary”, since the entire system is connected.) Even if San Antonio Bay is considered as a single estuarine system, as will be done in the remainder of this missive, the larger view is important as a reminder that the bay is

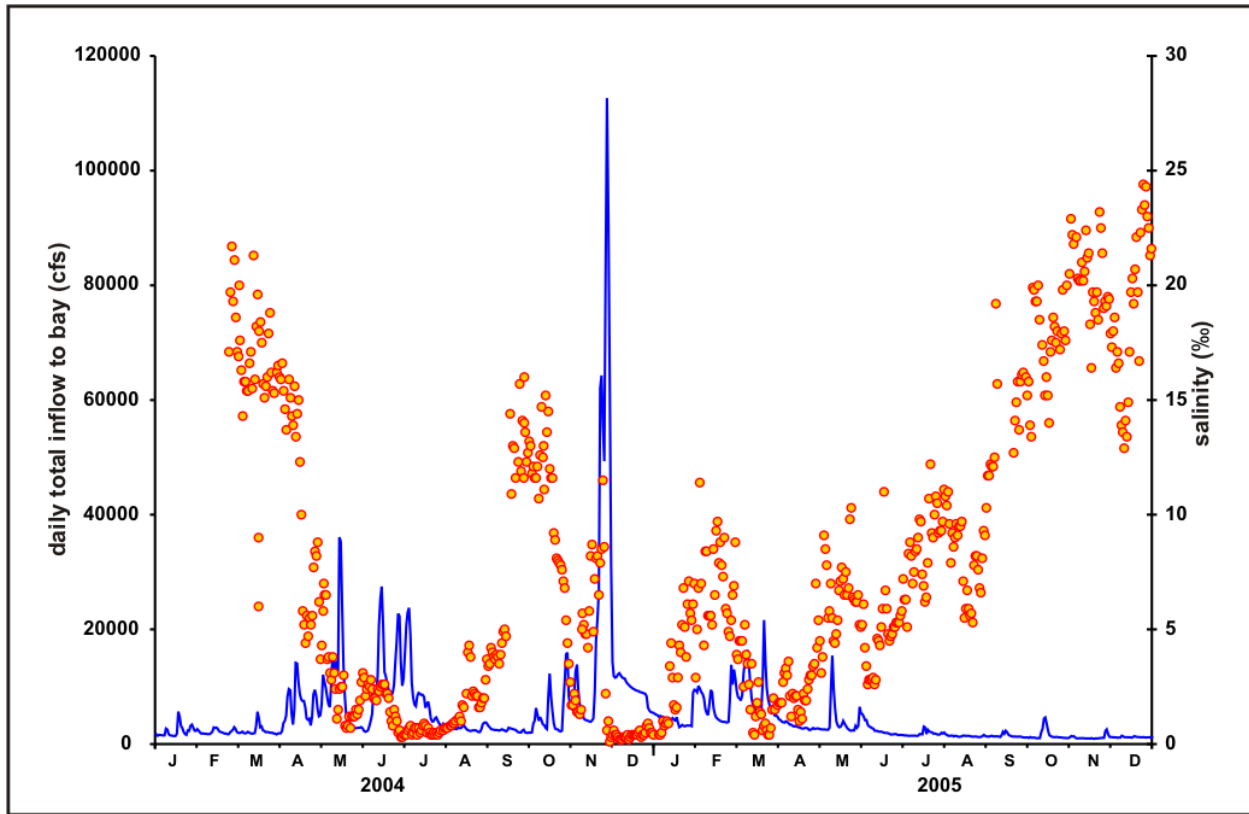


Figure 2-18 - Salinity response in San Antonio Bay at TCOON station GBRA-1 (see Fig. 2-17)

potentially influenced by the systems upcoast and downcoast, as well as by its own inflow and circulations.

Perhaps the most important geomorphological feature of San Antonio Bay is that it has no direct connection with the sea. As noted in Chapter 1, the influence of the ocean, notably tides and salinity intrusion, is exerted through the tidal inlets of Pass Cavallo (including the Entrance Channel) to the north, and Aransas Pass to the south. Cedar Bayou is minor in comparison and has been chronically closed since the 1970's, see Chapter 3. Corollary to the lack of an inlet to the sea, San Antonio Bay does not have a deep-draft ship channel, an important factor in the salination of the more industrialized estuaries on the Texas coast.

An example of salinity response to flood hydrographs in San Antonio Bay analogous to Fig. 2-15 is shown in Figure 2-18. This displays variation in the daily measurement of salinity in San

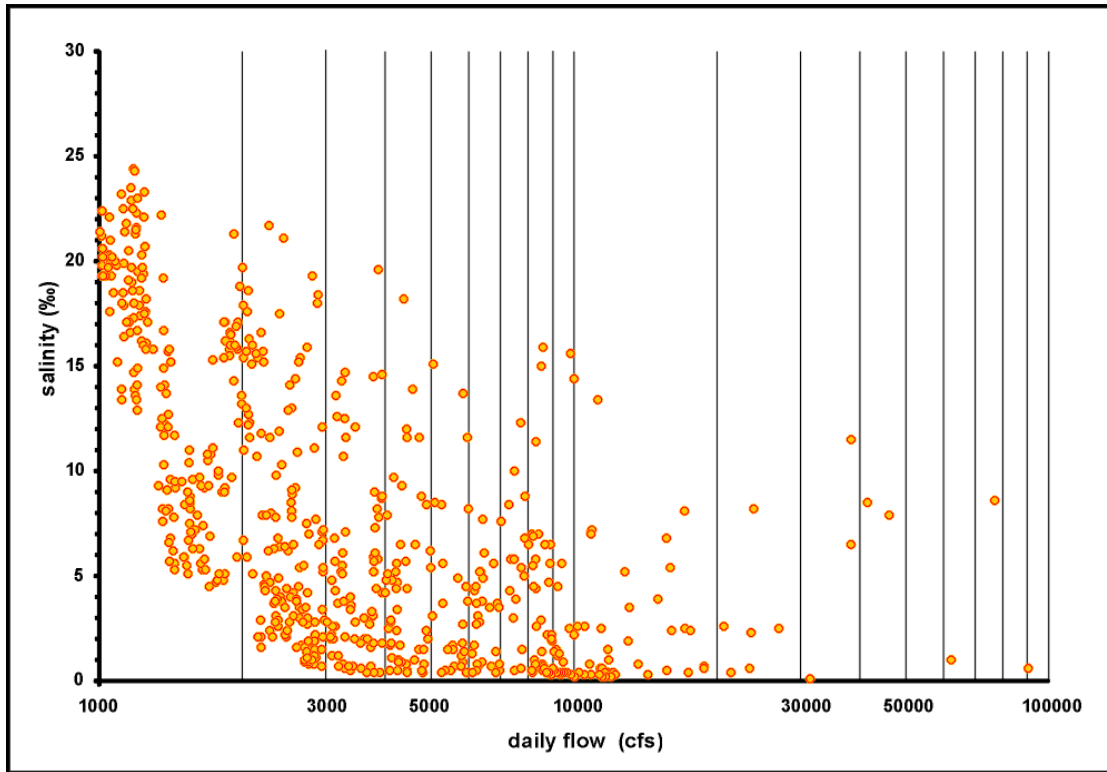


Figure 2-19a - Salinity at TCOON station GBRA-1 versus logarithm of daily inflow (cfs) to San Antonio Bay

Antonio Bay at Texas Coastal Ocean Observing Network (TCOON) sonde station GBRA-1 (whose location is shown in Fig. 2-17) along with the time signal of daily inflow to San Antonio Bay in cubic feet per second (cfs). (Sonde data of salinity are recorded hourly at this station. This time series was sampled daily at noon.) Figure 2-19a displays these same data plotted as salinity versus daily flow, rather than as a time series. (The abscissa is actually the logarithm of daily flow, to better resolve the data at lower flows.) While there is a general tendency to lower salinities at higher inflows, there is considerable scatter. The correlation proves to be about -0.62, i.e. a least-squares line through these data would explain about 38% of the variance.

Because salinity has a lagged, integrated response to inflow, it has “memory” of inflows preceding the date of measurement. One way to capture this memory is to use the averaged inflow over some period preceding the date of salinity measurement, rather than the inflow measured exactly on that date (as is the case for Figure 2-19a). Experimenting with various

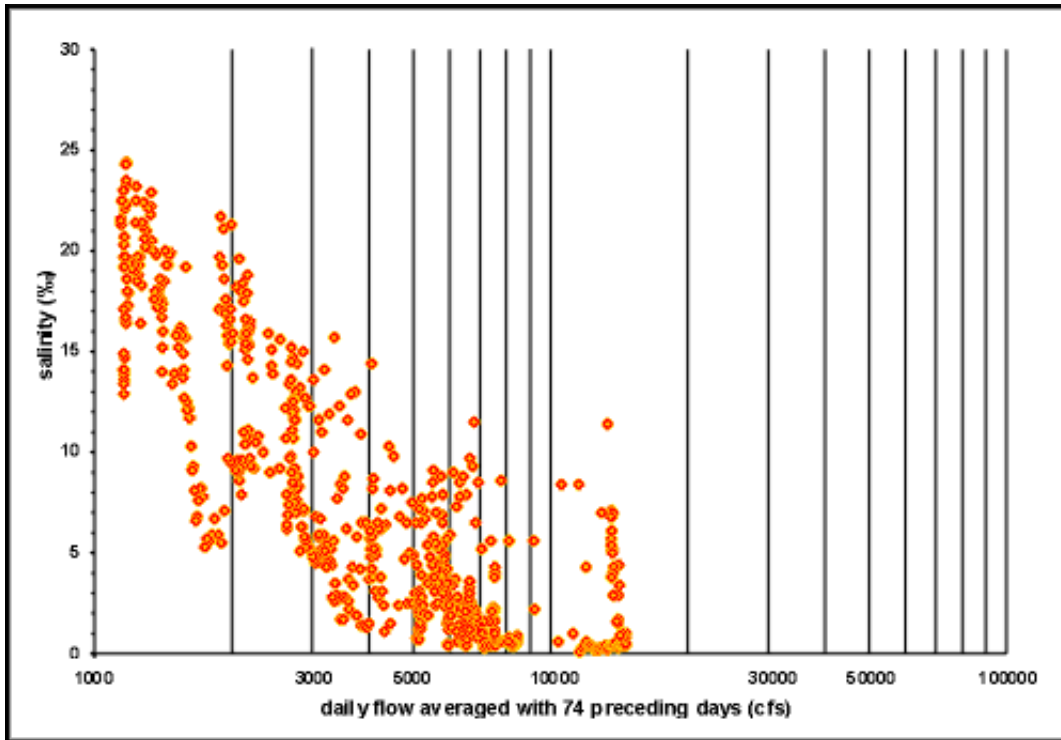


Figure 2-19b - As in Fig. 2-19a except versus logarithm of 75-day-mean inflow

averaging periods determined that a 75-day averaging period achieves the greatest predictive success for San Antonio Bay. Figure 2-19b repeats the plot of salinity versus daily inflow, except that the value of inflow used is the average of the 75-day period terminating on the date of measurement. Comparison of Figs. 2-19a and 2-19b discloses a reduction in scatter, the correlation between salinity and 75-day-averaged inflow being about -0.83, so that a least-squares line would explain nearly 70% of the variance in the data.

There still remains a great amount of scatter in the plot of salinity versus inflow. Moreover, it is rare to have an uninterrupted time series at a single location measured at a short interval of time (one day in the example of Fig. 2-18 *et seq.*). The usual practice of estuary hydrographers is to collect point measurements, usually from several monitoring programs, then group these within subregions of the estuary. This is the procedure employed in both of the National Estuary Program projects on the Texas coast to analyze salinity trends in Galveston Bay and Corpus Christi Bay (e.g., Ward and Armstrong, 1997). Such data are sparse in time, and the fact that

they are measured at different locations within a subregion is a source of scatter additional to those enumerated above.

2.2.3 Statistical regression of salinity on inflow in San Antonio Bay

In coastal management the need frequently arises for predicting the salinity in an estuary given the freshwater inflow. There are two broad strategies for approaching the problem: (1) mathematical modeling based upon deterministic laws of the physics of fluid motion, (2) statistical modeling based upon the fit of a mathematical function to measurements. For expediency, the latter is pursued here. This requires marshalling a data base of salinity measurements.

Data from the period 1982-2009 were gathered for the Lower San Antonio Bay (LSAB) region shown in Fig. 2-17. This is the region of San Antonio Bay that is adjacent to the Aransas National Wildlife Refuge (ANWR), but excludes the immediate vicinity (1 km) of the Gulf Intracoastal Waterway (GIWW). This was the region focused on in this study because this is typically where the main salinity gradient is located, the installation of the sonde station at GBRA-1 provided a reliable source of detailed data, and the resources of the project limited the areal scope of this part of the work. (Phase 2 will examine the entire area of San Antonio Bay and exploit a wider range of data.) There were three sources for this data compilation: routine water quality monitoring stations of the Texas Commission for Environmental Quality (TCEQ) (which includes data from the Texas Department of State Health Services), biological sampling stations of the Texas Parks and Wildlife Department (TPWD) Coastal Fisheries Program, and the robot sonde GBRA-1 operated by TCOON for the Guadalupe-Blanco River Authority (GBRA). As noted above, the sonde measures and records data every hour. Because of the high autocorrelation of salinity (two measurements an hour apart are likely to be nearly equal), most of these measurements are redundant, but their retention in the data base would overwhelm the other data, which are taken much more sparsely in time. To minimize the oversampling effect while still making use of the information in the automated record of GBRA-1, only the noontime values were retained in the data base (the same data plotted in Figs. 2-18 *et seq.*).

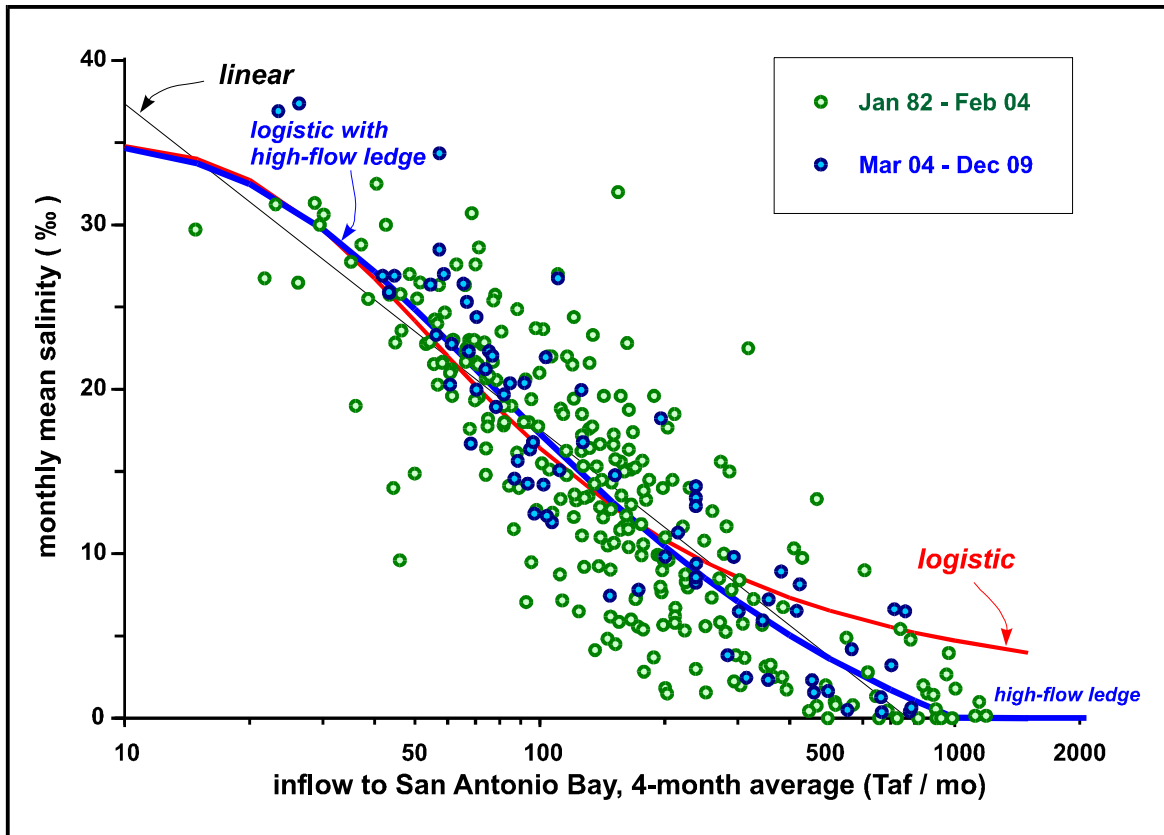


Figure 2-20 - Monthly-mean salinity in Lower San Antonio Bay (Fig. 2-17) versus inflow into San Antonio Bay averaged over four months terminating with the month of salinity data, with regression lines (see Table 2-8)

The present objective is to predict salinities at the lower inflow levels, to better diagnose salinities during drought events, such as that of 2008-09. It is more important therefore to focus on the long-term salinity responses to low flows, which typically are quasi-steady-state, rather than the more dynamic responses to flood events. For this purpose, the salinity data, already aggregated over the spatial area of LSAB, were averaged by month. The associated inflow data were also aggregated by month. This use of monthly-mean salinity and monthly inflow data is consistent with the resolution adopted by the G/SA BBEST (2011) in its salinity modeling work. Even considering flows and salinities with a monthly time resolution, there is still a memory effect, in which salinity exhibits a lagged, integrated response to inflows. This can be captured to some extent by averaging the inflows over several months, preceding and including the month

Table 2-8
 Regressions of monthly salinity versus inflows for Lower San Antonio Bay (Fig. 2-17)

<i>regression</i>	<i>equation</i>	<i>Expl var (%)</i>	<i>SEE (‰)</i>
(1) linear	$S = 57.15 - 8.598 * \log(Q)$	72.7	4.5
(2) logistic	$S = 35 [1 + \exp\{-24(1/\log Q - 1/\log 90)\}]^{-1}$	71.6	4.6
(3) logistic with high-flow ledge	$S = \max\{35 [1 + \exp\{-20(1/\log Q - 1/\log 210)\}]^{-1} - 15, 0\}$	74.4	4.4

where:

S = monthly-mean LSAB salinity in ppt (‰)

Q = total inflow into San Antonio Bay in thousands of acre feet (Taf) per month, present month averaged with preceding three (3) months (see text)

Expl var = explained variance of the regression (for the linear regression this equals R²)

SEE = standard error of the estimate

log denotes the naperian logarithm

for which mean salinities are available, in the same way that use of an averaged inflow in Fig. 2-19b reduced the variance of the relation from that of Fig. 2-19a. Numerical experiments with the 1982-2009 data disclosed that a four-month average inflow (i.e., the mean of the present and the preceding three months) achieved the greatest explained variance of the predicted monthly salinity. The monthly salinity data are plotted versus the four-month mean flows in Figure 2-20. Data points are differentiated as those before the GBRA-1 sonde became operational (i.e., before March 2004), and those afterward. The former averaged about 5 data points per month and the latter about 33, but there is no apparent bias between the two.

Selection of a regression form is based upon qualitative information about the observed behavior of the dependent variable on the independent. A linear regression is the obvious first choice, which achieves better than a 70% explained variance, see Table 2-8 and Fig. 2-20. Within the range of measurements, this would be satisfactory, but our purpose here is to better depict the response of salinities to flows perhaps lower than those represented in the data. For these the

linear relation has the unsatisfactory feature of predicting salinities substantially higher than sea water for extremely low flows. It also has the unpleasant attribute of predicting negative salinities for higher flows.

A better physical representation of the variation of salinity with flow is a sigmoid shape, in which the dependent variable approaches asymptotes at high and low values of the independent variable. We know that sufficiently high flows drive the salinity to zero, which defines the lower asymptote, and for low flows the salinity approaches seawater, which defines the upper asymptote. (Actually, with distance south along the Texas coast, the evaporative deficit at the surface increases, so that under low flows, especially in summer, salinities can exceed seawater. If we had more data at very low flows, it might have been possible to improve the specification of the upper asymptote, perhaps increasing it by a few parts per thousand. At present, an extensive data-recovery effort is underway through the support of GBRA and San Antonio River Authority. In Phase 2 of the present study, this more extended data set will be examined.)

There are a number of sigmoid functions on the market. For this work, a logistic function was selected. (The arctangent and the Gaussian error function were also tried, but proved essentially equivalent to the logistic.) A least-squares fit of the logistic to the salinity-inflow data was carried out iteratively (see, e.g., Cavallini, 1993), and the resulting regression is given in Table 2-8 and plotted in Fig. 2-20. A slightly more complicated version is a sigmoid with a ledge on either asymptote: in this case, a high-flow ledge was used to improve the function behavior at low salinities. This regression performs somewhat better than the simple logistic, see Table 2-8.

Although deterministic modeling of salinity is far beyond the scope of this study, it is of interest to compare the statistical accuracy of the regressions of Table 2-8 to results achieved with a deterministic model. As noted above, this type of modeling is based upon the numerical solution of complex partial derivatives in space and time. Modeling with these types of equations has been largely developed within the disciplines of meteorology and physical oceanography, from which modeling in the coastal zone has benefited. Recent surveys of the subject as applied to estuaries and the coast may be found in Dyke (2007) and Hearn (2008). The development of a hydrodynamic-salinity model for an estuary is a formidable undertaking. There is presently one

such model in existence for San Antonio Bay, namely the Texas Water Development Board's (TWDB) TxBLEND model. This model employs a two-dimensional depiction of the physical layout of the estuary (which means the governing equations are integrated in the vertical to eliminate the vertical dimension), and computes water level, north- and south-component currents, and salinity. A detailed description of the TxBLEND model application to San Antonio Bay is given in Longley (1994) and Guthrie (2010). Agreement with data is forced by adjusting several free parameters in the model, a process referred to as "calibration." A measure of model performance is the ratio of data variance about the model prediction, to variance about the mean of the data:

$$V = \sum (x - x_{\text{mod}})^2 / \sum (x - \bar{x})^2$$

where x is the measured values of the modeled variable with mean value \bar{x} , x_{mod} is the model predicted value corresponding to the measured value, and the sums range over all measurements. Therefore, the analogy to explained variance of a regression is the variance in the data explained by the model, i.e. $1 - V$. * Guthrie (2010) separately assessed model performance with GBRA-1 hourly data, TCEQ (including Texas Department of Health data), and TPWD point measurements in the vicinity of GBRA-1 for the period 1999-2009, finding the model-explained variances to be 0.86, 0.39 and 0.58, resp., with respective standard errors 3.9, 5.1, and 5.7%. The periods of analysis of Guthrie (2010) and the statistical regressions of Table 2-8 are different, the region of data evaluated by Guthrie is within, but only a small part of LSAB, and Guthrie employed hourly rather than daily values from GBRA-1. Therefore, these TxBLEND results are not directly comparable to the regressions examined in this study. Qualitatively, however, TxBLEND does not appear to be more accurate than the statistical models of Table 2-8, and may be less, judging from its performance on the east side of the bay (Guthrie, 2010).

* This has lately been accorded the elevated title of Nash-Sutcliffe efficiency index, though it did not originate with Nash and Sutcliffe (1970), and is only vaguely related to efficiency.

3. CEDAR BAYOU TIMELINE

3.1. Background

Cedar Bayou is a small inlet connecting Mesquite Bay to the Gulf of Mexico, see Figure 3-1. It is the formal boundary between San Jose Island and Matagorda Island. More importantly, it is the closest inlet to San Antonio Bay, which otherwise exchanges with the Gulf of Mexico through Aransas Pass in Aransas-Copano Bay to the south or Pass Cavallo/Entrance Channel in Matagorda Bay to the north. When open, Cedar Bayou serves as a migratory route between the bay and the Gulf for diadromous species (e.g., Simmons and Hoese, 1959, King, 1971), and it is generally expected that the abundance of such a species within the bay will be increased when such a migratory path is available. In anticipation of its function as a migratory access to San Antonio Bay, considerable effort, both physical and political, has been invested in its maintenance over the past seven decades.

Because the status of Cedar Bayou (*viz.*, open or closed) potentially affects the abundance of organisms within the estuary, it is essential to construct a timeline of the state of the inlet, by which a time series of organism data may be stratified for analysis. Not only will this information be immediately useful to other tasks in the present project, but it will also support analyses of the distribution and abundance of various species in San Antonio Bay being prosecuted in ongoing projects elsewhere.

Interest in the state of Cedar Bayou, particularly as a migratory access, dates back to the early Twentieth Century, the first attempt at dredging occurring before World War II. Several time lines of the pass have been constructed in the past, notably the summary by Hoese (1958), largely repeated in Simmons and Hoese (1959), a 1967 report by Turner Collie & Braden (which was not available to this study), and Shepsis and Carter (2007). While the information in these prior studies was employed as appropriate (and available), the general approach of the present

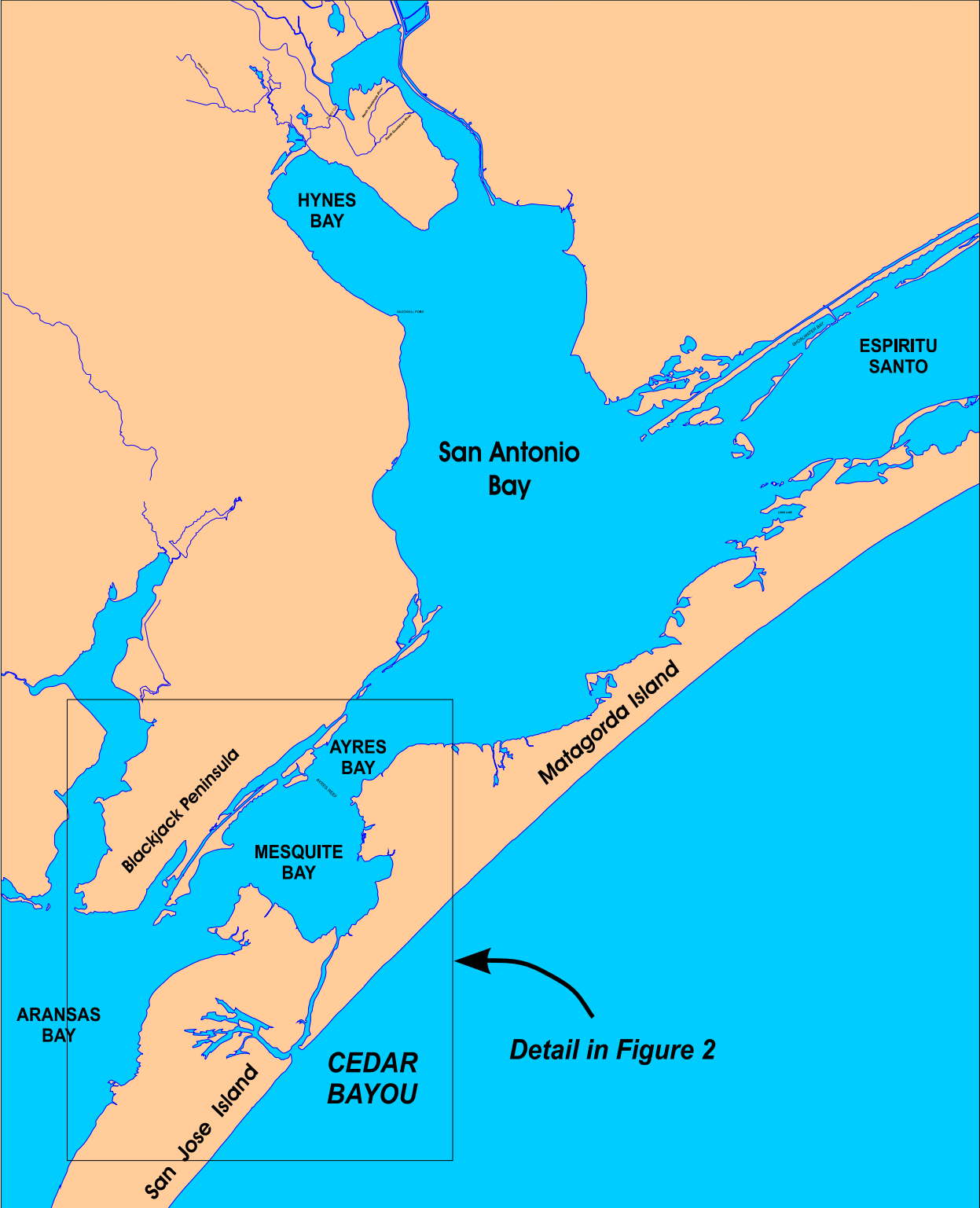


Figure 3-1 - Location map of San Antonio Bay

study was to seek and document information in the historical record of the status of the inlet that satisfies the following criteria:

- (1) the source is authoritative
- (2) the information is reliably dated, albeit of variable precision
- (3) the information is one of three types:
 - (a) data on the spatial configuration of the inlet allowing the inference of whether water freely flows through the main channel
 - (b) measurements of key dimensions of the inlet channel
 - (c) qualitative descriptions of the capacity of the channel to pass water

By “authoritative” in (1) is meant directly observed by a trustworthy observer and recorded objectively for general use in navigation, coastal management, engineering or science. Two important categories of information itemized in (3) are maps and aerial photography. This information must be capable of being dated, as specified in (2), although the precision of that dating may range from a specific day to a year or more. Many otherwise revealing maps must be discounted if the source date cannot be determined. With respect to the qualitative descriptions of (3c), we make the further distinction of an “observation,” in which the source personally examined the inlet or (say) its photograph, and a “report” in which a third party, presumed authoritative by the source, was responsible for the assessment of inlet status.

The scope of this study was narrow, and the resources were limited. Strictly, the time history presented in Appendix E satisfies—in fact exceeds—the contractual scope. Because it is of considerable interest to explore causes of the inlet’s behavior, in addition to information on the inlet *per se*, records were sought on events that might affect the status of the inlet or influence the interpretation of the above information. These events mainly consist of tropical depressions, heavy rainfall and/or riverine floods, seasonal high waters, and human activities of sediment removal or deposition. However, complete evaluation of the underlying causes for the time behavior of the inlet cannot be undertaken within the scope of the present study. In addition, sources of error or uncertainty were identified, especially where they affect the interpretation of hydrographic or photographic evidence of the status of the inlet.

3.2. Inlet structure and mechanics

Cedar Bayou forms the eastern boundary of an extensive washover fan and tidal delta complex that comprises the northern end of San Jose Island. The washover fan contains numerous minor distributaries that carry water only during rare extreme high-water events. The general structure of the Cedar Bayou environment is displayed schematically in Figure 3-2. Several zones may be identified that are characterized by differing physical processes. The washover fan is the western segment of the lobate end of San Jose Island, made up of mud flats and intervening sand mounds (of aeolian origin). The eastern segment, adjacent to the western shore of Cedar Bayou, is tidal delta, consisting of marsh and irregular ponds. (Andrews, 1970, presents maps of much greater detail, differentiating morphology, sediments, and flora.) Most important for the present purpose is the beach zone, dominated by transports of sand by wind and waves, extending from the shoreface to behind the line of active dunes (the “secondary dunes” in the terminology of Wilkinson, 1973). Beach zone is defined dynamically, but is generally a subset of the geomorphological concept of barrier nucleus (e.g., Andrews, 1970), which includes vegetated dune ridges.

The stability of the Cedar Bayou channel is determined by the interplay of two sedimentary processes: scour by flowing water through the channel, and deposition by gravitational settling from the water column. Scour is initiated when water velocity exceeds a value critical for the texture and cohesion of sediments in the channel bed. Deposition depends upon the concentration of sedimentary particles in the water column, their grain size and density, and the intensity of turbulence created by current or waves. Over the period of time for which inlet data were most densely accumulated, i.e. since the early 1950's, the back-bay reach of the channel appears to be stable. It is the beach-zone reach that shifts position and dimensions, and it is in the beach zone that the channel closes. This implies that it is the littoral transport of sands, overbalancing the scouring ability of water flowing through the inlet, that effects closure of Cedar Bayou. To summarize the mechanics of this inlet, each of these processes must be addressed.

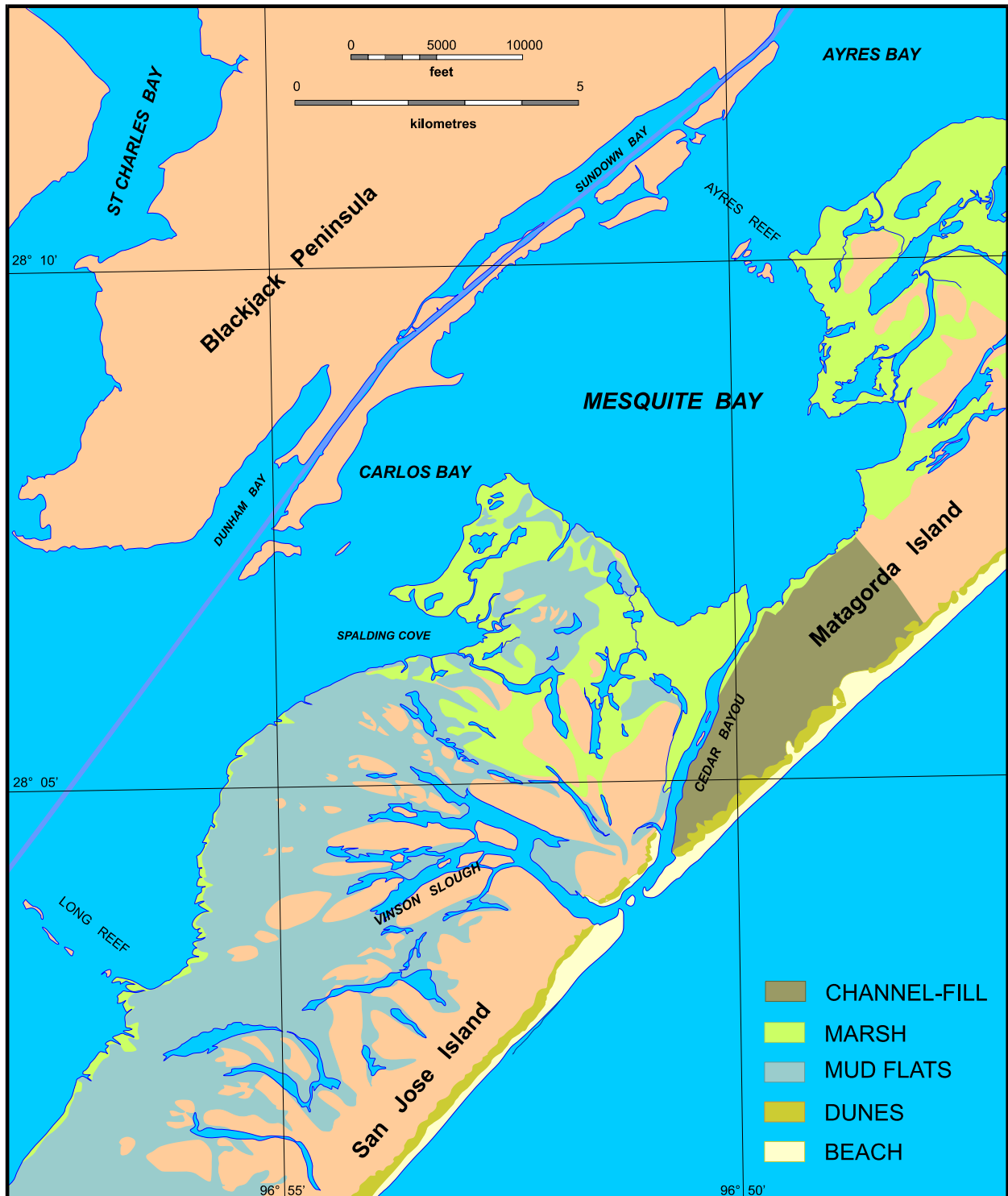


Figure 3-2 - Cedar Bayou and adjoining barrier island environments (see location map of Fig. 3-1)

When Cedar Bayou is open, its maintenance needs sufficient flow velocity through the inlet channel to limit deposition. This requires an imposed force to propel water through the inlet. There are two candidates, a slope in the water surface between the two ends of the inlet (more precisely, a gradient in pressure, but practically this will be dominated by the gradient in surface elevation), and the surface shearing stress exerted by wind. The latter becomes important only in the rare circumstance of extreme winds (gale force or more) directed along the axis of the inlet channel. So the former, a water-level slope in either direction between shoreface and backbay, is the primary mechanism, that is, a water-level differential (i.e., hydraulic head) between Mesquite Bay and the Gulf. The effectiveness of this water-level gradient in driving flow depends upon the water depth, in that the greater the water depth, the smaller the frictional resistance to acceleration.

Once Cedar Bayou has silted closed, two simultaneous physical factors are required to re-open it: (1) re-establishment of hydraulic continuity between Mesquite Bay and the Gulf, i.e., an open-water connection along the inlet, and (2) an imposed force to drive water through the inlet. For the latter, sufficient head gradient is needed that not only prevents deposition but also achieves scour. Put another way, re-opening the inlet requires that the inlet be inundated over its entire length and that there be adequate water-level differential between bay and Gulf. Some hydrographic events, if sufficiently intense, can accomplish both, e.g., the storm surge of a tropical cyclone, an energetic frontal passage, or, a large flood. More modest events can act in combination, i.e., one to create a high water (to achieve inundation) and another to produce a differential water level between bay and Gulf. Such hydrographic events are addressed in more detail below.

Whether the inlet is open, or is closed but temporarily inundated along its length, flow through the inlet is driven primarily by the hydraulic head gradient imposed along the length of the channel, that is, by the difference in water level between the nearshore Gulf of Mexico and that in Mesquite Bay. The principal physical factors that can force a water-level difference across the barrier island are (1) tides, (2) meteorology, especially variations in wind and pressure, (3) floods into the lagoon behind the barrier islands.

On a day-to-day basis, the most consistent potential generator of flow is the tide, by which is meant the “astronomical tide,” the variation of the sea surface induced by the orbital interactions of earth, moon and sun. As an example, the observed sea-level variation during June 2009 is shown in Figure 3-3 for three Texas Coastal Ocean Observation Network (TCOON) stations, Bob Hall Pier on the Gulf of Mexico seafront, Mesquite Bay (MANERR #1) and Lower San Antonio Bay near False Live Oak Point (GBRA #1). For clarity, these three time traces have been arbitrarily shifted with respect to each other to better display their individual variation. This month was selected because it is relatively free of meteorological disturbances, and the seafront tide is therefore almost entirely astronomical. Features of this figure exemplify several general observations about the astronomical tide on the Texas coast:

- (1) The range of the tide varies substantially over a period of about two weeks.
- (2) When the range is maximal, the tide has a 24.8-hour periodicity. (This is the length of the *lunar day*, the time required after the moon is overhead for the earth to rotate to bring the moon overhead again.) This is informally called the “diurnal mode” of the tide.
- (3) When the range is minimal, the tide has a 12.4-hour periodicity. This is informally called the “semi-diurnal mode” of the tide.
- (4) The average water level varies between the times of the diurnal and semi-diurnal modes with a periodicity of about two weeks. This variation in mean water level is referred to as the “fortnightly tide.”
- (5) The range of the tide is closely correlated with the *magnitude* of declination of the moon, i.e., the angle of the moon above or below the equatorial plane of the earth. The greatest declination is the angle between the equatorial plane of the earth and the orbital plane of the moon (which varies slowly as the orbital plane rotates, with a period of about 18.6 years). During its one-month orbit, the moon has a maximum (positive) declination at the top of its orbit, then a zero declination as it crosses the earth’s equatorial plane, then a maximum – but negative – declination at the bottom of the orbit, then another zero declination as it once again crosses the equatorial plane.

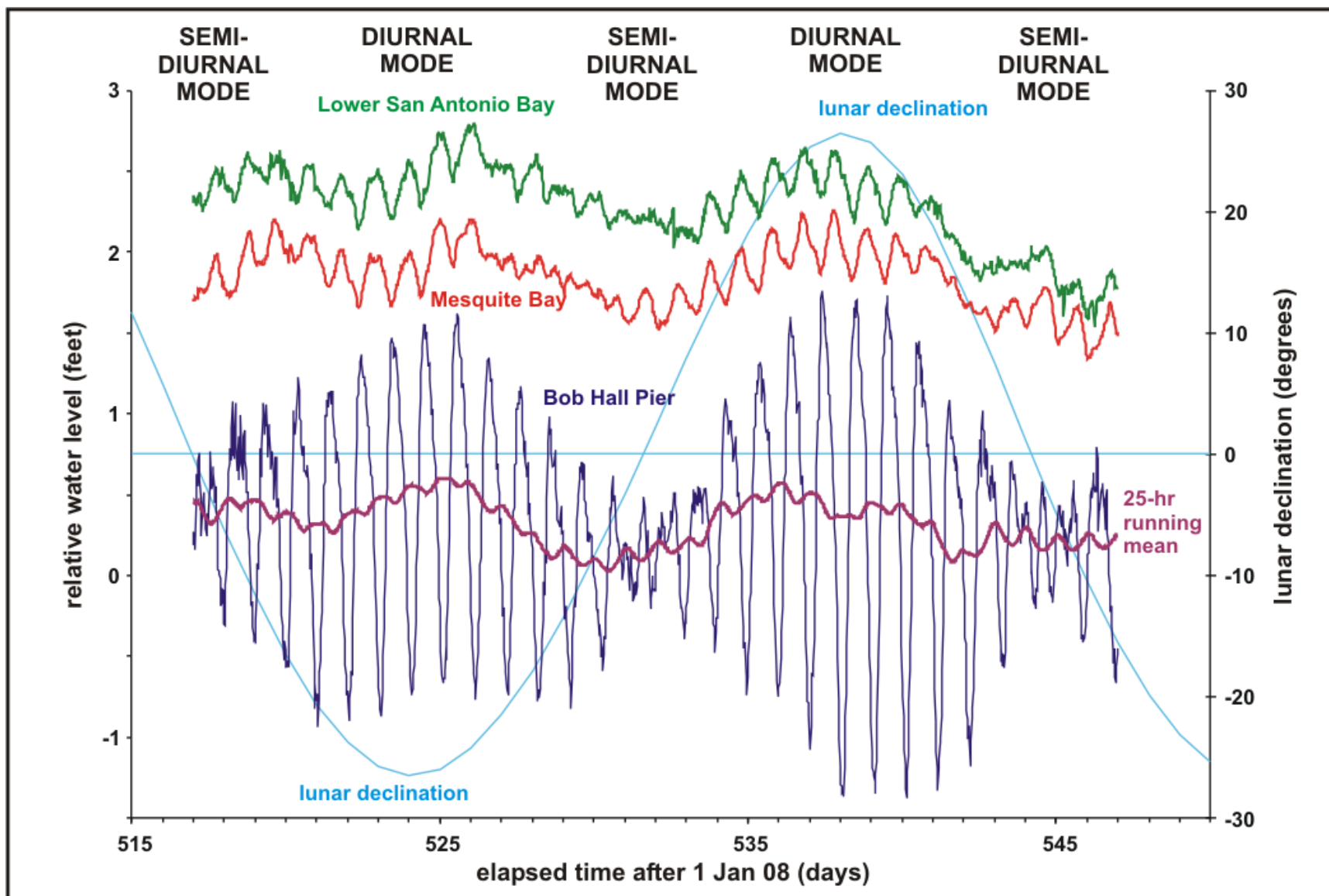


Figure 3-3 - Tides in vicinity of Cedar Bayou, June 2009. Data from Texas Coastal Ocean Observation Network. Tide traces are displaced vertically by arbitrary shifts for clarity.

- (6) The maxima in absolute value of lunar declination correspond to the diurnal tides, with maximal tidal range. The zeroes of lunar declination correspond to the semi-diurnal tides, with minimal tidal range. For this reason, the diurnal mode of the tide is sometimes called the “great-declination tide,” and the semi-diurnal mode, the “small-declination tide.”

The Gulf seafront tide has been succinctly described as a superposition of a 12.4-hour semidiurnal and 24.8-hour diurnal tide, modulated by a 27.2-day signal tied to the declination of the moon (Ward, 1997). It is worth noting in passing that, despite the physical elegance of the relation between spring and neap tides and the phases of the moon—a relation which appears in standard oceanography textbooks and piloting manuals—and despite the frequent description of the variation in range of Texas tides as the spring-neap cycle, including some local guidebooks, lunar phase has little effect on the tide on the Texas coast.

There is one more component of sea-level variation in the western Gulf, which like the above tides is cyclic and relatively predictable, and is an important mechanism for the exchange of water between the bays and the Gulf, namely the secular semi-annual “tide”. This is exposed by averaging water levels over a long enough period that the semidiurnal, diurnal and fortnightly tides are removed. Figure 3-4 displays the observed water levels at Bob Hall Pier after being subjected to a running 29-day average, then being further averaged over the 1990-2010 record for each day of the year. The resulting, greatly-smoothed annual variation exhibits two maxima and two minima, whence the name “semi-annual”. High waters occur in the equinoctial seasons, the higher occurring in the fall, and low waters occur in the solstitial seasons, the lower being in winter. The smoothed curve of Fig. 3-4 correctly depicts the calendar occurrence of these events but greatly diminishes the extent of water-level variation, as demonstrated by the superposed annual extrema (from the 29-day mean smoothed annual variation for each year). While the mechanics of this “tide” are not well-understood, there is no doubt that climatology plays some rôle in the annual signal, including but not limited to a steric response to the solar cycle, and that meteorology contributes both inter-annual and intra-annual variation. When the seasonal high water, most notably that of the fall, coincides with other factors that elevate sea level, e.g., a great-declination tide or an intensification of the trade winds, beaches and nearshore structures

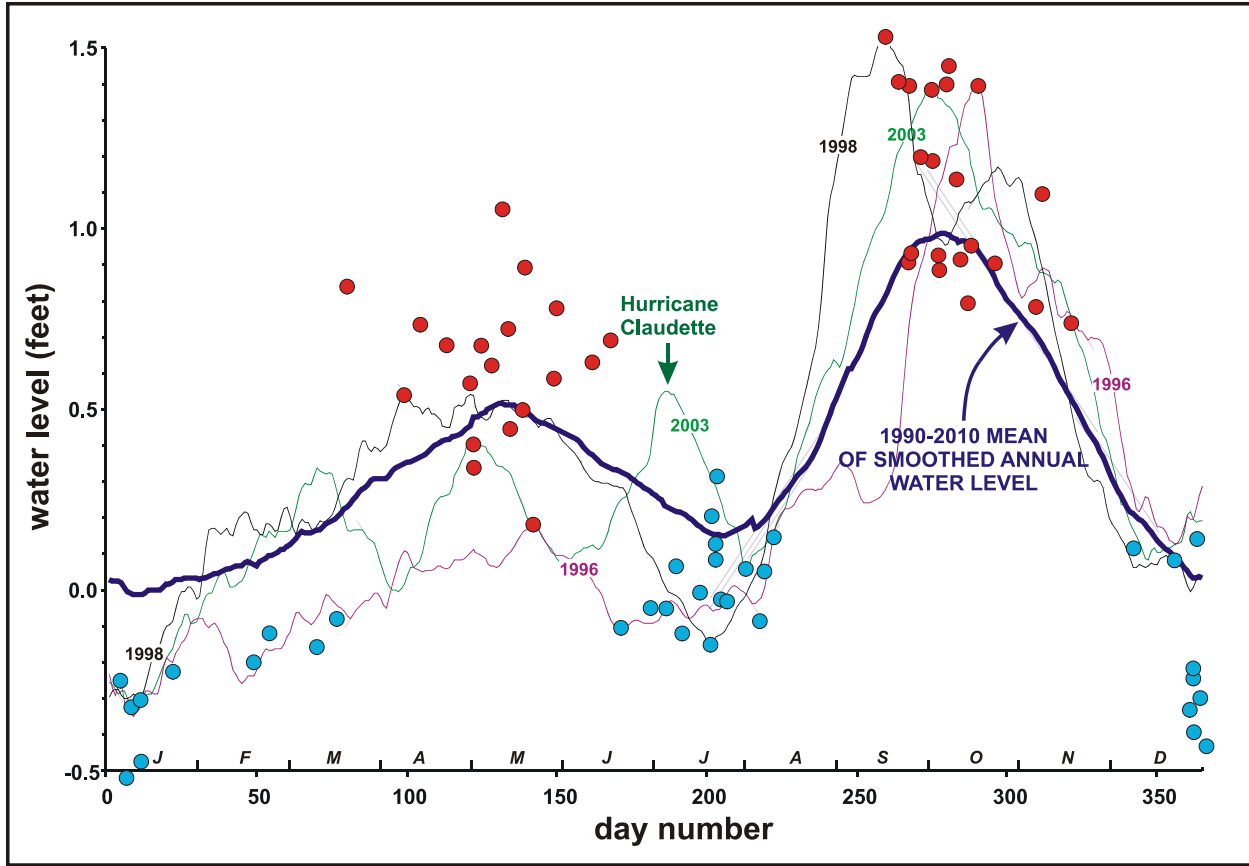


Figure 3-4 - Annual water-level variation at Bob Hall Pier after 29-day running mean, 1990-2010 average and selected years. Extrema of individual years plotted as red circles (maxima) and blue circles (minima).

such as the JFK Causeway may be flooded. The conventional practice when this occurs is to ascribe the cause to a tropical storm in the Gulf of Mexico, no matter how feeble or remote (see Ward, 1997).

The Gulf tide described above is considerably modified as it passes through the inlets into the Coastal Bend bays, a manifestation of the "stilling well" effect, in which the inlet behaves as a small port or ajutage connecting a large oscillating chamber of water (the Gulf of Mexico) with a much smaller chamber in co-oscillation (the bay behind the barrier island). For example, the 24.8-hr diurnal tide loses about 75% of its energy in passing through Aransas Pass, and the 12.4-hr semidiurnal tide loses nearly 90% of its energy (Ward, 1997). Similar losses occur through Pass Cavallo and the Entrance Channel. The effect is a considerably reduced tidal range at these

frequencies within the bays. As the tide passes from the main body of the bay into the secondary bays, e.g. through the ajutages of Nueces Entrance into Nueces Bay, Copano Pass into Copano Bay, or Espiritu Santo into San Antonio Bay, its semidiurnal and diurnal variations are reduced even further in amplitude. This is evident in the tide traces for San Antonio Bay and Mesquite Bay in Fig. 3-3. However, the fortnightly and semi-annual tides, being of longer periods, lose very little energy in passing through the inlet. In Fig. 3-3, it should be noted how closely the Mesquite and San Antonio Bay tides track the 25-hr running mean of the seafront tide. A stilling well, it will be recalled, filters out the short-period variation due to surface waves, so that the water surface in the well follows the average level of water outside.

While the astronomical tide (including, for convenience, the semi-annual “tide”) is an important regular mechanism of water-level variation, the Gulf and the interior bays are dominated by atmospheric forcing, especially arising from time variations in wind and atmospheric pressure. The wind regime in the Texas coastal zone can be characterized as a sustained onshore flow from the Gulf of Mexico, interrupted by frontal passages, and modulated by the sea-land breeze circulation (Ward, 1997). The operative agent is the wind stress on the water surface, which accelerates the water in the direction of wind and increases its elevation along the windward shore. Informally, the water is said to “pile up”. (The technical term is *denivellation*, the distortion of a free fluid surface by an applied stress.)

Under strong trade winds, characteristic of summer, water levels are gradually increased on the Texas Gulf shore. Within the bays water levels are raised on the interior shore and depressed on the shoreline behind the barrier islands. The inlets see a water-level differential from Gulf to bay, and water is driven from the sea into the bay. Under strong northerlies, such as following a winter frontal passage, these relative elevations are reversed, the Gulf being set down along the shorefront and the water surface within the bays tilting up from the inland shore to the barrier island. Water flows, often at a relatively fast rate, from bay to sea through the inlets, reducing the water volume within the bay. Direct measurements show that this volume driven from the bay by a frontal passage is typically greater than the great-declination tidal prism (Ward, 1980). While a vigorous front can evacuate half the volume of the bays on the upper coast, those on the lower coast, including San Antonio and Aransas-Copano, exhibit a more limited response to frontal passages.

The largest proportion of volume exchange was found by Ward (1997) to be about 10% of the bay volume. This more modest response to frontal passages on the south and central coast, compared to the upper coast, is probably due to the more constricted inlets of Matagorda and Corpus Christi Bay, and their reduced hydraulic capacities, and additionally to the reduction of energy of the frontal system in penetrating to the more southerly latitudes of the Coastal Bend area. Notwithstanding, the response of the bays and inlets to frontal passages dominates the astronomical tide and is a major mechanism of exchange between the bays and the sea.

An additional effect of wind that must be mentioned is that of the seabreeze. This is a diurnal variation in the onshore wind induced by the differing heat exchanges with the atmosphere over land and ocean, most prominent in the summer. Due to the rotation of the earth, the seabreeze *component* of the wind turns clockwise, describing a circle every 24 hours. Because this component is of smaller magnitude than the normal onshore flow, it is sensed as a variation in the windspeed, which directly at the coastline amounts to a change of a factor of three in windspeed, from about 0600 CST (when the seabreeze component is opposed to the onshore flow and reduces the total windspeed) until about 1800 CST (when the seabreeze reinforces the onshore flow). In confined bays with a suppressed astronomical tide, the seabreeze can induce a pure 24-hour variation in water level (see Ward, 1997).

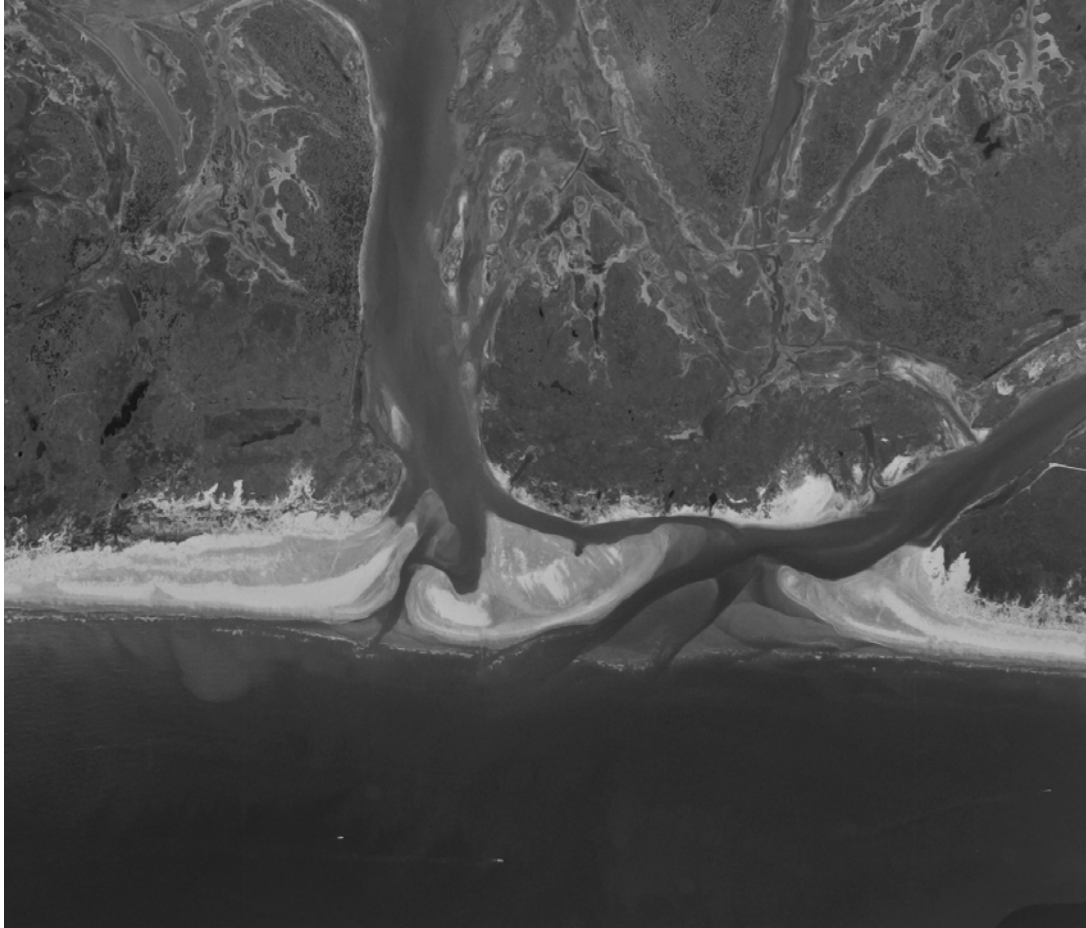
Probably the most dramatic meteorological response of the Texas coast is that due to wind and surge of a tropical cyclone. (These systems also generate waves and mobilize sediment, but these processes are considered later.) These storms are large-scale atmospheric vortices driven by the release of heat energy when water vapor, evaporated from the warm ocean surface, is condensed into ice and water. The circulation around these storms is counterclockwise. Relative to the point of landfall, the wind to the right (looking inland, in the direction of storm movement) is onshore, and to the left, offshore. The zone to the right is therefore favored for wind stress and wave run-up, both of which contribute to the elevation of water referred to as the “surge”. It is, however, more complicated than this. Water is also elevated by the depressed pressure within the storm (the “inverse barometer” effect), at a rate of about one foot per 30 millibars depression. There is an additional inward (radial) component of wind at the surface that feeds the convection in the storm and moves seawater toward the eye (e.g., Anthes, 1982). These processes create a

mound of water beneath the storm that evolves as the cyclone moves. When the storm enters the continental shelf zone, water depths become shallower and this mound of water, conserving its volume, is forced upward. Far offshore, its elevation above the surrounding sea level may only be one or two feet for a moderate hurricane, but as the storm moves into the nearshore zone, its elevation increases markedly to exceed ten feet or more.

A large zone of the coast, extending both to the left and the right of landfall, is potentially exposed to surge, though wind and surge will be greater to the right. The influence of the storm is dictated by its intensity (measured by central pressure anomaly and maximum sustained windspeed), size, trajectory and speed of movement. To pick one illustrative example, Carla in 1961 was a Category-4 hurricane (McAdie et al., 2009), whose impact was augmented by its relatively slow movement into the Texas coast. Landfall was at Pass Cavallo, where the surge (as determined by high water marks, see Harris, 1963) was about 12 ft, and in the Cedar Bayou area, to the left of landfall, the surge was around 10 ft. (Of course, much higher surges were experienced within the bays due to the convergence of cross section, the maximum being 22 ft at Port Lavaca.)

Appendix F presents a summary timeline of tropical storms and hurricanes that potentially could have affected the Cedar Bayou area, drawn mainly from the authoritative compilation of the National Climatic Data Center (NCDC) and the National Hurricane Center (NHC), published in McAdie et al. (2009).

It is difficult to offer a definitive statement on the ability of river flow to open or maintain Cedar Bayou from mechanical considerations. Delivery of a large volume of flow from the San Antonio Bay watershed into the bay would raise water levels throughout the adjacent bays of Espiritu Santo and Mesquite (in addition to San Antonio Bay itself), but Aransas Bay to the south and Matagorda to the north offer large cross sections opening onto enormous surface areas, so would represent the path of lesser resistance for the majority of the river flow. Nonetheless, a flood large enough might still raise water levels sufficiently in Mesquite Bay to inundate Cedar Bayou. The best guide to what level of flow would be required would be observational



**Figure 3-5 - Detail of Cedar Bayou beach zone during high flow event, 22 April 1969.
(From USGS AR1VCFI00010053 Roll 1 Frame 53)**

experience. Two vertical aerial photographs are available under high flow conditions, USGS 1 Feb 1979 and USGS 22 Apr 1969 (see Appendix G). In each of these the date of the photograph is embedded in a 3-4 month period of high flows. In the 1979 photo, while the inlet is open, there is no indication of elevated water levels. In the 1969 photo, shown in Fig. 3-5, it is apparent that much of the beach area is underwater, as evidenced by the extensive shallow (but submerged) bars. The flow conditions for the 1979 photo exceeded about 80% of the period of record data*, while those for the 1969 photo are higher, exceeding about 90% of the data. Since

* Based on the Texas Water Development Board compilation of total monthly flows into San Antonio Bay for the period 1942-2008.

this photo was taken in mid-April, it is possible that the water-level elevation is more associated with the spring high-water (the semi-annual “tide” of Fig. 3-4) rather than with river flow. This photo is consequently rather flimsy evidence for drawing any conclusion, but provisionally it appears that a flow well in excess of the magnitude of that of April 1969 (about 400 Maf/mo) would be required to inundate the inlet through the beach zone. Of course, the question of whether this level of inflow would be additionally sufficient to force a flow through the inlet is a separate matter, to be addressed in Section 3.4. We observe that in Fig. 3-5 the channel out from Cedar Bayou is clear, as well as the opening out from Vinson Slough. There is no indication of sediment discharge through the inlet, i.e., no plume in the nearshore Gulf and no turbidity difference between Vinson Slough and Cedar Bayou, which would have been expected if there were a substantial flow through the inlet.

As noted at the beginning of this section, the maintenance of Cedar Bayou depends upon the ability of flows in the inlet to scour and erode sediments during high velocities that settle to the bottom of the inlet during low velocities. The fact that the inlet is observed to close in its beach zone means that the source of sediments (notably, the fine sands making up the beach) settling in the inlet channel exceeds the scouring ability of inlet throughflow. A primary source of sands in this zone is littoral transport into the inlet mouth by longshore drift, driven in turn by waves (primarily swell) whose crestlines approach the beach at some acute angle. (There is a vast literature on beach sediment dynamics, of which the work of Bagnold is fundamental, e.g., Bagnold, 1963, Inman and Bagnold, 1963. The *Coastal Engineering Manual*, née *Shore Protection Manual*, of the U.S. Army Corps of Engineers is a comprehensive source, USCE, 2008, especially Part III Chaps 2 & 6, Part IV Chap 3. While much work has been done on conditions for settling and incipient motion by flowing water, and on the mechanics and sense of littoral transport, the computation of the actual volumes of sand transported in either process remains elusive.)

It has been long recognized that—assuming the crestlines of swell propagate in the direction of the wind—the prevailing onshore winds impingent upon the concave Texas coastline create a zone of *net* littoral drift convergence in the general vicinity of Aransas Pass (e.g., Carothers and Innis, 1960, Watson, 1971), exemplified by the asymmetric accumulation of sand at barriers such

as jetties along the coast. As the onshore winds range from E to S over the course of the summer season, the actual zone of convergence migrates along the coast. Cedar Bayou lies within the region through which the point of convergence passes. Like almost all of the Texas shoreline, this region evidences long-term retreat, but at a much more modest rate—about a foot per year—than the beaches farther south or north, according to BEG (2010). An earlier study by Morton (1977) found a net shoreline accretion over the period from the 1880's through the mid-1970's. This net long-term accretion was the integrated effect of two very different shoreline behaviors: until the 1930's this shoreline was accreting at a substantial rate, but this reversed in the 1930's, the shoreline eroding thereafter. That Matagorda Island is not eroding as quickly as the beaches upcoast and downcoast may be attributable to the longshore transport of these eroded sediments into the area, especially from upcoast. For Cedar Bayou, unlike the larger, jettied inlets of Matagorda Entrance Channel or Aransas Pass, this exposure to longshore littoral drift is probably more than enough to overbalance the relatively low flows through the inlet.

3.3. Evolution of inlet

The segment of the Texas coast containing Cedar Bayou has received considerable attention from geologists over the years. Of immediate relevance to the evolution of the inlet is the American Petroleum Institute Project 51 (Shepard and Moore, 1955, Shepard et al., 1960). The study area of this project (“Area 51”) included San Antonio, Aransas and Copano Bays, and the adjacent barrier islands, Matagorda and San Jose. More recently, the washover fan adjacent to Cedar Bayou to its south (Fig. 3-2) was given detailed study by Andrews (1970), and Matagorda Island by Wilkinson (1973), see also Deal (1973) and Wilkinson (1975). From these, a picture of the geological evolution of Cedar Bayou and environs emerges, as follows:

- (1) The nascent Matagorda Island was a sand shoal, which migrated inland as sea level swiftly rose following the close of the Pleistocene, about 12,000 years BP. During this period, the Pleistocene river valleys were inundated by rising sea level and filled with sediment.

- (2) Around 4000-5000 yrs BP, the rate of sea-level rise sharply declined, and the island stabilized in more-or-less its present location, as a low sandbar with numerous passes between the Gulf and an elongated lagoon, or sound, behind the sandbar.
- (3) With sea-level rising much more slowly, the island began prograding seaward, and by 3000 yrs BP, it had nearly doubled its width. At this time, three major passes through the island remained active, all of the others being filled. There was an even larger pass at the southern end of the island, whose location was in the vicinity of the present washover fan to the south of Cedar Bayou (Fig. 3-2).
- (4) The island continued to prograde, creating a sequence of dune ridges separated by swales, now in its interior, marking successive positions of the island dune chains.
- (5) At some point in time after 3000 BP, a narrow channel, the primordial Cedar Bayou, opened between the pass at the southern end of Matagorda Island and the next pass to the north, at the eastern boundary of the channel-fill area of Fig. 3-2. There is a suggestion by the recurvature of the dune ridges just to the east that this was the site of a much older tidal pass, dating back to the early progradation phase of the island (Wilkinson, 1973).
- (6) After Cedar Bayou formed, probably around 2400 yrs BP (Andrews, 1970), the accretion of a tidal delta began on the west side of the inlet. Interestingly, this predates the *oldest* sediments in the washover fan (ca. 1700 yrs BP, Andrews, 1970).
- (7) Around 2000 yrs BP seaward progradation ceased. All of the passes through Matagorda Island filled. The pass at the south end of the island (as well as that at the north end, Pass Cavallo) remained active.
- (8) Approximately 1700 yrs BP, the washover fan adjacent to present Cedar Bayou began to form, associated with the tidal pass to the south, at first rapidly prograding into the bay.
- (9) About 1500 AD, around the time of Columbus, the major tidal pass at the south end of the island silted closed. Progradation of the washover fan

ceased at this time (based on the youngest radiocarbon dates found in bayside fan sediments by Andrews, 1970). Subsequently, Cedar Bayou migrated to the south, in the process obliterating the earlier ridge-and-swale topography, and creating the channel-fill zone of Fig. 3-2.

- (10) Certainly since the 1880's, probably since the Civil War (given the 1867 chart of Felix Blucher), and most likely earlier, the gross physiographic features of Cedar Bayou channel, notably its NNE-SSW trend and the washover fan to its west, have not substantially changed.
- (11) Sometime after 1900, the fore-island dune chain on Matagorda Island began migrating inland, to form the present maximum-elevation ridge of the island. These are much higher than the relict dune ridges (now stabilized). These dunes reached their present position around 1935 and have become stabilized by vegetation. Since 1935, a new line of dunes has formed just inland from the backbeach.

Figure 3-6 displays a detail of the Cedar Bayou channel showing three mapped shorelines from the Twentieth Century. Sources for these shorelines are:

- 1934 - Nautical chart, U.S. Coast & Geodetic Survey 1285
- 1952 - USGS 1:24,000 topographic quadrangle St Charles Island SE
- 1973 - USGS 1:24,000 topographic quadrangle St Charles Island SE photorevised

While such map sources are generally regarded as authoritative, the applicable dates have considerable uncertainty. The 1934 nautical chart, for example, is based upon surveys in the area in the early 1930's and earlier. It would be necessary to consult the USC&GS reports (*viz.* descriptive reports filed by the survey parties, chart letters or field examination reports, and history sheets, archived at the National Oceanic and Atmospheric Administration) to establish the applicable date for this shoreline. The 1952 USGS map is compiled from a combination of photogrammetry based on photography in the 1940's, after WWII, and plane-table surveys in the area in 1952. Which of these sources (and in what combination) are the basis for the shoreline, and therefore the corresponding applicable date(s) is unknown without extensive archival



Figure 3-6 - Detail of Cedar Bayou showing three shorelines from the Twentieth Century, see text. The least back-island width and the throat width are based on the 1973 shoreline.

searching. Finally, the 1973 photorevision is the publication date, not necessarily the date of the photography source. We can be sure that the date is no later than 1973, and probably from the late 1960's or early 1970's. Again, a considerable effort of accessing the photography used by USGS would be necessary to establish this precisely. (The image of Fig. 3-5 was no doubt one of these sources. However, the emergent islet in the inlet mouth shown on the 1973 quadrangle is absent or underwater in Fig. 3-5, and the open pass to the south, connecting Vinson Slough is not depicted on the map.)

There is exactly one (1) historical survey of Cedar Bayou in which cross sectional profiles were measured, namely the February 1954 survey performed by Lockwood and Andrews (1954). It is worth noting that, excepting the Lockwood & Andrews survey, the 1934 map of Cedar Bayou is the *latest survey* including both widths and soundings of the channel *in an open state* available to this study, and perhaps extant. This is a frustrating information deficit. Even a simple measurement of controlling talweg depth (and approximate location in the channel) at various intervals over time would have been of immense value to the present study. Such data would be easily and inexpensively obtained, especially given the frequent visits to Cedar Bayou by technical personnel as well as knowledgeable boaters.

Despite the imprecision in dates, these shorelines illustrate that the back-island configuration of Cedar Bayou has remained fairly stable in the Twentieth Century, while the beach zone has exhibited considerable variation. Two quantitative measures in the horizontal plane are indicated in Figure 3-6, the least width in the back-bay reach, and the throat width in the beach zone. The least back-bay width, as the name suggests, is the minimum width of the Cedar Bayou channel anywhere in the reach from approximately Grass Island to the opening of the channel in Mesquite Bay. This least-width location generally falls in the vicinity that is shown in Fig. 3-6. In the beach zone, the "throat" is defined for present purposes to be the least width in the channel segment that trends southwest from the dune line, i.e. from the dune line to the point at which the channel turns seaward. For the 1973 shoreline, the least back-bay width is 290 ft, and the throat is 650 feet.

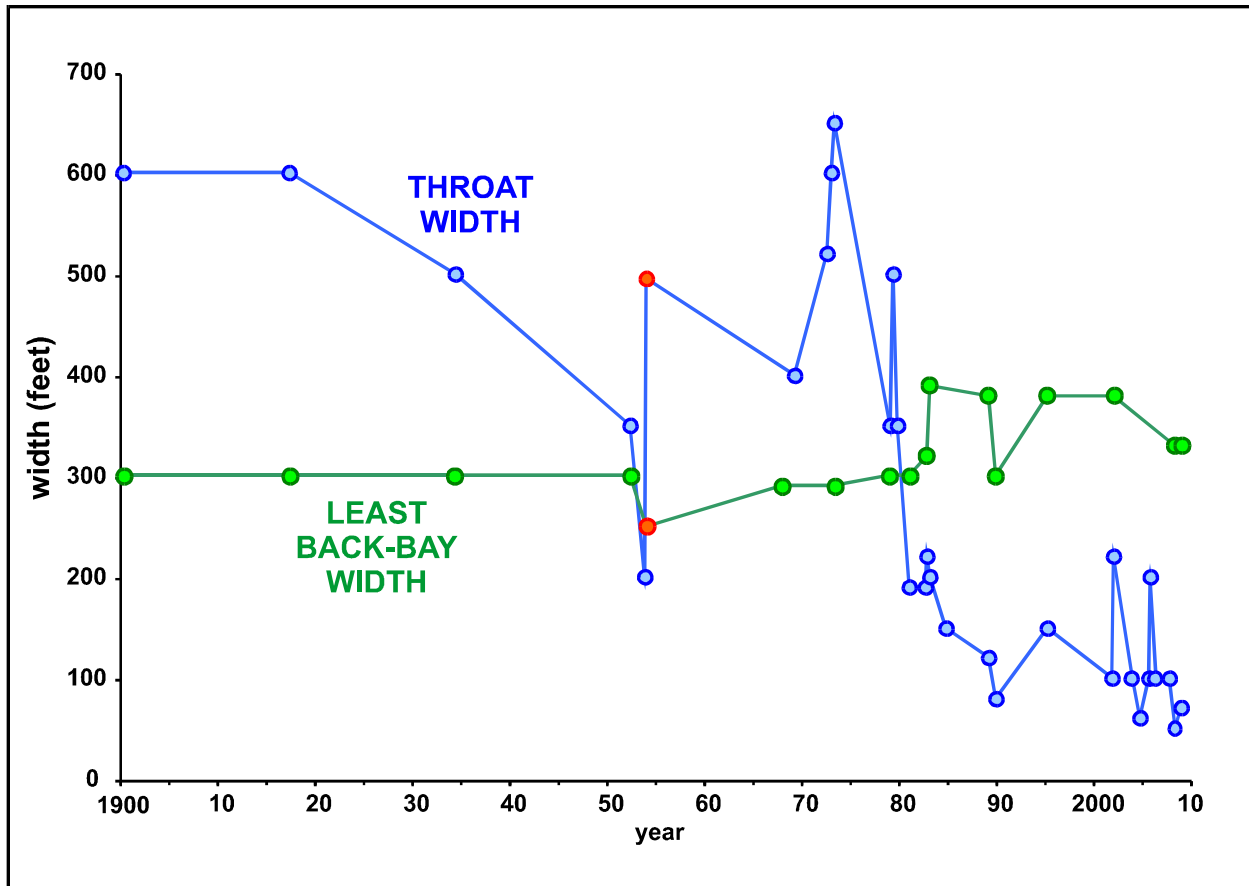


Figure 3-7 - Time history of width measures for Cedar Bayou. Red data points are from Lockwood & Andrews (1954) survey.

The variation over time for each of these width measures is shown in Figure 3-7. The stability of the least back-bay width is clearly demonstrated, ranging 300-400 ft over the century, while the throat width is much more variable, but generally trends downward. Not all of this variation in width is natural. The channel has been dredged in its entirety, or in limited reaches, four times in the past century, in 1939, 1959, 1987-88 and 1995. Unfortunately, there was no reliable information available to this study as to the specific reaches dredged or the volumes removed. In addition to these dredging events, the Gulf entrance has been opened by dragline (1956) and closed by bulldozer (1979).

3.4. Inlet time series 1900-present

In assembling a timeline on Cedar Bayou from the various information sources, the objective was to render the status of the inlet quantitatively. Unfortunately, many of the historical *observations* about the status of the inlet are qualitative, e.g., “open” or “open at high water”. Moreover, the typical *data* are either a map (without depths), a reported depth (without a map, or specific location), or an aerial photograph. The best single source of information is a set of cross sectional profiles along the channel. There is but one such survey extant for Cedar Bayou, from 1954. Next best is a hydrographic survey chart with soundings. As remarked above, the *latest* such survey available of Cedar Bayou *in an open state* is the 1934 USC&GS nautical chart.

The Coast and Geodetic Survey (USC&GS, formerly the Coast Survey, now the Office of Coast Survey of the National Ocean Service) has historically been responsible for precise determination of the nation’s shoreline, as well as operation of tide gauges, prediction of tides, and establishment of horizontal and vertical control. Prior to WWII, shorelines were surveyed by the use of planetables. The procedures and field protocols of the USC&GS are detailed by Shalowitz (1964). While USC&GS references bathymetry and submerged hazards to some low water datum for navigation purposes, such as mean low water or mean lower low water, the shoreline position on its maps is at mean high water. USGS apparently follows a similar convention. Only since WWII has photogrammetry become incorporated into the process, so that modifications to the shoreline can be readily incorporated into new maps. Earlier surveys were performed infrequently and therefore provide only a very spotty record of shoreline history.

The primary source of information on shoreline position in the present study is aerial photography, mainly vertical photography. From these, the shoreline can be identified, and if an accurate scale can be constructed, key dimensions may be measured. Oblique photographs are difficult, sometimes impossible, to rectify and assign an accurate scale, so were given only limited use to qualitatively establish features of Cedar Bayou.

Aerial photography offers, in principle, a superior data source on shoreline position because the photograph can be precisely dated (presumably). This precision is limited to the calendar date,

because the clock time is generally omitted from the readily available metadata. For several otherwise excellent photos, the date was given only to the month.

An instantaneous shoreline position, such as exhibited by photography, is subject to considerable uncertainty arising from the unknown variation in water level in coastal regions. Ideally, tide data would be obtained from the nearest gauge and translated to the Cedar Bayou area, then used to adjust the photographed shoreline position to that of mean high water. This is a complex procedure for which the extant tide information is often inadequate. While this was manifestly beyond the scope and resources of this study, without an accurate acquisition time for the photograph, it is impossible to relate an aerial photo to concurrent water level. Therefore, the stage of the tide, including meteorological effects, remains a source of uncertainty in interpreting aerial photography. (It should be noted that this is also a source of uncertainty in the mapped USC&GS shoreline position, because tidal adjustment could be effected only based on tidal variation recorded by the survey crew during the short period of time while in the area.)

The order of magnitude of this uncertainty can be estimated from the background information of Section 3.2, above. The diurnal tide can range from less than 0.5 ft for small declination to 3.5 ft at great declination. The fortnightly tide can contribute another 0.5 ft, and the semi-annual secular tide has a nominal range of another foot, but can be more than twice this in some years. All of these are independent contributors to the total water level variation (and we have not even addressed the additional factors of wind denivellation or flood events). A nominal composite uncertainty from tide variation alone is as large as 5 ft. From USGS topography, the detail map of Figure 3-8 indicates the area potentially subject to inundation due to these tidal variations only. Even a rise of 2-3 ft in water level can significantly encroach into this zone and influence the apparent shoreline position.

Key dimensions of the Cedar Bayou channel are the *throat width* and *backbay width*, as defined in the previous section (see Fig. 3-6 and associated text). These are least-width measures in specific reaches of the channel. To these we add one more, the *aperture width*, which is defined to be the least width of the segment of the channel running across the beach zone to the Gulf,

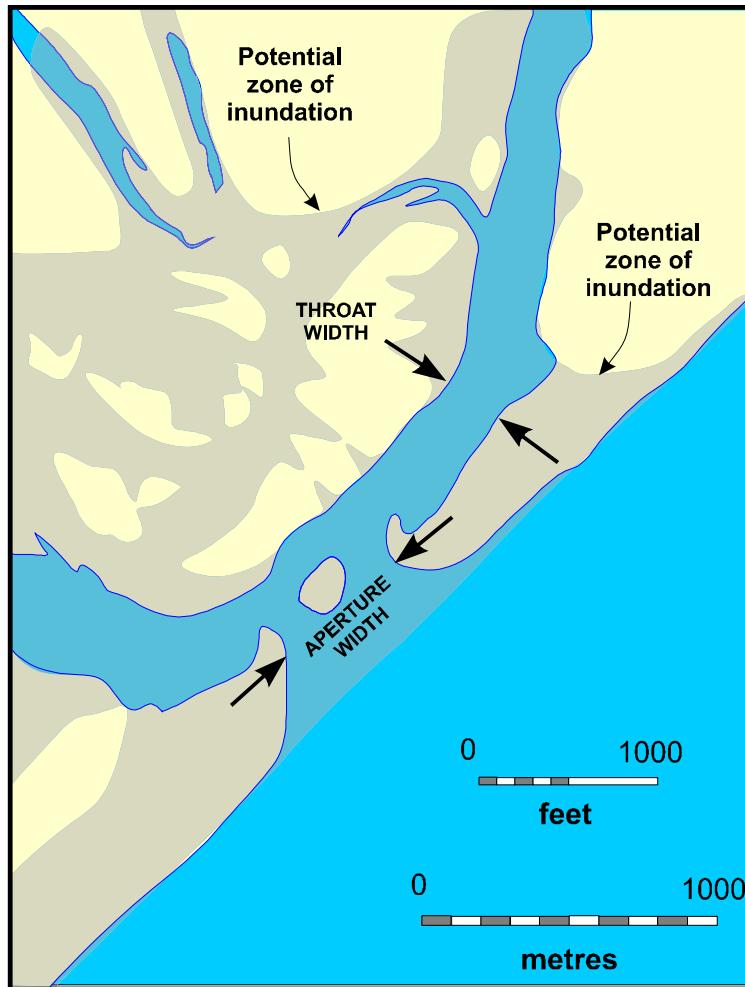


Figure 3-8 - Detail of Cedar Bayou entrance with 1973 shoreline, showing region subject to inundation by normal tidal and seasonal water-level variations (grey area)

generally orthogonal to the shoreline, indicated in Fig. 3-8. The most desirable measure of each of these is not the width or the depth, but the cross sectional area, because this is the parameter most closely related to the capacity of the channel to carry flow, to its ability to exchange water between estuary and sea, and to its effectiveness as a migratory access. Moreover, cross section area depends sensitively on both width and depth, and the smallest value in the entire Cedar Bayou channel (usually the smaller of the throat or the aperture) is the controlling section for these physical processes.

Since we are able to determine widths (without depths) from maps and photos, and occasionally find a depth reported (without width), an estimate of cross section area is at best only approximate. A simple cross-section geometry is assumed, that depth across the channel is a parabolic function of width with apex at the talweg, and the measured cross section from the 1954 survey together with the three (3) instances in the historical record in which *both* talweg depth and channel width are reported were used to establish the parameters of this relation. Details are given in Appendix H. (Any such measurements used to determine channel shape are limited only to those occasions when the channel shape represents the response to normal forces of deposition and scour. After dredging or hurricane events, this relation cannot be expected to hold, even approximately.) The resulting estimated cross section should be regarded only as a numerical *index* to the functional dependence of section area on width or depth, not as an accurate computation of cross section. Indeed, profile irregularities, multiple channels, and shelf regions will undermine the accuracy of the parabolic channel approximation. For the survey of 1954, the actual channel area was overestimated by about 30%.

The measured Cedar Bayou channel widths from maps and photography, surveyed or reported depths, the associated estimated channel cross sections, and the single set of surveyed profiles from 1954 make up the core of the inlet chronology assembled in this project. These were compiled into a time series extending from 1900 through 2009 (which we define as the “present” thereby preserving the academic tradition of always being behind schedule). In addition, occasional reports of the depth over the bar (meaning the shoal directly out from the Gulf mouth of the inlet), controlling depth (without width) in the channel, and typical talweg depth, as well as controlling depth after dredging, were included in the compilation for informational purposes.

The literature is replete with qualitative reports of the status of the pass as “open” or “closed”, or some equivocal partial measure such as “open at high water,” “shoaled at low water,” or “occasionally open.” These are valid observations when reported by reliable observers, but are not readily quantifiable. The exception, of course, is the “closed” state, which is taken to mean that the aperture has zero width (and zero cross section). To include these sorts of observations in the chronology, they were translated to three categories, “open”, “closed” and “marginal”. The last of these, “marginal” includes all of the equivocal reports, as well as oblique photographs

that display an inlet with apparently very small dimensions. Quantified cross sections (from maps and vertical aerial photographs) were incorporated into this *categorical* compilation by assuming “marginal” to apply to those with cross sections less than 100 sq ft, and anything larger to be “open”. By this artifice, the time series of inlet *category* becomes the longest and best-populated chronology of an inlet feature that we can construct.

To this compilation was added (1) tropical cyclones that offer some potential for affecting the Cedar Bayou area (or were invoked in a literature report as explaining some observed behavior of Cedar Bayou), (2) human activities affecting the inlet, *viz.* dredging or closure, (3) flood events entering San Antonio Bay, (4) any other events (e.g., meteorological) that might be of use in interpreting the response of the pass, or the behavior of water quality (e.g., salinity) or biology (e.g. abundance). The complete compilation of these data is presented in Appendix E. It is intended to be organic, and to continue growing as new entries are found, validated and entered.

The data on tropical disturbances are particularly important in seeking to explicate the observed behavior of Cedar Bayou. The ultimate authority on tropical storm data is the National Hurricane Center, which continues to sort and sift through historical data on these storms to improve their track lines and characterization. For this compilation, McAdie et al. (2009) was the primary source, supplemented by additional references where warranted. Three classifications of intensity are used in McAdie et al. 2009): “tropical storm”, “hurricane” and “major hurricane”, in which a major hurricane is Category-3 or higher on or about landfall, on the Simpson-Safir scale. In the chronology of Appendix E, the storm name, intensity classification, date of landfall, approximate landfall location, and comments regarding the behavior of the storm or reported effects on Cedar Bayou are given. A more complete listing of storms landfalling in Texas or potentially (however remote) affecting Cedar Bayou or the neighboring coast is tabulated in Appendix F. Which storms from Appendix F were ultimately included in the chronological compilation was a matter of judgment. The effects of such storms, especially those of marginal intensity, are frequently exaggerated, not only in the press but occasionally in scientific reports: there is a tendency to connect any unusual hydrographic behavior on the coast to a tropical disturbance somewhere. The usual effect of such a storm is considered to be the opening of inlets, especially on the barrier island north of the landfall.

These storms can also increase the littoral sand load by generating swell, which becomes surf in the nearshore zone, and both mobilizes sediment and forces a longshore drift.

It is sometimes stated that flood events play a rôle in maintaining Cedar Bayou or in re-opening the inlet after it has closed. This no doubt arises from the observation that Cedar Bayou is now open, or is larger than it was before, on some occasion that happens to follow, perhaps by some weeks, a flood event, especially on the Guadalupe or San Antonio rivers. Such connections can be specious. When precisely the inlet opened or enlarged is often unknown. Flood events frequently happen in association with seasonal high waters in the spring or fall, and perhaps with frontal passages, so it can be difficult to separate which hydrographic effect, if any, might have been responsible. To allow the examination of relations between the inlet and inflow, the total inflow into San Antonio Bay, based largely upon the data evaluation, analyses and modeling of the Texas Water Development Board, was included in the present data compilation.

Figure 3-9 is a graphic depiction of the chronological compilation of Cedar Bayou history starting in 1910. This is rather information-dense. For clarity, it is divided into three segments, each consisting of 40 years (the last two segments having a 10-year overlap with the previous segment at their beginning). Quantitative data on the inlet state, as measured by the estimated controlling cross section (i.e., the minimum of the throat and the aperture), are shown as prominent data points, while the categorical state (open, marginal, or closed) is indicated by the shaded zones. (The actual observations or reports used to define these zones are evident as small data points on the zone boundaries. Consultation of Appendix E will disclose the nature and source of the observation.) On this time graph are superposed the tropical disturbance events, dredge or fill events, and a time series of monthly flow into San Antonio Bay. Tropical disturbances are shown as vertical arrows at the top of the diagram, their length and pen-weight indicating the strength of the event (tropical storm, hurricane, major hurricane), along with the general area of landfall. Dredge and fill events, in contrast, are depicted as vertical red arrows at the bottom of the diagram. The monthly flow into the bay is the green trace starting in 1942. The left ordinate serves as the axis for both estimated cross section (square feet) and total flow (millions of acre-feet per month).

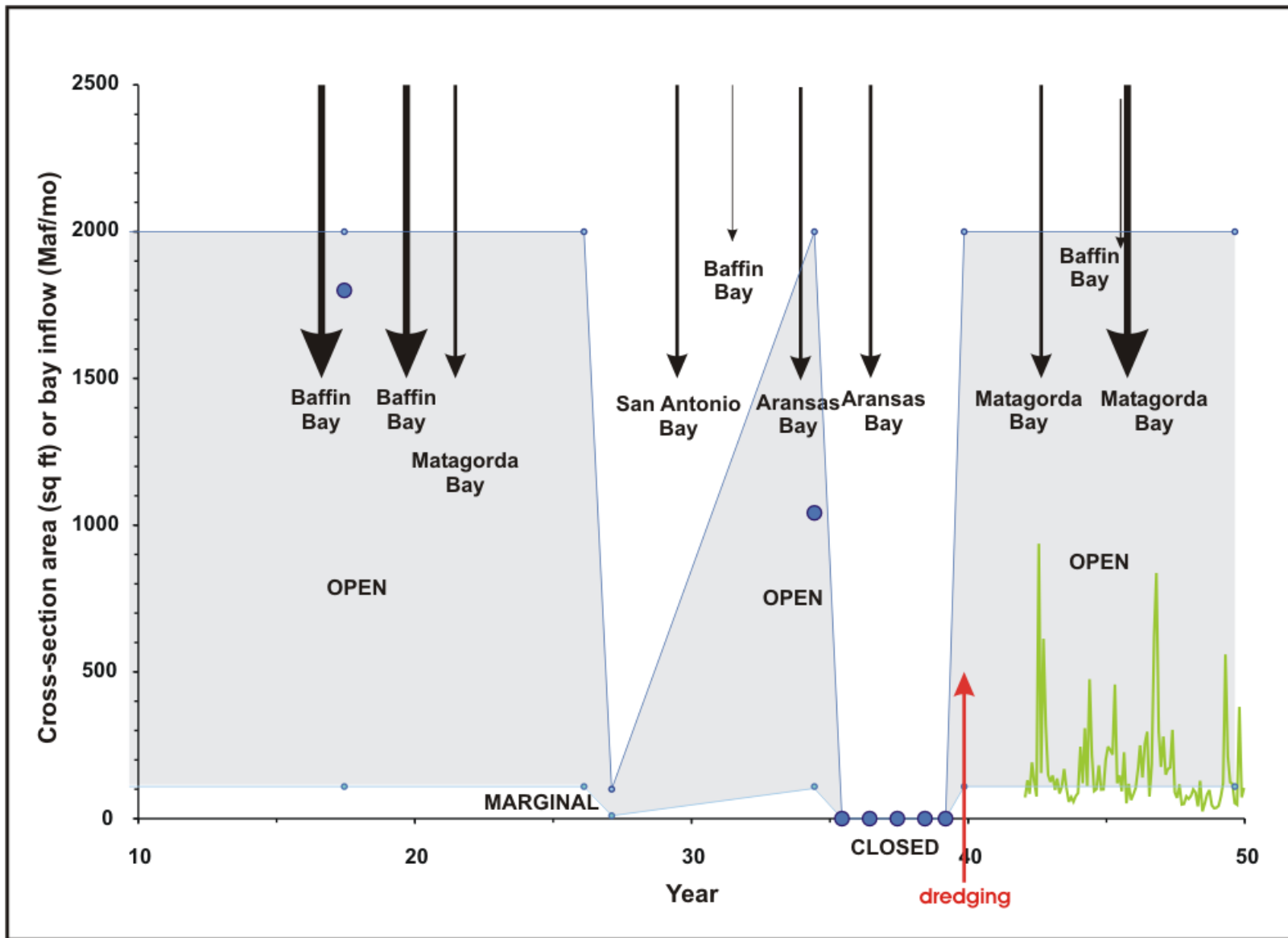


Figure 3-9a - Time history of Cedar Bayou, from chronological data (see text), 1910-1950.

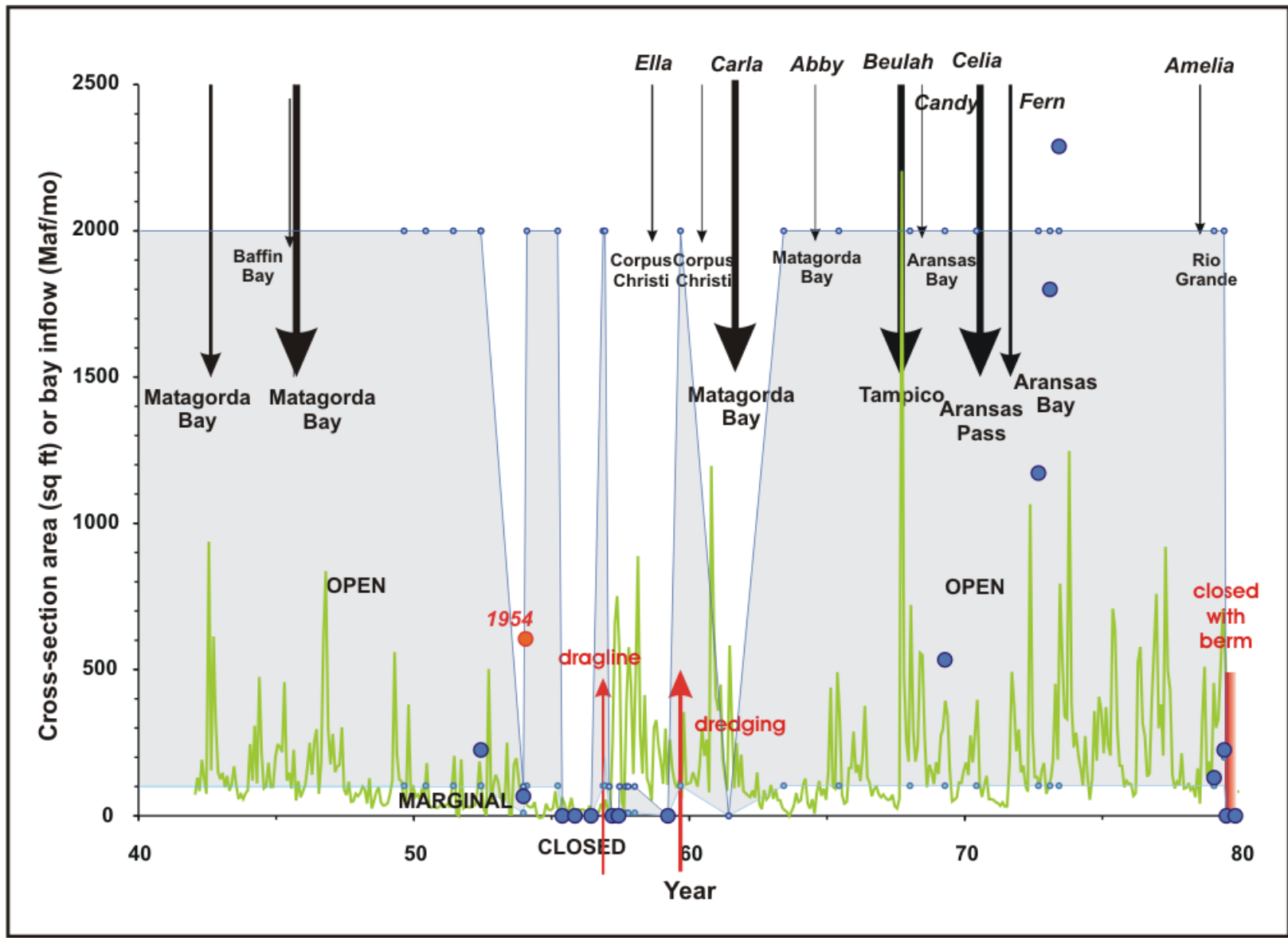


Figure 3-9b - Time history of Cedar Bayou, from chronological data (see text), 1940-1980.

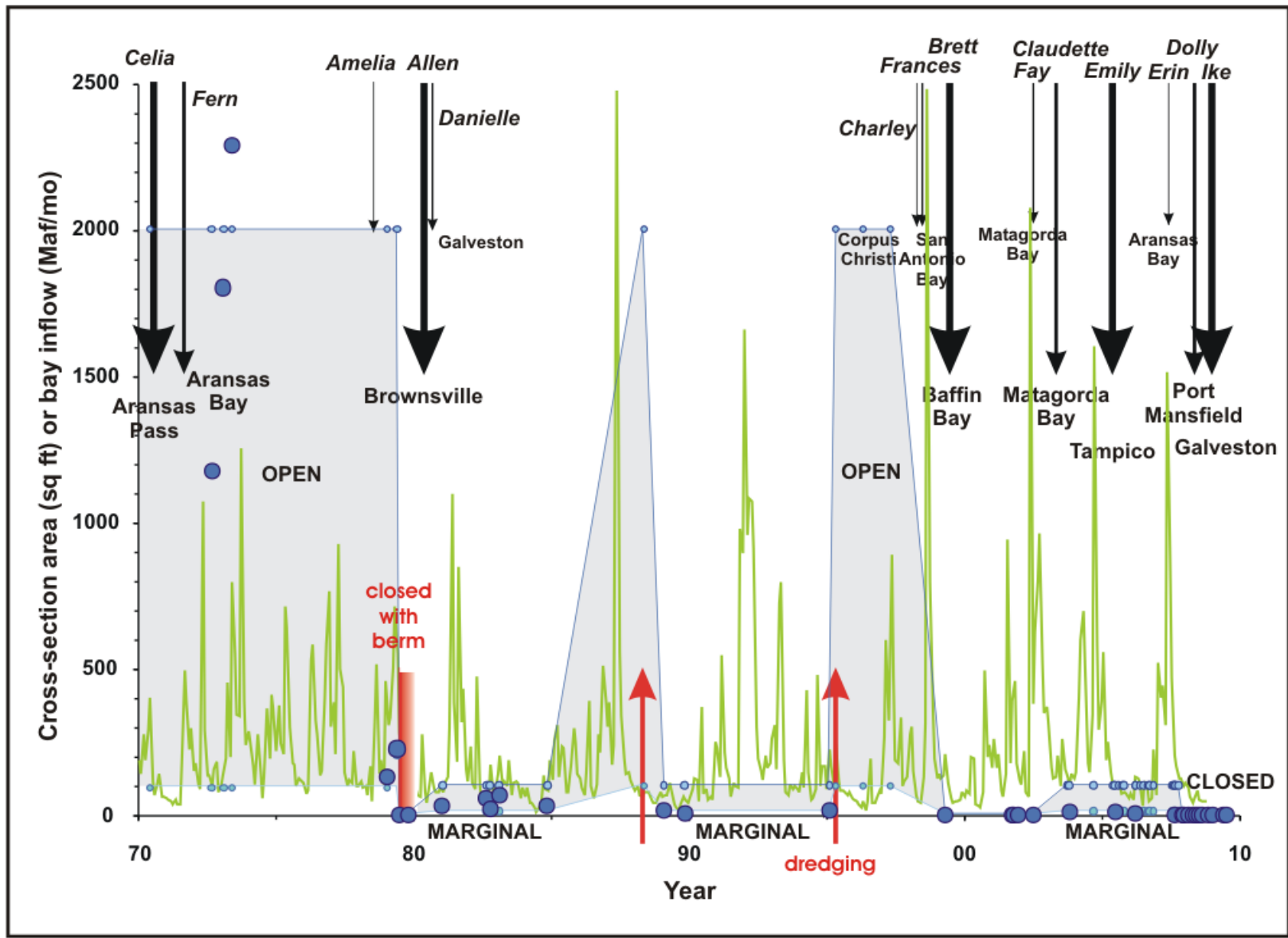


Figure 3-9c - Time history of Cedar Bayou, from chronological data (see text), 1970-2010.

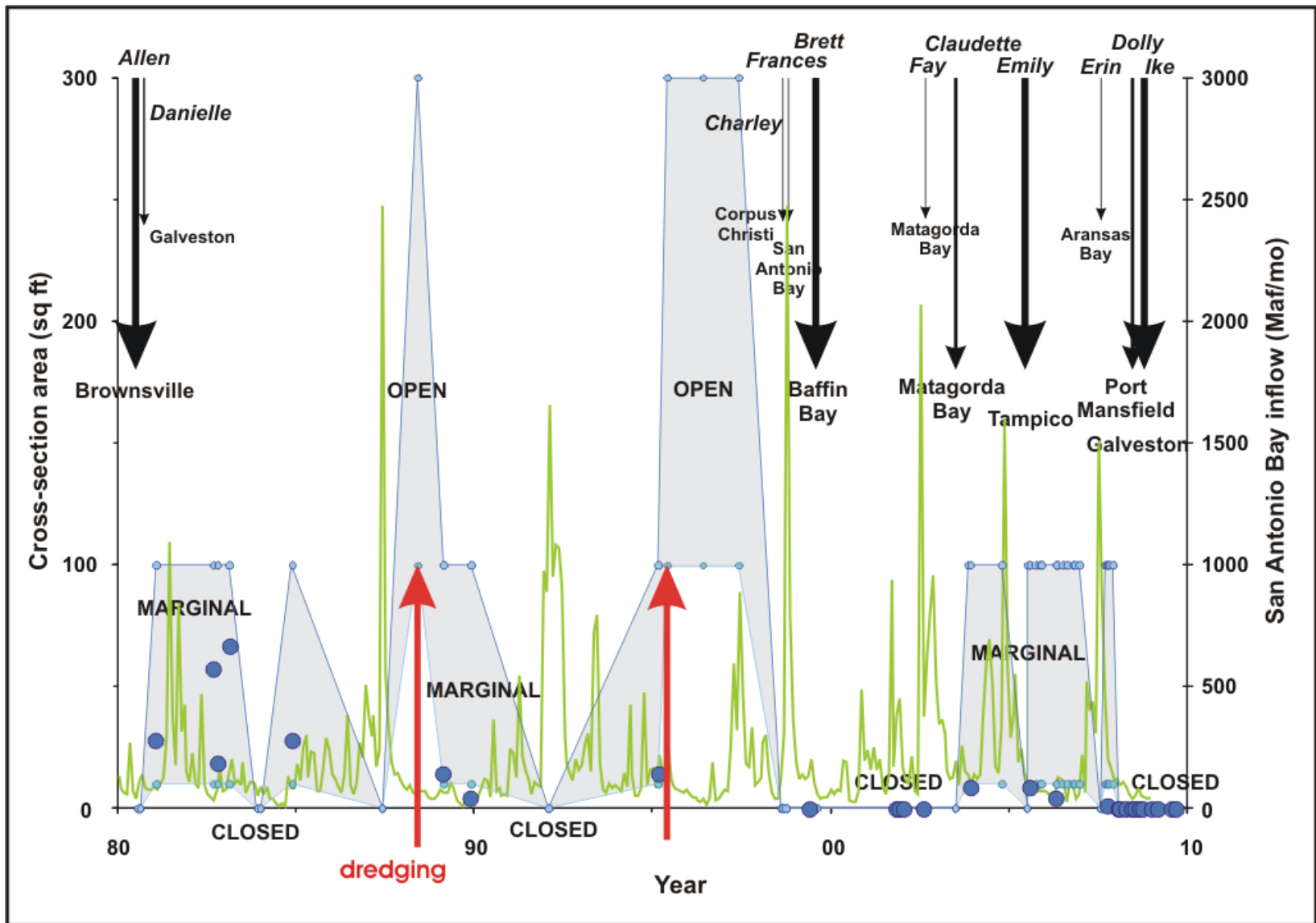


Figure 3-10 - Time history of Cedar Bayou, from chronological data (see text), 1980-2010, with better resolved cross-section data.

Generally, over the past 100 years, Cedar Bayou has declined in cross section, despite the efforts to open the inlet by dredging. Because of the recent activity in this respect and the importance of interpreting the inlet's behavior, Figure 3-10 shows a more resolved display of inlet cross section for the time period 1980-2010 (also somewhat better resolved in time than Fig. 3-9). In this period, there is no quantitative measure of inlet area that exceeds 100 sq ft (our qualitative category of "marginal"), despite two dredging projects, numerous tropical storms and record inflows to the estuary. A detailed examination of the history of the inlet offers insight into this fact.

In the first half of the Twentieth Century, the inlet was generally open, except for closing during the 1950's drought. This general statement is, however, based on four surveys in the area and qualitative reports in the literature. What is probably more significant is the size of the inlet in those years, with cross section exceeding 1000 sq ft (when open). The controlling (i.e., least) depth was found in the inlet aperture, and there was no indication of shoals in the throat area. Although there are numerous reliable later reports that the inlet was "open", the next quantifiable data does not appear until the early 1950's, when the inlet was evidently shoaling and ultimately closed. Unfortunately, there is a data gap after the 1959 dredging project of TGFC until 1969 (Fig. 3-9b), a crucial segment of the inlet's history. (The one report that the inlet was closed in 1961 appeared in the *U.S. Coastal Pilot* for 1962, and is of dubious authority. Apparently, after the inlet's first appearance in the 1958 *Pilot*, no new reports were received so the *Pilot* continued to post the last known status of the inlet. All later *Pilot* reports were ignored in this data compilation.) The 1969 aerial (see Fig. 3-5) indicates a controlling cross section of 500 sq ft (during a high-water event). For the next decade, the inlet began to increase, achieving its largest recorded historical size in 1973. At the close of the decade (with a 6-year gap in coverage), the inlet has shoaled to marginal dimensions.

In summer 1979, to prevent contamination from the Ixtoc oil spill, Cedar Bayou was bulldozed closed, as evident in Figure 3-11. There is no reliable information available as to how long this berm remained, though there are reports that the inlet was re-opened by Hurricane Allen. Certainly by 1981, while there is a remnant of the berm, the inlet channel has shifted to the north, see Figure 3-12. By September 1982, the channel had re-occupied its original southernmost



Figure 3-11 - Aerial photograph 11 Nov 79 showing Ixtoc berm in place



Figure 3-12 - Aerial photograph 2 Dec 81 after inlet abandoned bermed channel



Figure 3-13 - Aerial photograph 6 Mar 89 within months of completion of 1988 dredging

channel, and there was no vestige of the berm remaining. From this point in time on, as depicted in Figure 3-10, the inlet remained in a marginal condition apart from two or three years after the 1995 dredging project.

For the remainder of the 1980's the inlet appears much as it did prior to the berm installation of Fig. 3-11, i.e. extending over the entire reach of the beach zone and debouching to the sea in the southernmost channel location. Hoese (1958) and Simmons and Hoese (1959) describe the evolution of the inlet from its open state in November 1939 (after the TGFOC dredging project) to its closure in 1955 as proceeding from a channel to the sea at the northern end of the beach zone, as an extension of the main axis of the interior channel, to one positioned at the southern end, via spit accretion from Matagorda Island and erosion of the San Jose Island shoreline. This is consistent with the migration of the larger tidal passes on the coast, notably Aransas and



Figure 3-14 - Aerial photograph 18 Mar 95

Cavallo, under the influence of dominant littoral drift from the northeast. The 1988 dredging project was reported to have resulted in an “open” inlet, but there are no photographs available or quantitative soundings. In any event, within the year, the inlet was marginal again (Fig. 3-10). Its configuration in March 1989 is shown in Figure 3-13. Probably the inlet was opened by again dredging to the sea in the direction of the main axis of the interior channel, i.e. opening the channel on the north end of the beach zone, but information is not available to confirm this. Following the pattern reported by Simmons and Hoese (1959), the aperture channel migrated to the south. There is a hiatus in photography and reports for the first five years of the 1990’s, until just before the 1995 dredging project, Figure 3-14, then another hiatus for the next five years.

In considering the morphology of Cedar Bayou, one notable change is evident between its state in the mid-Twentieth Century and that at the close of the century, as disclosed by a close examination of Figures 3-2 (1969), 3-12 (1981), 3-13 (1988) and 3-14 (1995), namely the growth of substantial bars and shoals in the lower section of the interior channel upstream from the beach zone. This is first evident in Fig 3-12, by a spit prograding upstream in the center of the main channel. By 1988, bar structure has developed well into the interior reach (note the shoals upstream from the emergent island in Fig. 3-13), and by 1995, these shoals have become complex and occupy the majority of the channel, Fig. 3-14.

There is little evidence in these time series that tropical disturbances are the operative agent in keeping the inlet open anywhere near its original size. There certainly has been no shortage of such events since 1998, yet the state of the inlet seems impervious. The only apparent distinction between the storms during the 1970's compared to those more recently is that the earlier storms made landfall squarely on Aransas Bay, with three storms within a four-year period. If such storms do play a rôle in the maintenance of the inlet, it will have to be exposed by a much more careful and quantitative analysis than merely correlation in time.

In Section 3.2 above, a plausibility argument for the rôle of floods in inlet maintenance was proffered by which the operative mechanism is an elevation of water behind the barrier island that forces a flow through the inlet. It was judged that such an event would have to exceed at least 400 maf/mo to inundate the inlet, and more would be needed to force a flow sufficient to scour the inlet. In the chronology depicted in Figures 3-9 and 3-10, there are ample events exceeding even three times this level of flow. The fact that most of these have occurred in the modern period of Figure 3-10, including record levels of flow and cumulative discharge, yet the pass has remained chronically closed or minimal, would refute the notion that somehow inflow events maintain Cedar Bayou.

3.5. Conclusions

The assembly of data establishing a chronology for Cedar Bayou is intended to continue, because there are additional sources of data that have not yet been located for inclusion in the data base. Therefore, it is premature to represent any conclusions from this work as final. At best, this provides a data base for potentially examining whether the state of Cedar Bayou is an operative factor in the variation of abundance of species within the estuaries of San Antonio Bay, Aransas-Copano Bay and their secondary systems, which was, after all, the objective of the project. The time and resources available to this study limited the archival work to sources readily available. We expect that holdings of state agency files (notably, Texas Parks & Wildlife Department coastal laboratories), private aerial photography sources and public sources limited to hardcopy only (such as Galveston District Corps of Engineers), and the files of individual coastal researchers, will yield more information on the history of the pass.

What has emerged thus far is that Cedar Bayou has tended to diminish in size from the surveys of the early Twentieth Century to the aerial photography of the Twenty-first Century. The mechanisms that operate to scour and maintain tidal inlets, *viz.* tides, seasonal water-level variations, set-up and set-down from meteorological disturbances, surge from tropical storms, and inflow events, seem to be operating now at roughly the same intensity and frequency over this period, except perhaps for freshwater inflow, which is trending upward. There is apparent no ready hydrometeorological or hydrographic explanation for the declining trend in inlet dimensions, though this certainly warrants detailed study. It may be that the answer lies in alterations in the littoral sand budget along this area of the coast.

The data reported by King (1971) demonstrated the importance of Cedar Bayou as a migratory access route for diadromous species. In light of the chronology depicted in Figure 3-9, it is important to realize that the pass in the years of the King study was much larger than it has been more recently, certainly since around 1980. It is unlikely that, even when presently “open”, it will now have anything like the effect that it had in the 1960’s, though this must be tested by data analysis.

4. BIOLOGY AND ECOLOGY OF THE BLUE CRAB

In this chapter is presented a survey of the literature about 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. While features of the structure and function of the organism 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. Specific objectives of this survey are:

- (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) 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.

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 Van den Avyle and Fowler (1984), Hill et al. (1989), Millikin and Williams (1984), Patillo et al. (1997) and, especially, the monumental pandect edited by Kennedy and Cronin (2007). 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,

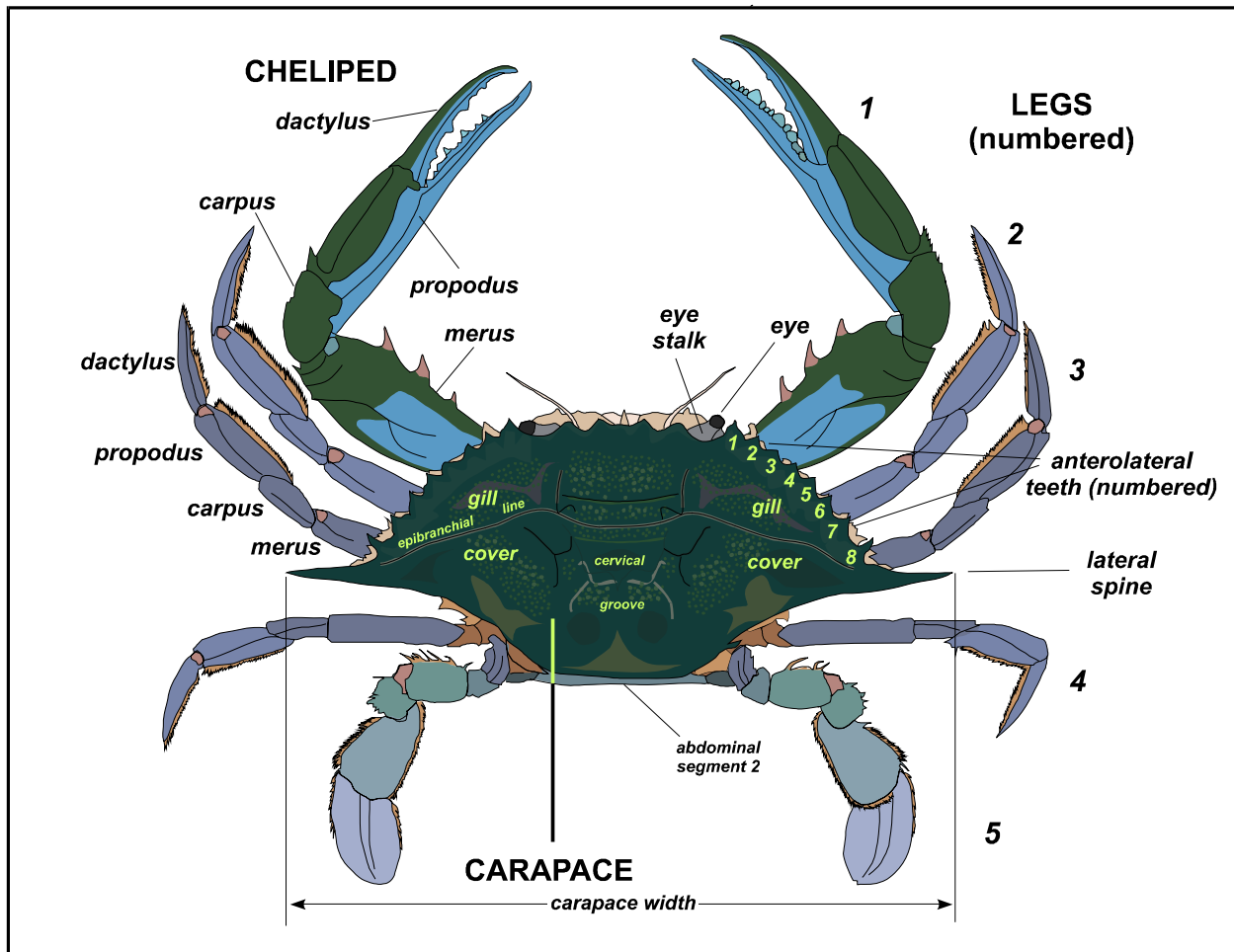


Figure 4-1 - Anatomy of blue crab, male, dorsal view

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

4.1 Anatomy and physiology

4.1.1 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 4-1 and 4-2. The crab

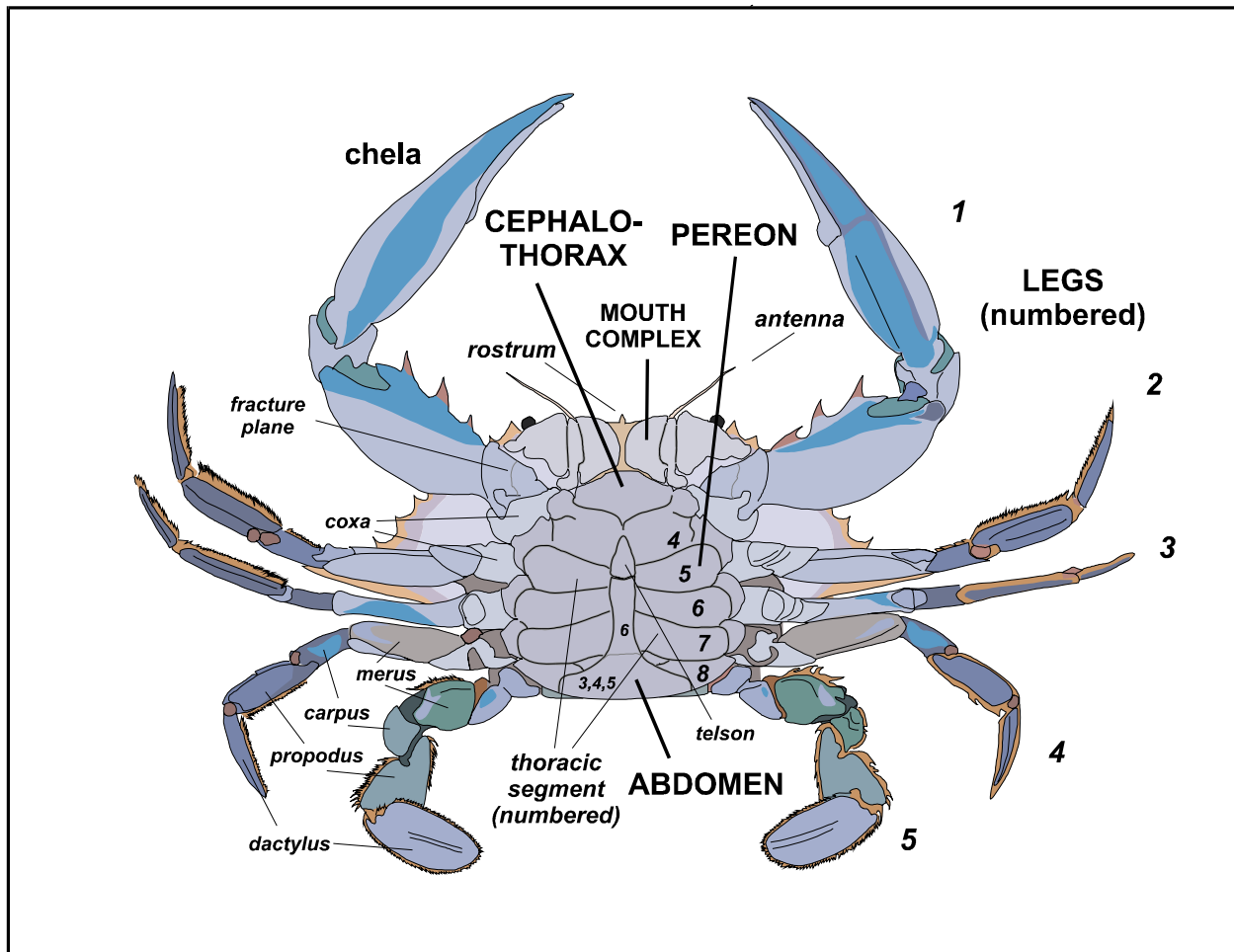


Figure 4-2 - Anatomy of blue crab, male, ventral view

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. 4-1). 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. 4-1. (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:

$$M = A W^b \quad (1)$$

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 I). 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 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 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 I.

Table 4-1 collects various least-squares fits (see Appendix I) of blue-crab data to equation (1), and the corresponding graphical relations are shown in Figure 4-3. The bold black line is the relation resulting from the count-weighted averages of the parameters A and k (see Appendix I). 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 $\pm 20\%$, and about $\pm 12\%$ and $\pm 15\%$, 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

Table 4-1
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

<i>Geographical region</i>	<i>b</i>	<i>A</i> (<i>g/mm^b</i>)	<i>number</i> <i>of data</i>	<i>R</i> ²	<i>source</i>
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 I)
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

Department (TPWD) for many years, underestimates crab weight by about 20% for males and over-estimates crab weight by 5-10% for females. (The traditional application that TPWD makes of this relation, for monitoring of year-to-year variation in potential harvest weight, is unaffected by a proportionate error.)

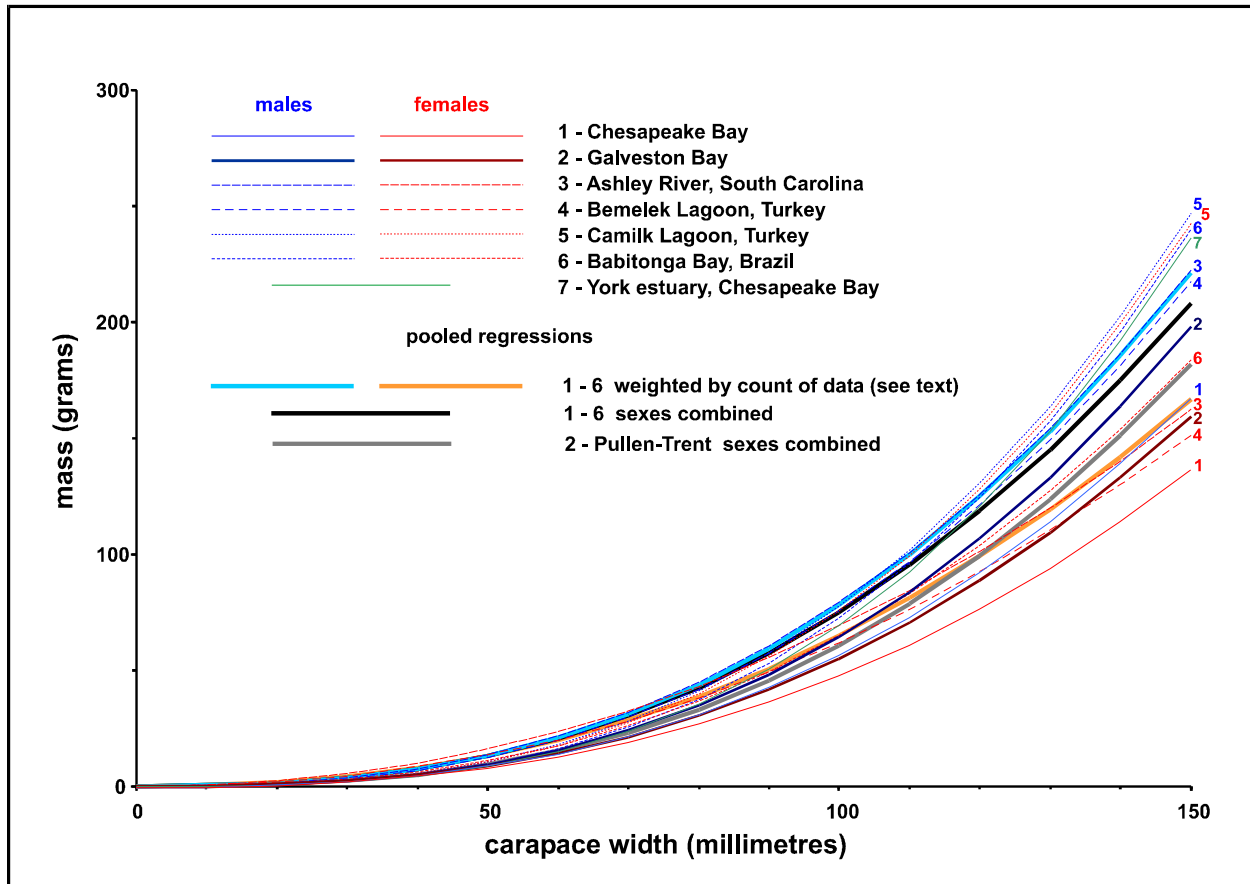
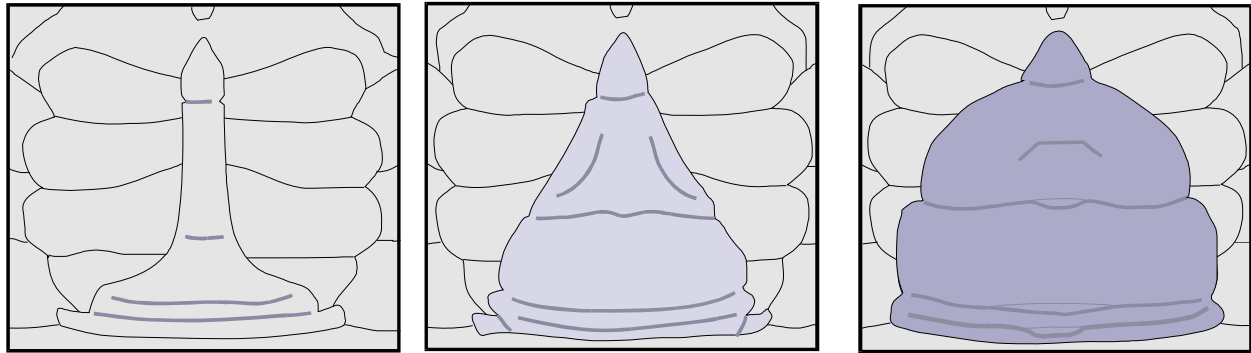


Figure 4-3 - Literature relations of blue crab mass versus carapace width

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 cephalothorax, the remaining five thoracic stomites comprising the pereon. The ventral surface (Fig. 4-2) 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. 4-2). 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 Bouchard, 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 4-4, but early juveniles are more difficult to sex.



(a) Male

(b) Female, immature

(c) Female, mature

Figure 4-4 - Differentiation of sex from abdomen or “apron” shape

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. 4-2. The segments (podomeres) of 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. 4-1) 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 4.3.1.1. The coloration of Figs. 4-1 and 4-2 is schematic only.

4.1.2 Function

4.1.2.1 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 cm³/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 cm³/min for a 200 g crab, ranging 22-400 cm³/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. 4-1). 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 per gram of body mass (wet weight) per hour. The measurements of McGaw and Reiber (2000) ranged 50-60 $\mu\text{mol/kg/min}$. 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 $50\% \pm 10\%$ 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 $\text{O}_2/\text{g hr}$ 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).

4.1.2.2 *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 4.2.1.)

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 ($\text{Na}^{++}\text{K}^{+}\text{-ATPase}$), 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‰.

4.1.2.3 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, 2007), 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 (2007). 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).

4.1.3 Locomotion and mobility

The newly hatched Zoea I larvae (see Section 4.2.3) 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 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 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 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. 4-1 and 4-2) 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 Section 4.4.

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 benthic nutrient fluxes (e.g., Graf and Rosenberg, 1997, Bertics and Wiebke, 2009).

4.2 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.

4.2.1 *Molting*

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

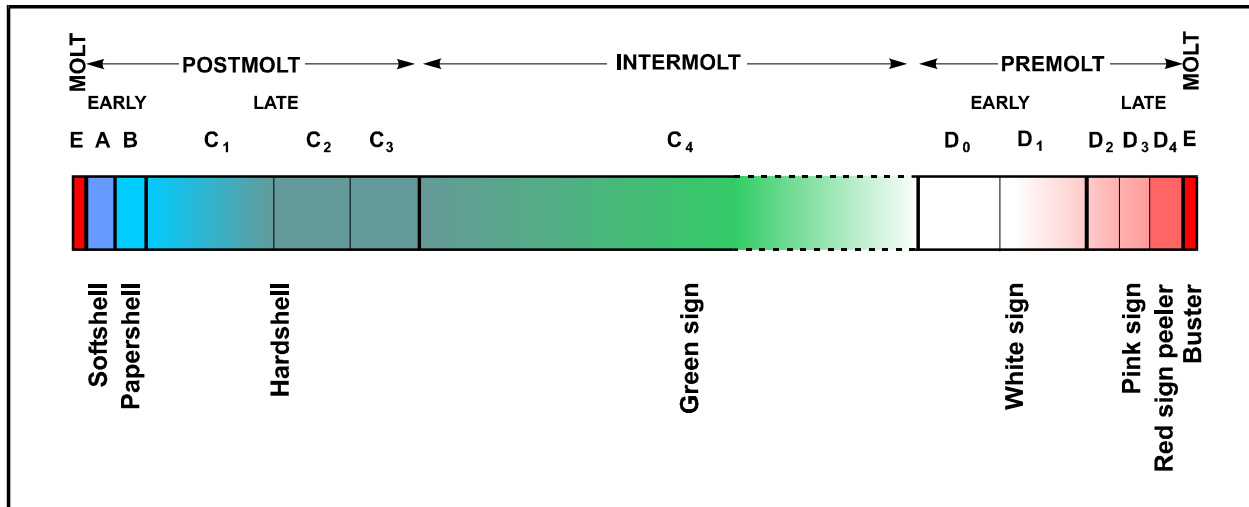


Figure 4-5 - Intermolt stages showing durations proportional to the total intermolt period (horizontal bar), with common descriptors (below), after Passano (1960), Mangum (1985) and Smith and Chang (2007)

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 4-5, in which the horizontal bar represents the total time period between molts, and the length of each individual stage (A, B, C₁, etc.) is the proportional duration of that stage. The total time period of Fig. 4-5 is 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, in which the sequence of Fig. 4-5 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). An analogous stage sequence applies to megalops as well,

based upon retraction from the cuticle exhibited in the maxillipeds and uropods (Metcalf and Lipcius, 1992).

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 D₄, intake of water by drinking and osmosis begins and the rate increases sharply by the end of the stage (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, see Section 4.2.3), remains constant for the remainder of the cycle until the next molt. Stage C₄ 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. 4-5). 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). Also, stage C₄ is of variable duration (Freeman et al., 1987), indicated by the broken lines of Fig. 4-5.

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 the 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 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:

$$\Pi(t) = \int_{t_0}^t \max\{0, T(t) - T_{min}\} dt \quad (2)$$

where $T(t)$ is the instantaneous water temperature time function, t measured in days, t_0 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 \bar{T}_i , then (2) becomes

$$\Pi(t) = \sum_{i=0}^N \max\{0, \bar{T}_i - T_{min}\} \quad (3)$$

where i denotes the time duration in days after t_0 , 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 anecdyosis”) 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 appears 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 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 4-6. 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. With 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. 4-6.)

4.2.2 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. 4-4(b), which becomes dark blue or purple prior to the terminal molt. After the terminal molt, the abdomen is dome-shaped and dark, Fig. 4-4(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

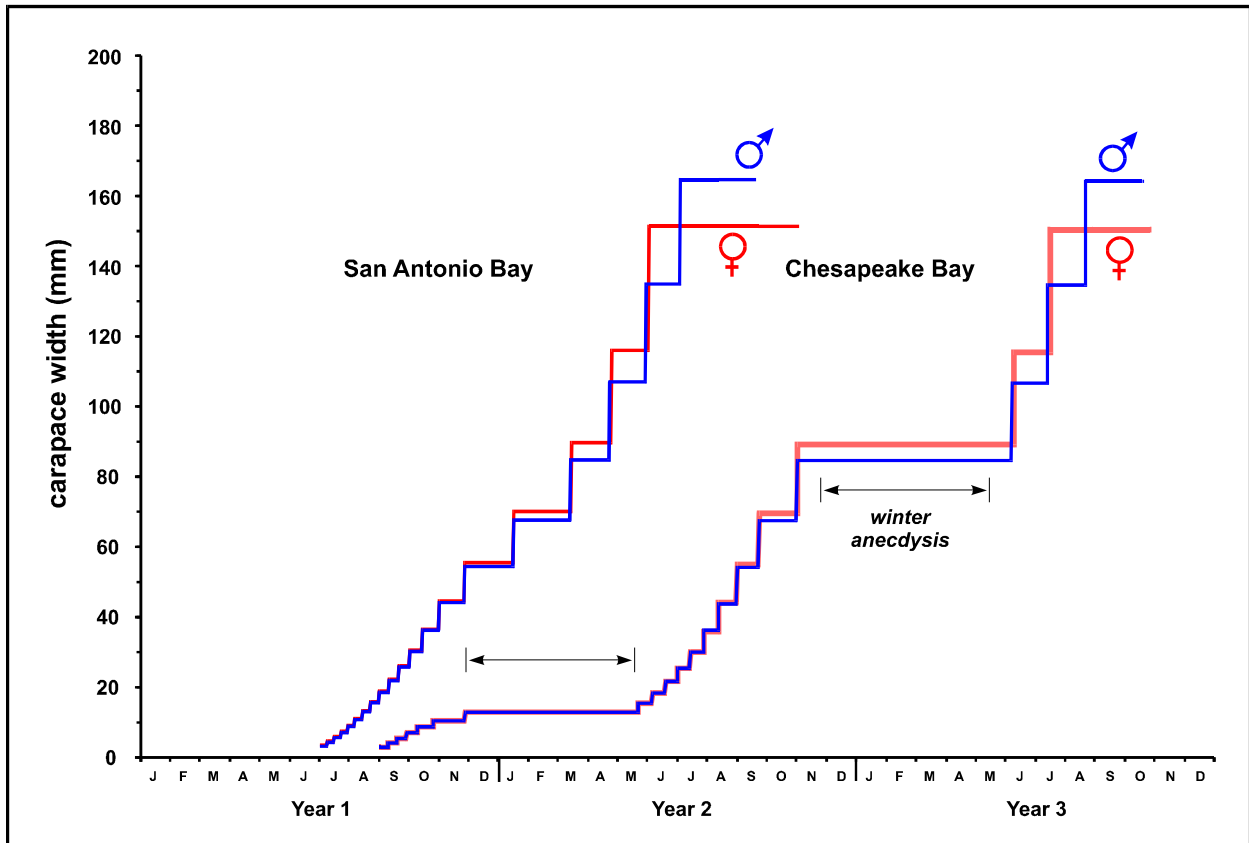


Figure 4-6 - Simulated growth of blue crabs in Chesapeake and San Antonio Bay, starting at first month of peak settlement, with cycled 2004-08 averaged daily water temperature. Based on model of Smith and Change (2007).

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 indicates that as the number of his conquests increases, the male is more likely to simply eat the female (Wolcott et al., 2005).

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 broods. 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.

4.2.3 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 K. In this report, larva means zoea (and prezoeta), 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 K.

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 4-7 and 4-8 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. 4-7 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 prezoa 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,

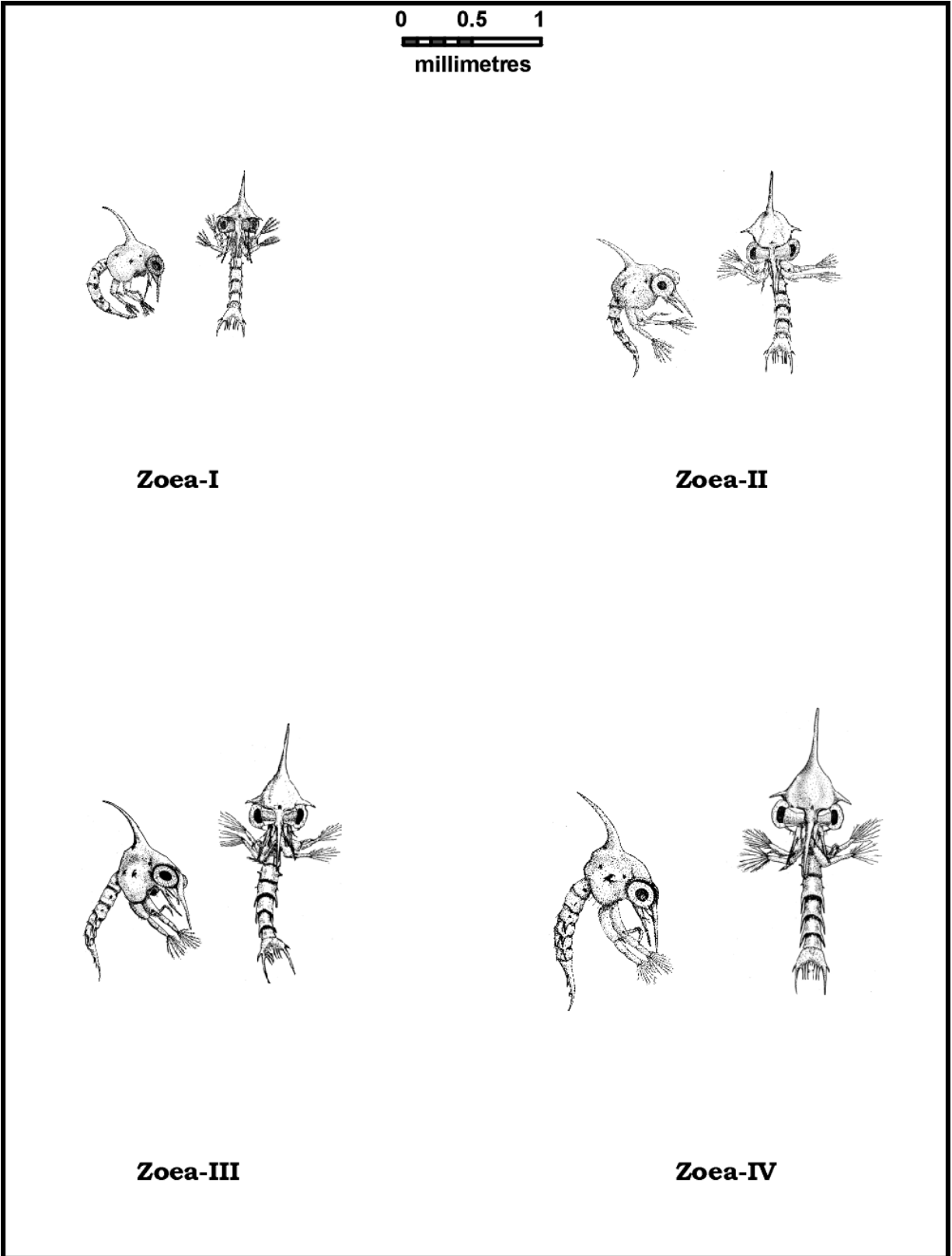


Figure 4-7 - Sketches of side (left) and ventral (right) views of blue crab zoeae, adapted from Costlow and Bookhout (1959)

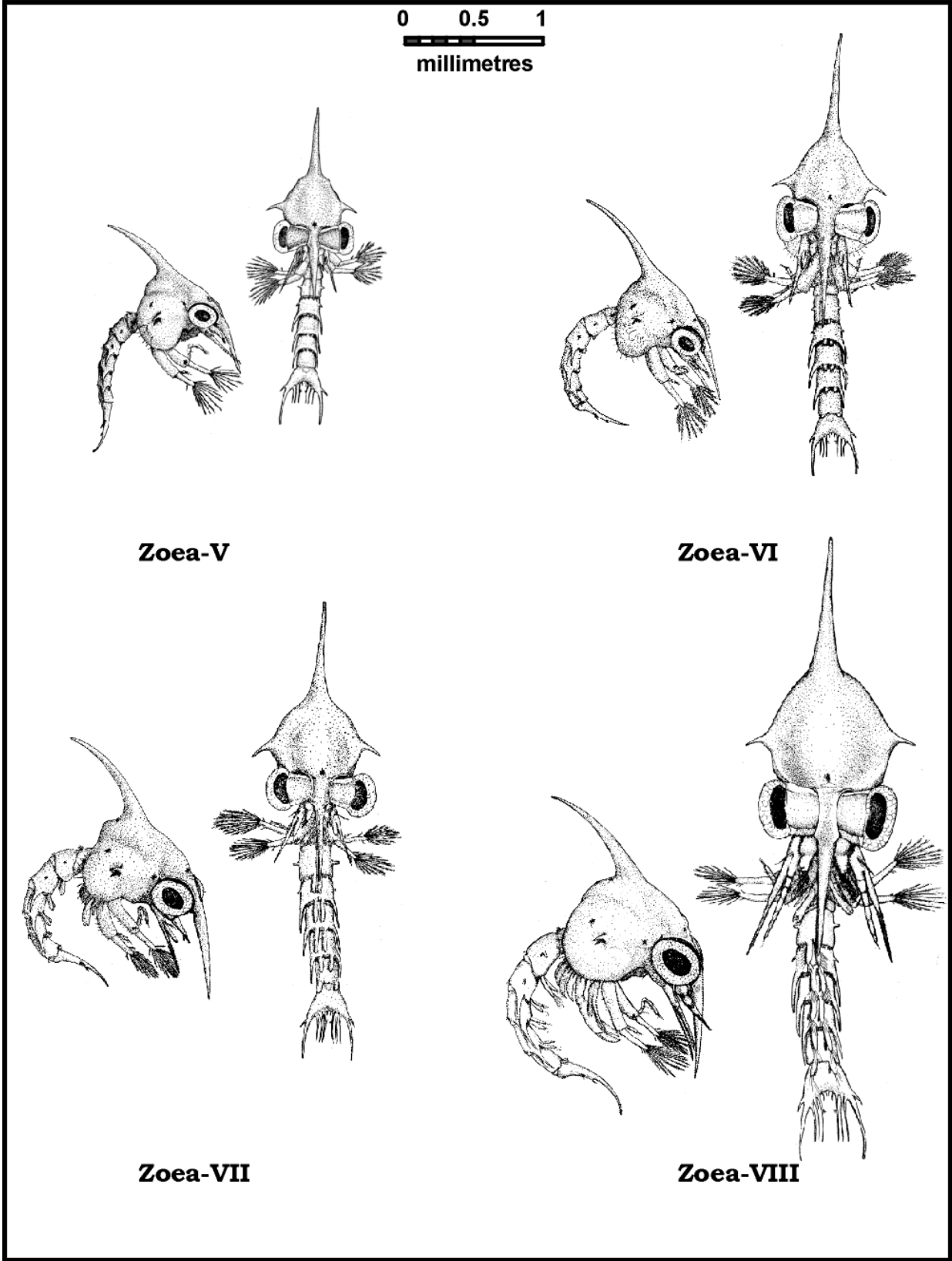


Figure 4-7 - continued

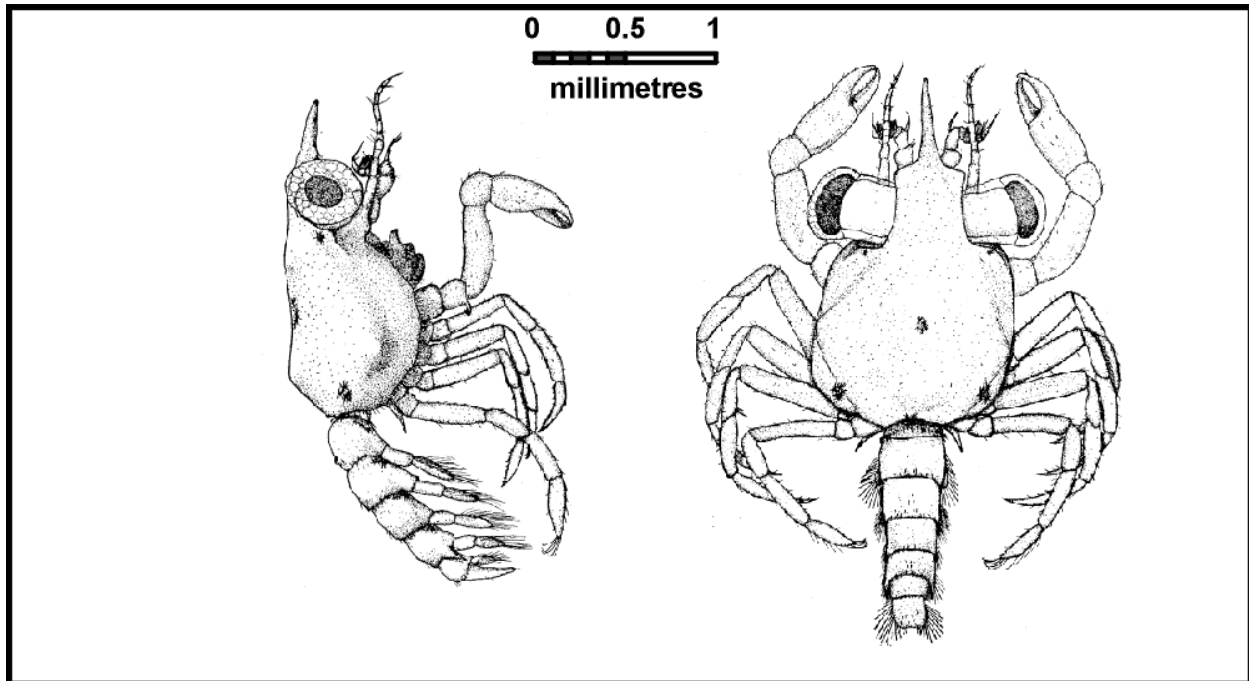


Figure 4-8 - Sketches of side (left) and ventral (right) views of blue crab megalop, adapted from Costlow and Bookhout (1959)

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 growout 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.

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 4-9. (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. 4-9, these data have been combined.) Survival of the larvae

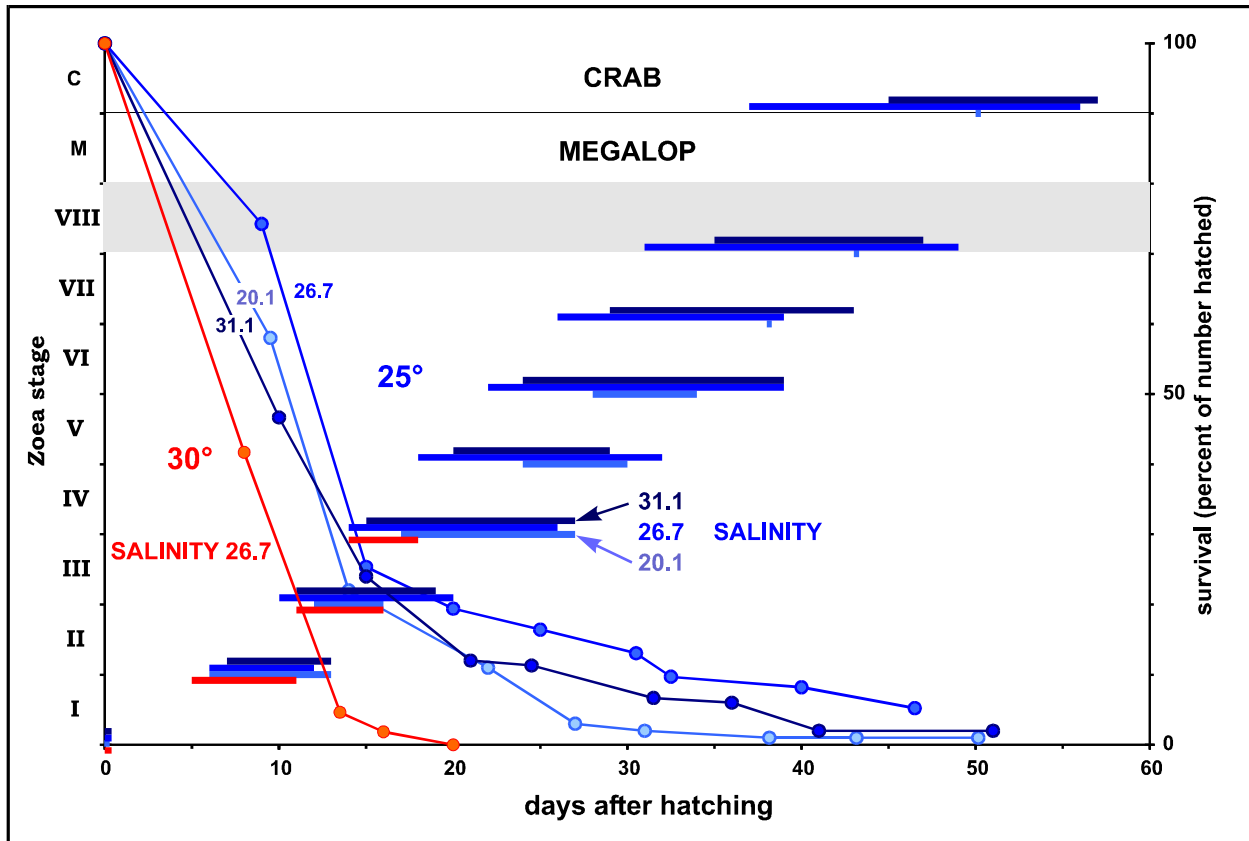


Figure 4-9 - Range of time after hatching for molt of blue crab larvae (horizontal bars), and survival (connected data points) from data of Costlow and Bookhout (1959)

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. 4-9 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. 4-9, 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 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

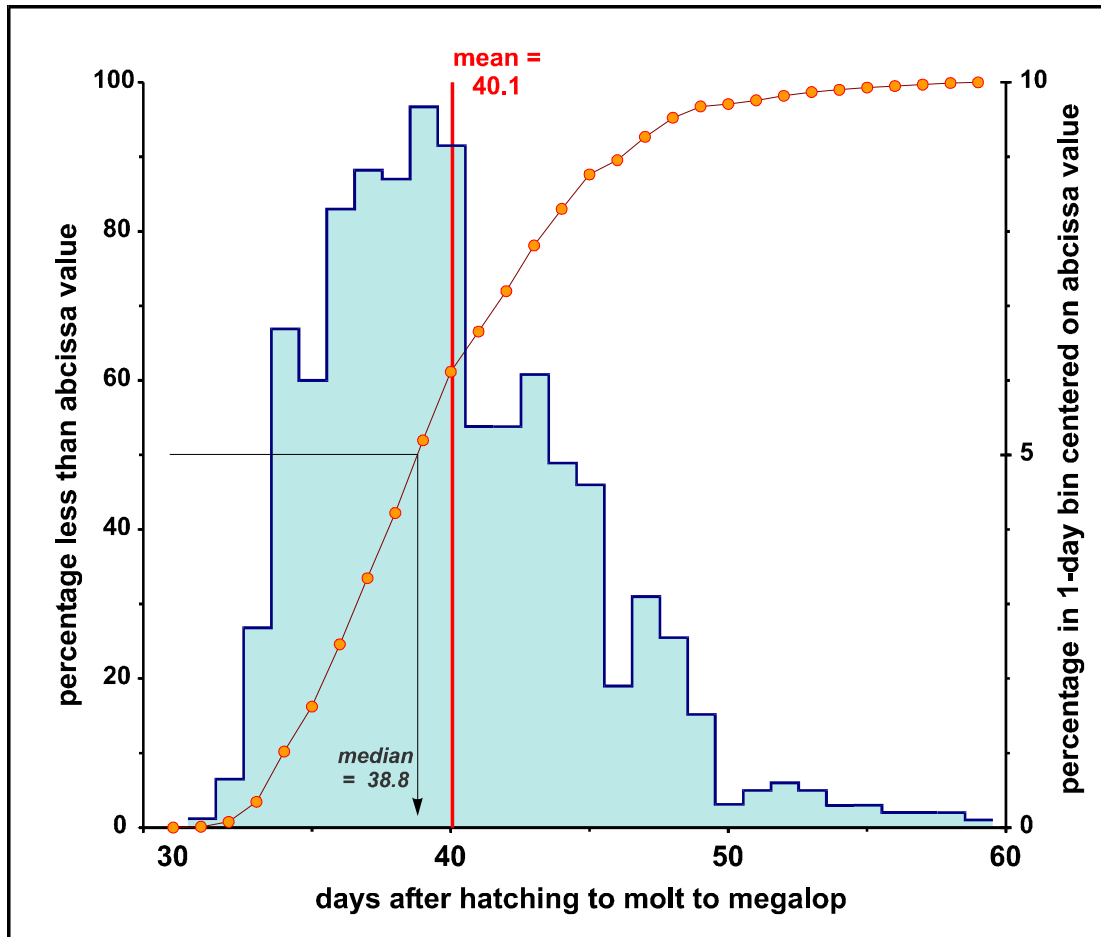


Figure 4-10 - Range of time (days) after hatching for molt to megalop, of 1,157 sibling larvae at 23°C and 30‰, from data of Sulkin and Van Heukelem (1986). Mean = 40.1 days, standard deviation 4.7 days. Cumulative frequency ogive (connected data points) left axis, frequency diagram right axis.

and replotted as frequency distribution and ogive in Figure 4-10. 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. 4-8) 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

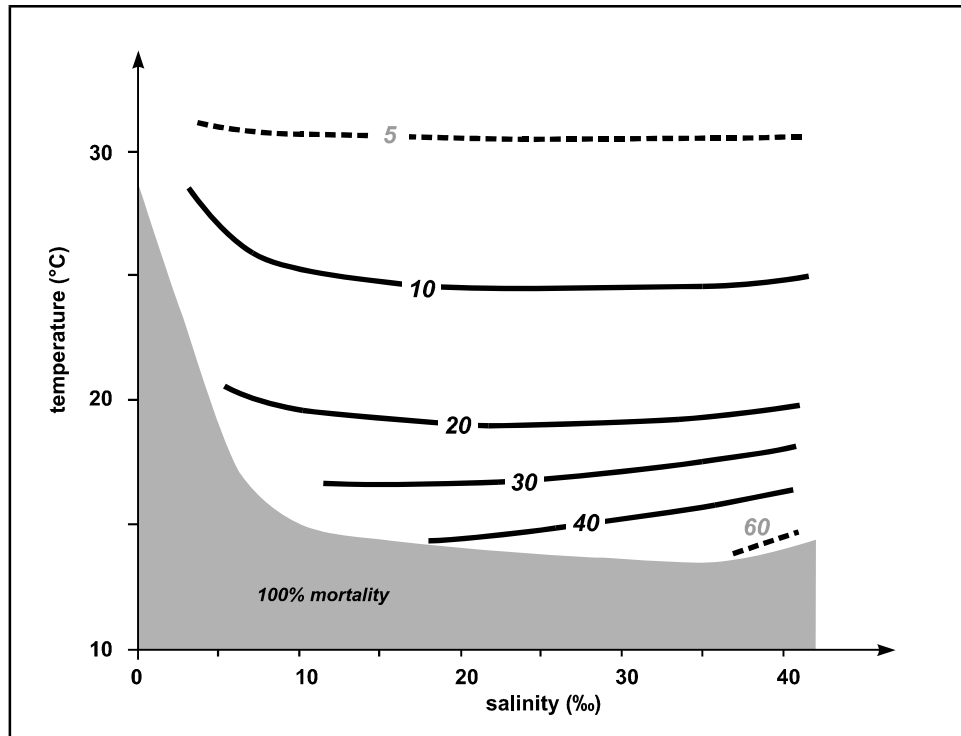


Figure 4-11 - Duration (days) of megalop stage from data of Costlow (1967). Broken contours extrapolated from range of data.

days at 31.1‰ (all at 25°C), but the small number of individuals (Fig. 4-9) 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 4-11 (cf. Fig. 4-14). 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 period with salinity.

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. 4-10, i.e., the individuals attaining the megalop stage on days 33-39 after hatching, which represents 43% of the individuals of Fig. 4-10, 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 4.4.4).

The next molt is a second metamorphosis, this time from the megalop to the juvenile crab. Although the relative 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 J.) 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 4-12 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. 4-12).
- (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).

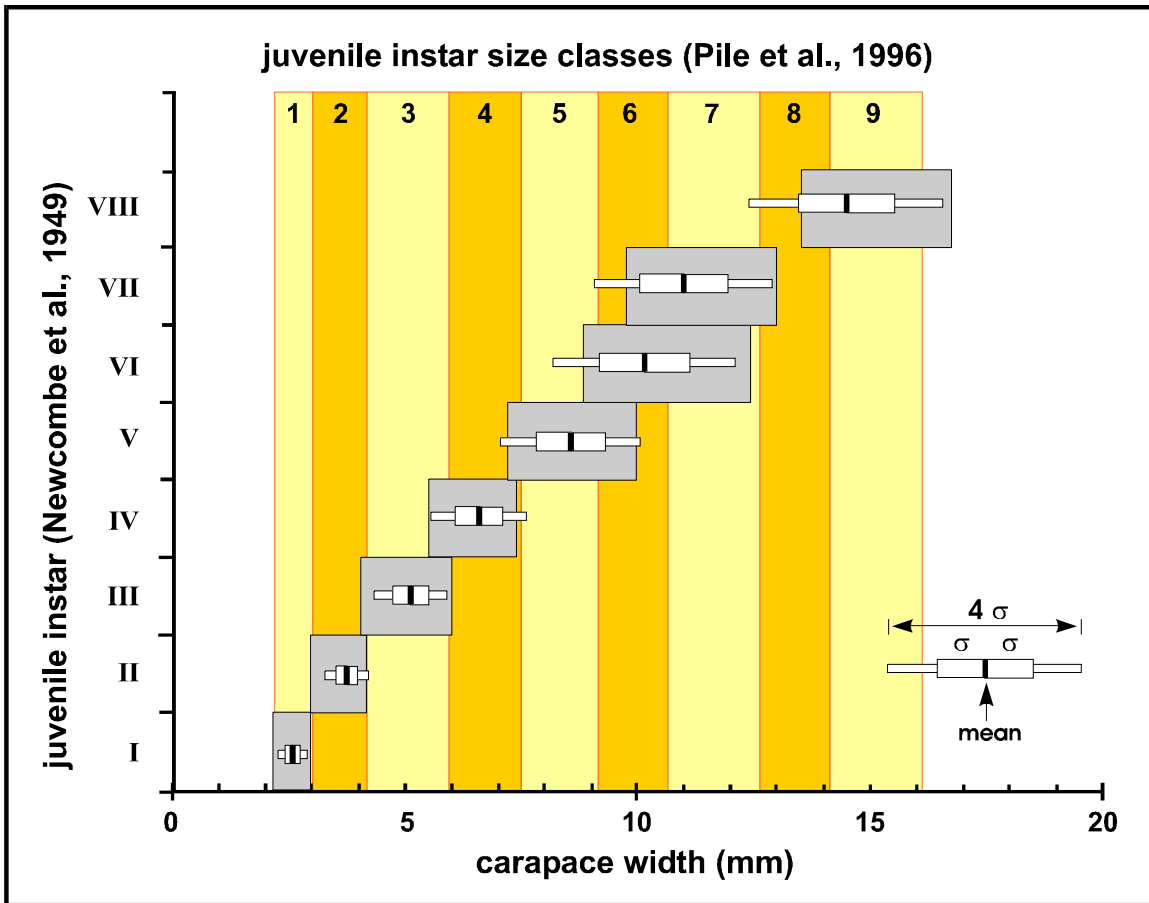


Figure 4-12 - Instar size ranges from Newcombe et al. compared to current convention of size classes. Grey boxes indicate size ranges for instars I – VIII from Newcombe et al. (1949), with mean, 2 x and 4 x standard deviations (68 and 95% of population, resp.), see Appendix J. Vertical bands indicate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

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 4-2 may be extracted. (Details are given in Appendix J.)

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

Table 4-2
Probabilities of given instar falling in size categories of Pile et al. (1996)

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

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 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 4.2.2).

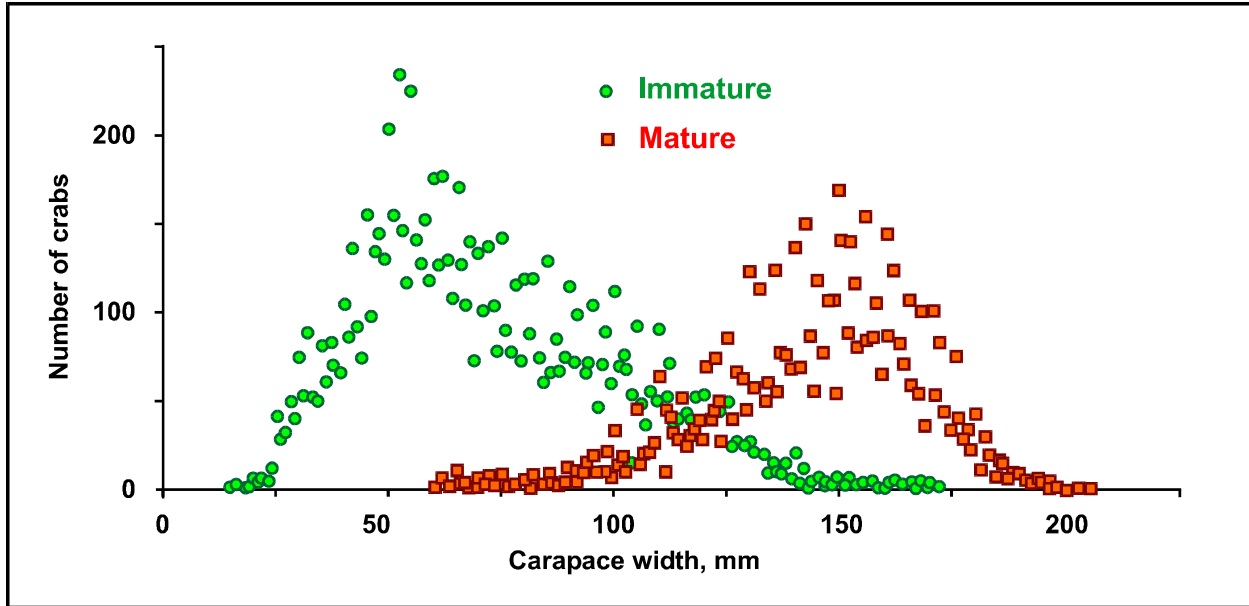


Figure 4-13 - Distribution of female blue crabs taken in TPWD trawls and seines for Texas coast 1984-87 versus carapace width. Data of Fisher (1999), replotted.

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 4-13. It is apparent that both immaturity and maturity extend over a wide and overlapping range of carapace size.

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

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

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

<i>instar</i>	<i>CW</i> (<i>mm</i>)	<i>instar</i>	<i>CW</i> (<i>mm</i>)
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

where R is the molt increment as a fraction (not a percent) of the pre-molt width. Assuming a carapace width w_l 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 4.2.1), the resulting widths after molting are given in Table 4-3. Tagatz (1968b) reports two crabs he tracked after metamorphosis to the first instar, finding that one required 10 molts to reach 20 mm, the other nine molts, which closely agrees with Table 4-3. (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 J, then the appropriate calculation is

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

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 J).

4.3 Ecological interactions

4.3.1 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 4.3.1.4, below.

4.3.1.1 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. (2005). 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., 2005). This diel migration would expose the postlarvae to daylight predators in the coastal zone, and is counter to that exhibited during estuarine reinvasion, so its ecological value is not immediately clear. (This becomes apparent in the larger context of migration, see Section 4.4.4, 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 4.3.1.2 below.

Careful laboratory experiments have failed to induce a circatidal response in movement or depth regulation of blue crab megalops (Forward et al., 1997, 2003b). Laboratory experiments by Forward et al. (2005) determined that vertical movement of megalops was distributed uniformly with respect to tidal variation, i.e., there was no circatidal rhythm.

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. (2005) used wild-caught or newly hatched first and second 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 addressed larger juveniles 6-9 mm (4th and 5th instars according to Fig. 4-12), 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 is noisy, with periods ranging from 23 to 25.5 hours, but showed no coherence with tides, so is 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 4.3.1.2, 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. Darnell et al. (2010) 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 4.3.1.2, 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.

4.3.1.2 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 when the direction is favorable to be

carried by the current. 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 4.3.1.1).

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) 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 $5 \times 10^{-4} \text{‰ s}^{-1}$, with a constant, even declining, response for rates of increase greater than $1 \times 10^{-3} \text{‰ s}^{-1}$. 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 $1 \text{ cm}^2\text{s}^{-2}$ 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, they 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 4.3.1.1, 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 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

* 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.

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 tide after larval release, in contradiction 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).

4.3.1.3 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 4.4.4. 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 4-4. Inspection of this table

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

<i>Estuary</i>	<i>Measurement</i>	<i>Data period</i>	<i>Lunar association</i>	<i>Citation</i>
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)	substrate	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 plankton 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 plankton 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, higher settlement during small- declination, i.e., minimum tidal range	Rabalais et al. (1995) Hasek & Rabalais (2001a)
Galveston Bay	substrate	1990-91	higher settlement during 1st lunar quarter but no year-to-year consistency	Rabalais et al. (1995)

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.

4.3.1.4 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 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 difficulties 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 difficulty 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 4-4. 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 4-4), which is reviewed in Section

4.3.4.4 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).

4.3.2 *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 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 recent 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.

4.3.2.1 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). 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 generally homogeneous and well-mixed (see Ward and Armstrong, 1997, for detailed evaluations 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. 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. 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 4.2.3, 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. 4-9, 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. 4-9 – 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 4-14 (*cf.* Fig. 4-11). The nearly horizontal isopleths in the range of salinity 10-35‰ show the principal control on both mortality and megalop duration to be 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 4.2.1 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

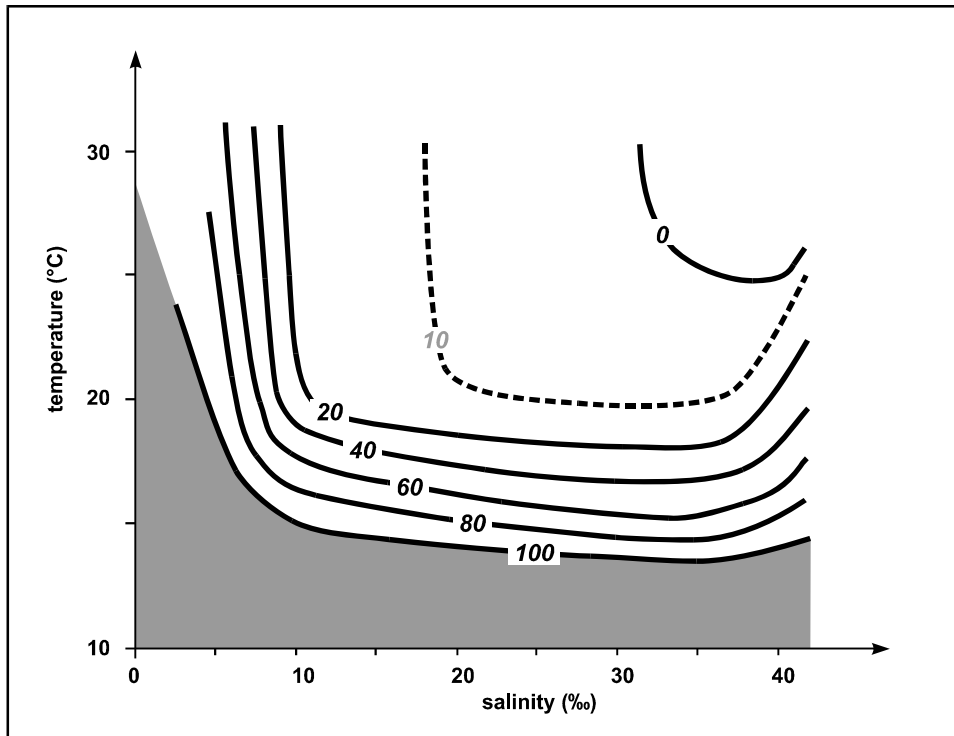


Figure 4-14 - Megalop mortality (percent of megalops failing metamorphosis to first crab stage), from data of Costlow (1967)

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 4.2.1, 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.

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 4-5.

Table 4-5
Upper and lower* lethal limits of temperature for blue crab
determined experimentally by Tagatz (1960), average 48-hr LC50 in °C

	<u>juvenile</u>		<u>mature female</u>	
<i>20% seawater</i>	2.3	35.2	2.3	35.0
<i>100% seawater</i>	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.

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 harrisi*, 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 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 4-5. 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 4-5. The field data of Rome et al. (2005) from dredge surveys of overwintering crabs, shown in Figure 4-15, are not directly comparable, because time of

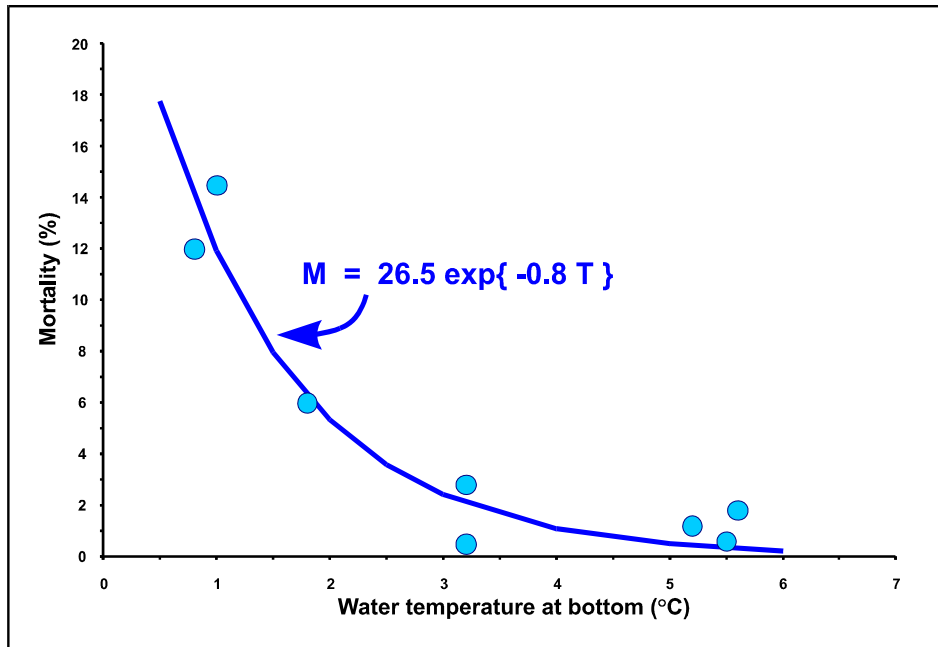


Figure 4-15 - Mortality of overwintering crabs in Chesapeake Bay versus February mean water temperature, data from Rome et al. (2005), replotted. Best-fit exponential, explained variance = 93.1%.

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 came. 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 4-5 are averaged over all acclimation temperatures.)

4.3.2.2 Salinity

Unlike temperature (or dissolved oxygen, see Section 4.3.2.3), 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, ranging 32 – 36‰, and sometimes higher, 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 4.3.2.1 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. 4-9, 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 osmoregulatory 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 4.3.2.1 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. 4-14. 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 4.1.2.2. 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 4.1.2.2. 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.

4.3.2.3 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 the specific DO requirements of the crab. 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 L), 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 4.1.2.1) 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.

4.3.3 *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 perniciosus*. This is the agent responsible for “grey crab disease”, which has caused major mortalities 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 perezii* is found in the Atlantic and Gulf of Mexico nearshore environments, in waters of high salinity (greater than about 11‰), and frequently infects crustaceans, including the blue crab. The infection is usually 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. perezii* 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 (cercariae) 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. The good news is that this fluke itself has a parasite, the protozoan *Urosporidium crescens*, which renders the metacercariae 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 nemertean, *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 essentially 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 of the crab response 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 4.1.2.2), 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 4.1.2.1). 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.

4.3.4 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, like that of zoeae, is unknown, however. Like zoeae, the main predator of megalops is thought to be planktivorous fish (Morgan and Christy, 1996), see Section 4.4.2. Megalops may more successfully evade predators because of their better swimming capability, including bursts of 20 cm/s (see Section 4.1.3).

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 Schlicht, 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 saxatilis*) 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 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 Louisiana Department of Wildlife and Fisheries. Their results for the top eight predators are given in Table 4-6. (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

Table 4-6
 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 (<i>Sciaenops ocellatus</i>)	545	Spotted seatrout (<i>Cynoscion nebulosus</i>)	24
Sea catfish (<i>Arius felis</i>)	110	Gafftopsail catfish (<i>Bagre marinus</i>)	3
Black drum (<i>Pogonias cromis</i>)	33	Atlantic croaker (<i>Micropogonias undulates</i>)	2
Sheepshead (<i>Archosargus probatocephalus</i>)	26	Southern flounder (<i>Paralichthys lethostigma</i>)	1

of proportionality is unknown, because Guillory and Elliot do not report the units of the net data or the species weight.) Since Table 4-6 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.

The organism that is both prey and predator for the blue crab is the organism itself, i.e., cannibalism. 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 4.4.4 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 remove 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.

4.4 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 4.2.2. 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 about 215 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 4.2.2, 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 that the development process 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.

4.4.1 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 movement on the order of several kilometers per day. This behavior is reviewed in more detail in Section 4.3.1.2, 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 – 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 direction is unclear. Because of the low freshwater inflow, the bay general 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 movement 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.

4.4.2 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). While 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; and in Texas, Daugherty (1952) reported that hatching occurs offshore in the Gulf (as much as 10 miles, from indirect evidence) — 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 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 1.5 km 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-

* 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. The main invertebrate predators seem to be ctenophores (notably *Mnemiopsis leidyi*) and hydromedusae (notably the cabbagehead, *Stomolophus meleagris*). See Morgan (1992).

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 report 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 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 mature 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.

4.4.3 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 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 through the megalop stage (e.g., Smyth, 1980), which requires some three to six weeks depending upon conditions, mainly temperature. 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, 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 4.1.3) so their movement and distribution devolves to 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 4.1.3). 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 elusive (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.

4.4.3.1 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 former 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) 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

* 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.

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 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

$$U_E = \int_{-h}^0 u \, dz \quad V_E = \int_{-h}^0 v \, dz \quad (6)$$

(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:

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

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 4-16. Spatial variations in wind direction translate to spatial variations in the 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

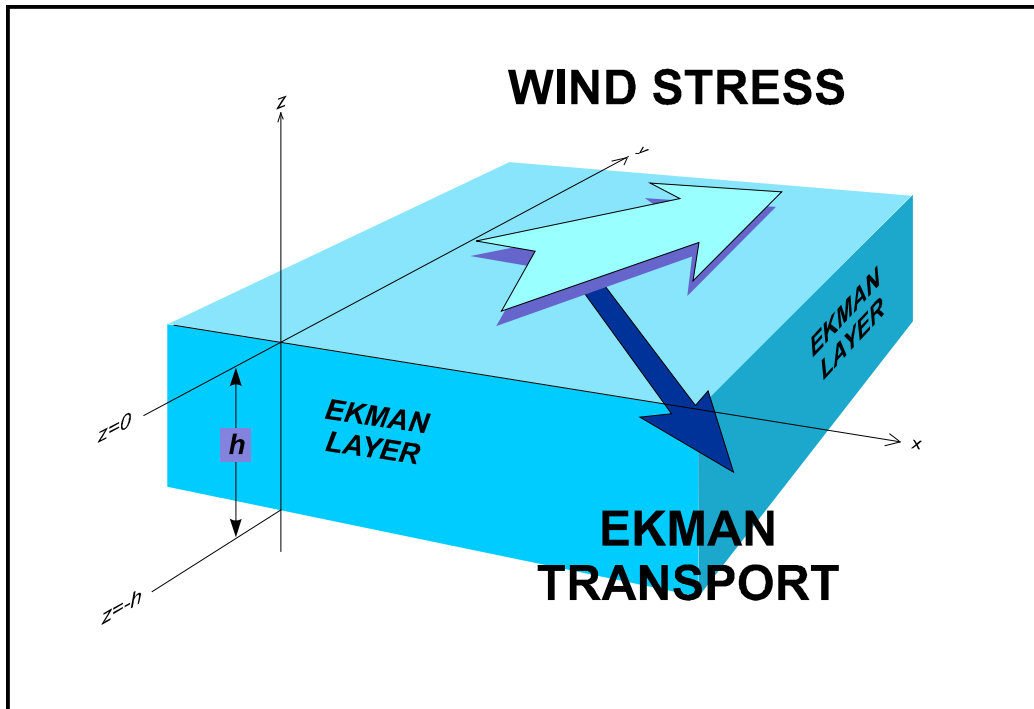


Figure 4-16 - Diagram of Ekman transport driven by wind stress at the ocean surface (northern hemisphere)

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

* 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.

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, 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 a hidden 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

* 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).

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 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 zoeae I southeast from the entrance to Chesapeake Bay, and megalops to the east-northeast (his Figure 2). The former would correspond to the outflow plume from the bay, and

the latter to the null zone, so this distribution is consistent with the notions of Tilburg et al. (2007). McConaugha (1988) interpreted these distributions as two limbs of a cyclonic circulation around the mouth of the bay.

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.)

4.4.3.2 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). 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 carried to the east coast of the U.S. (Walker et al., 1994). However, the Mississippi 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).

The elements of the circulation of surface waters are sketched in Figure 4-17, 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 4-17 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. 4-17 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

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

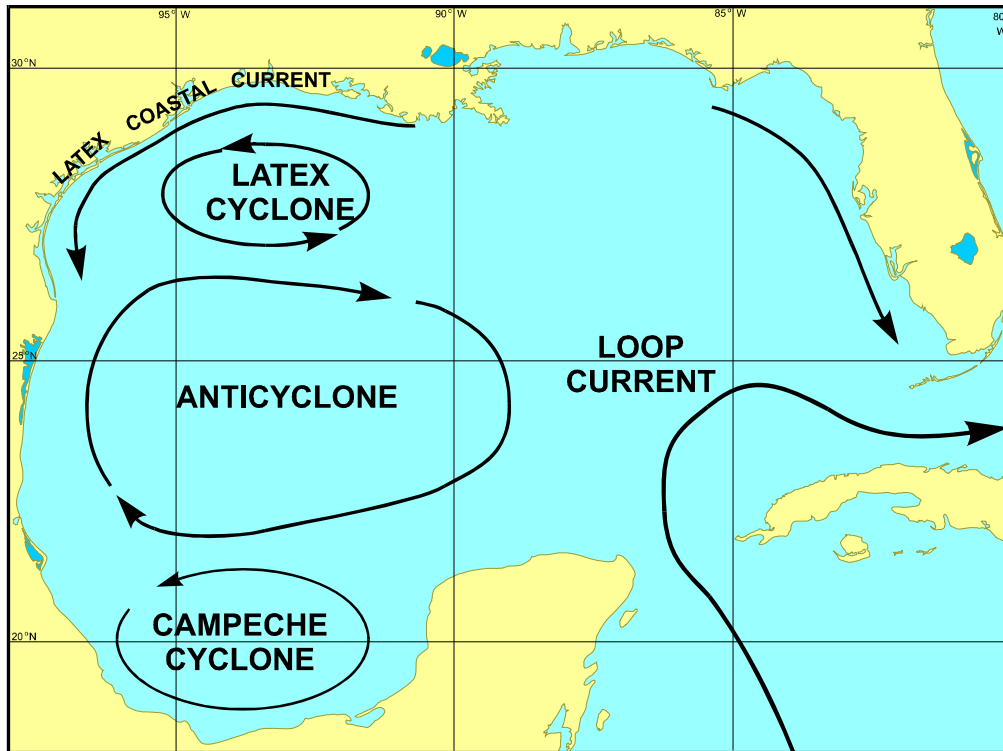


Figure 4-17a - Schematic of surface currents in Gulf of Mexico, nonsummer conditions

the wide west Florida shelf, Fig. 4-17b, 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. 4-17a.

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 northeastern 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

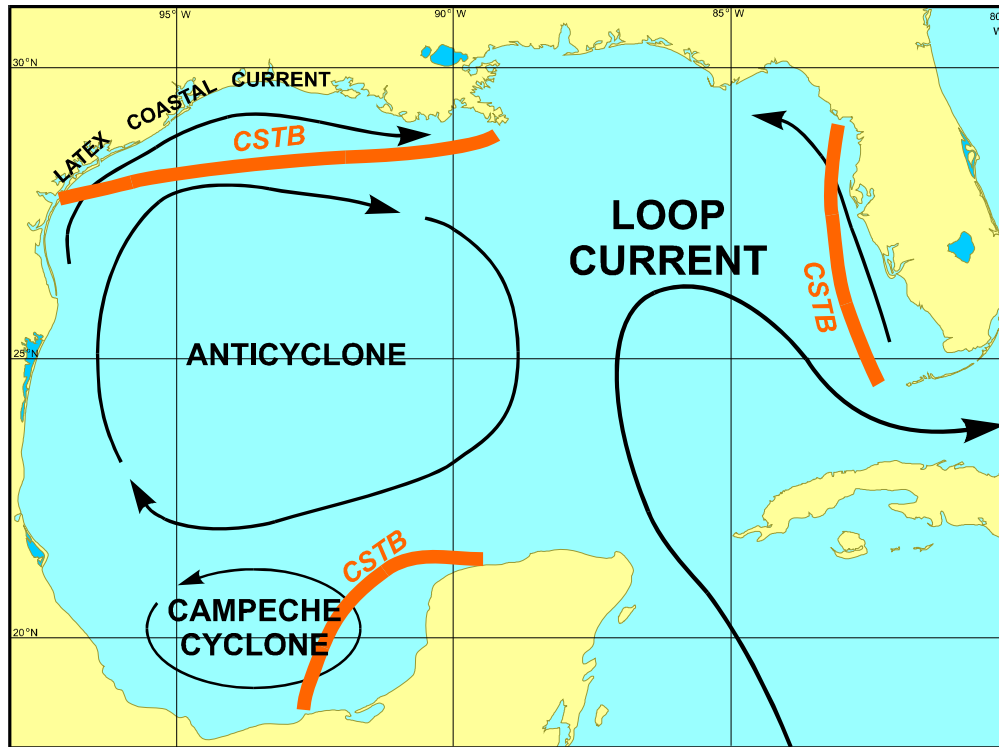


Figure 4-17b - Schematic of surface currents in Gulf of Mexico, summer conditions. CSTB denotes cross-shelf transport barrier, see text.

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 Structure (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. 4-17b. 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 Louisiana-Texas coast from the Mississippi delta to the Coastal Bend, as well as one adjacent to Yucatan, also shown in Fig. 4-17b. 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 Louisiana-Texas (LATEX) coastal current sets west then southwest down the coast paralleling the isobaths, Fig.4-17a. In late summer, July through August, it reverses, setting northeast along the south Texas coast, then east along the east Texas coast, see Fig. 4-17b. Its speed is about 5 km/day, but varies a factor of two or more about this mean. As noted in Section 4.4.2, 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 above).

4.4.3.3 Summary

This brief survey of the blue crab larva's sojourn on the nearshore and shelves has now grown larva-like to mimic 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 crabs 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 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, it is not clear that there is a mechanism to return these larvae to the nearshore. However, 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 mechanism in 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.
- (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 truer for the Texas coast, where there has been much less observational research on the development, transport and distribution of megalops.

4.4.4 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 4.1.3), 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.

4.4.4.1 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, McConaugh, 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 4.4.2 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.

4.4.4.2 Mechanism

Another aspect of megalop reinvasion that was controversial during the last two decades of the twentieth century was the mechanism of reinvasion. Among the proposed mechanisms were 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 4.3.1.2). 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 4.3.1.2.

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 4.3.1.1). 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., 2005). 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 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 their 16-month study of Mense and Wenner (1989) in tidal creeks around Charleston Harbor 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 4.3.1.2 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.

4.4.4.3 Settlement

Observations of settlement of megalops have confirmed its rôle as the main recruitment stage of the blue crab (e.g., Orth and van Montfrans, 1987). The swimming ability of megalops (Section 4.1.3) 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 4.2.3, 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). (*Cf.* 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 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 settle instead 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 instars this young. However, it is likely some megalops settle in unsatisfactory regions and perish.

4.4.4.4 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 Institute 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 the “clinging” (thigmotactic) response of the megalops, 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 substrates 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 4-18. 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. 4-18.

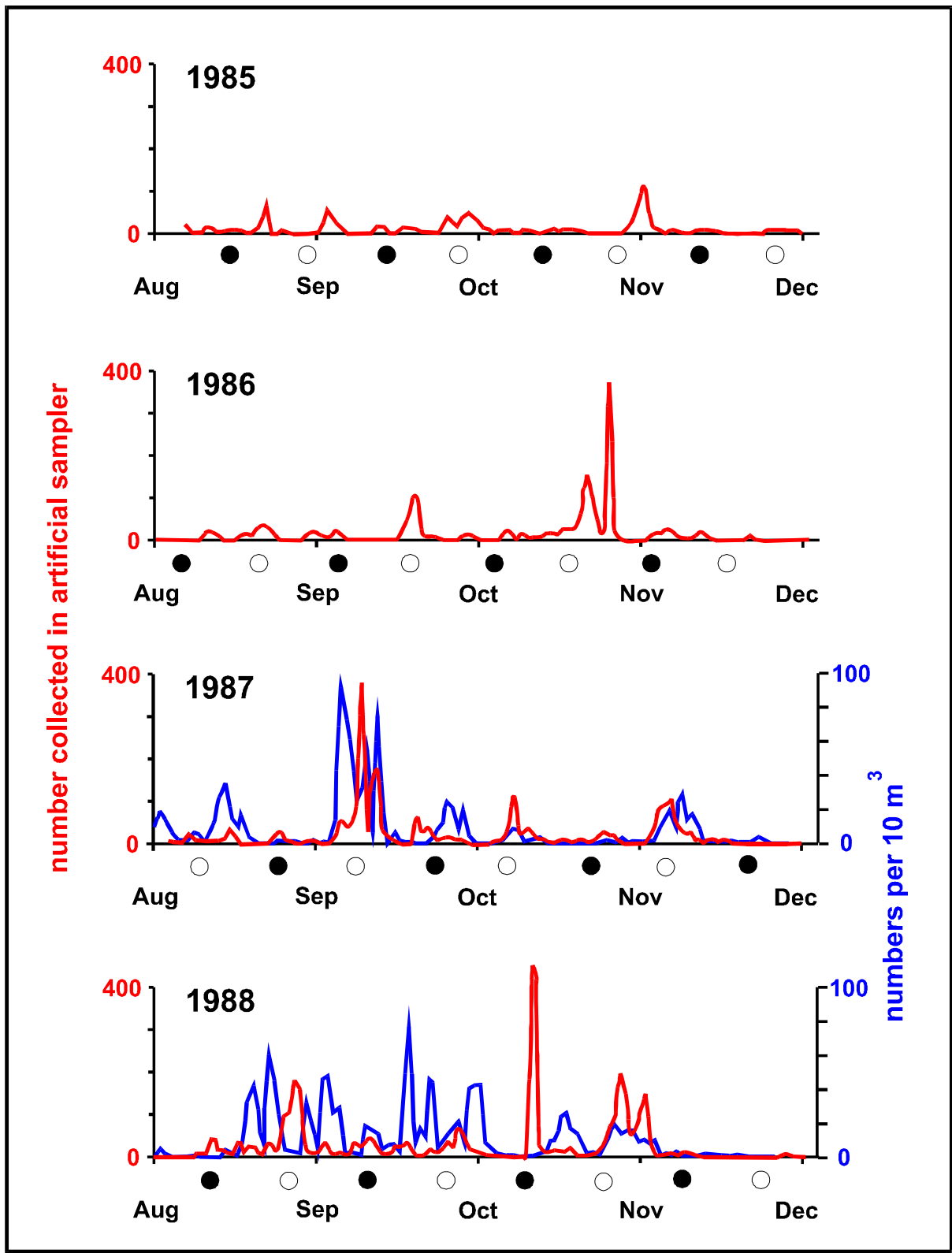


Figure 4-18 - Time histories of daily megalop collections on artificial substrates (red) and plankton nets (blue) in York Estuary, lower Chesapeake Bay, showing association with lunar phase. Redrawn from van Montfrans et al. (1990) and Olmi (1995).

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 (indicating northeasterly winds on the mid-Atlantic coast) or the direct stress of wind (indicating 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 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 ofmax 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. 4-18. 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 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).

The 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 4-7. 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

Table 4-7
Deployment sites for coordinated artificial-substrate monitoring
by the Blue Crab Recruitment Group, see text

<i>Site</i>	<i>Estuary</i>	<i>Monitored</i>	<i>Relevant citations</i>
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 Fontaine 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)

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 4-19 and 4-20, 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 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 4-7, 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 (see Section 3.2 and Ward, 1997). They found that pulses of settlement were strongly associated with onshore (south) winds, when these winds were strong, and with small declination tides. Winds

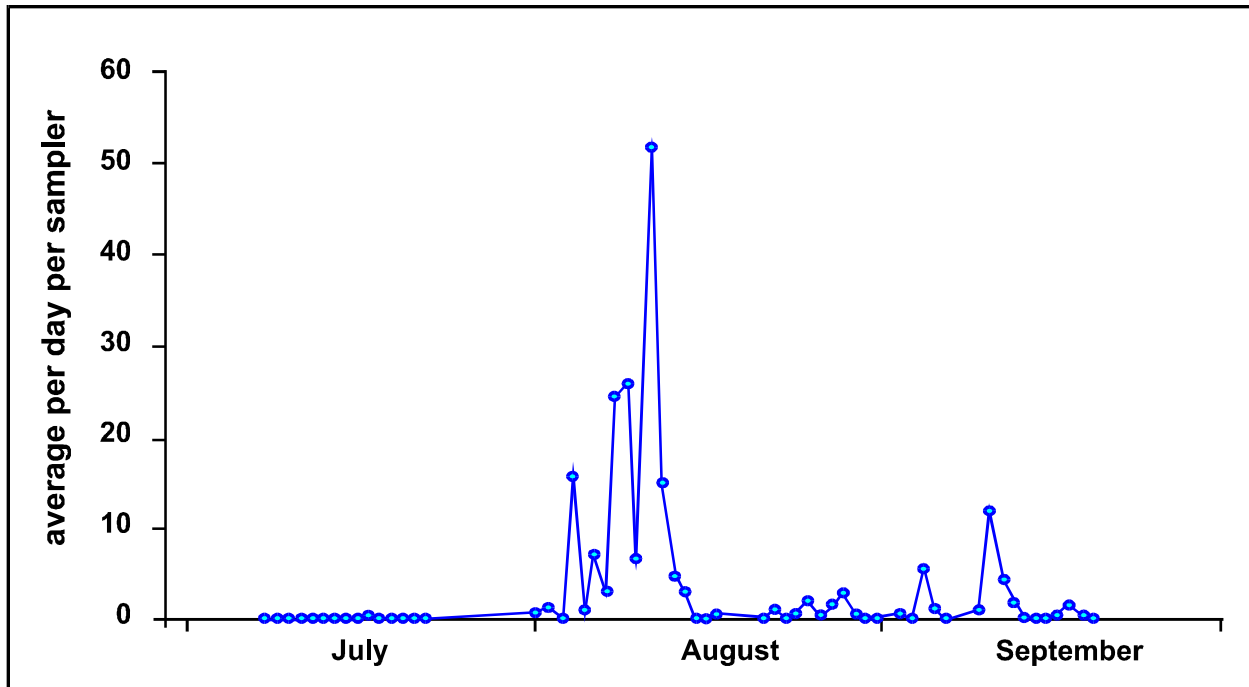


Figure 4-19 - Times series of megalop data from artificial substrates at Hatteras Inlet Coast Guard Station, data of Mense et al. (1995) replotted

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-

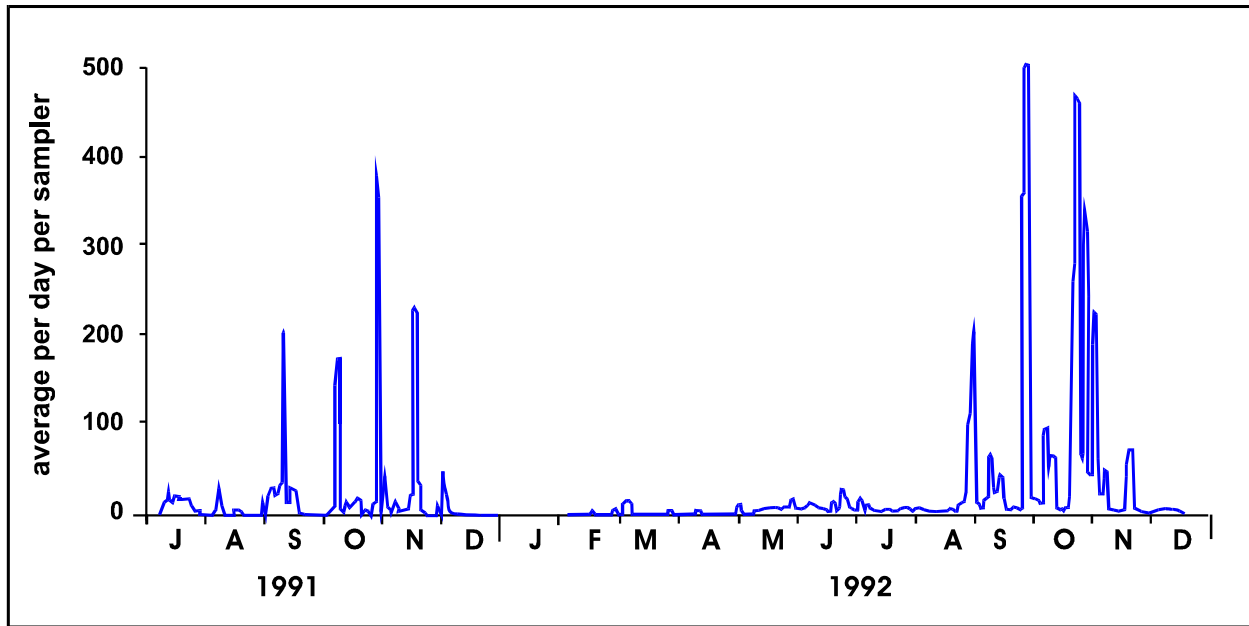


Figure 4-20 - Times series of megalop data from artificial substrates at Galveston Coast Guard Station, data of Rabalais et al. (1995) replotted

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 4.3.4 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 growth 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 4.4.3), neglecting tides and variation in longshore current. “Settlement” in the model occurs when larvae ascend to the megalop stage at the entrance of the estuary. This model roughly simulated the four years of megalop data from the Broadkill (Table 4-7), 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 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 4-7). An example from the four years of simulation is shown in Figure 4-21. 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 4-21 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

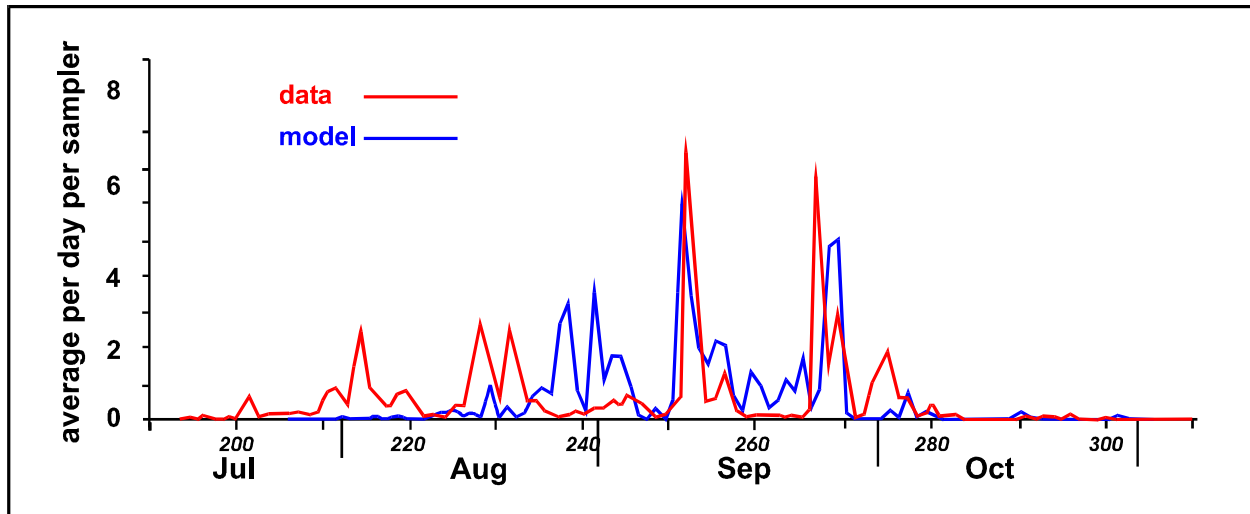


Figure 4-21 - Observed (red) and modeled (blue) times series of megalop data from artificial substrates at Broadkill station, Delaware Bay, see Table 4-7. From Garvine et al. (1997) and Tilburg et al. (2008b) replotted

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 artificial-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 flood tides. 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 artificial-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, which is measured by a conventional plankton net. This is suggestive that the collector is related to the planktonic density of megalops. The comparison of plankton density of Omni (1995) with collector data of van Montfrans et al. (1990) in the York, shown in Fig. 4-18, 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.

4.4.5 Recruitment and the rise through the ranks

4.4.5.1 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. 4-12) 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 4.4.4, 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. 4-12) appear in the marsh creeks, evidently migrating from the seagrass beds. After they exceed about 16-20 mm (ninth or tenth instars, Fig. 4-12), 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 Chesapeake 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 Harbor 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).

4.4.5.2 *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) concludes 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 Louisiana (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% by 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. 4-12) 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 4.2.1, 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, 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 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 4.4.1). 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.

5. THE BLUE CRAB IN SAN ANTONIO BAY

This purpose of this chapter is to illustrate and exemplify the distribution of blue crab in space and time in the San Antonio Bay system, and relate this distribution to the general life cycle principles summarized in Chapter 4.

5.1 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 as a function 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 N. 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.)

* 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. 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 5-1
1986-2005 average biomass density of seined and trawled blue crabs
in TPWD Coastal Fisheries collections by major bay system, in mg/m³

<i>estuary</i>	<i>bag seine</i>	<i>otter trawl</i>	<i>estuary</i>	<i>bag seine</i>	<i>otter trawl</i>
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	<i>average over all bays</i>	96	86

5.2 General assessment of blue crab abundance

In Table 5-1, 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 4-1), 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 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 N, 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 5-1.

* 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.

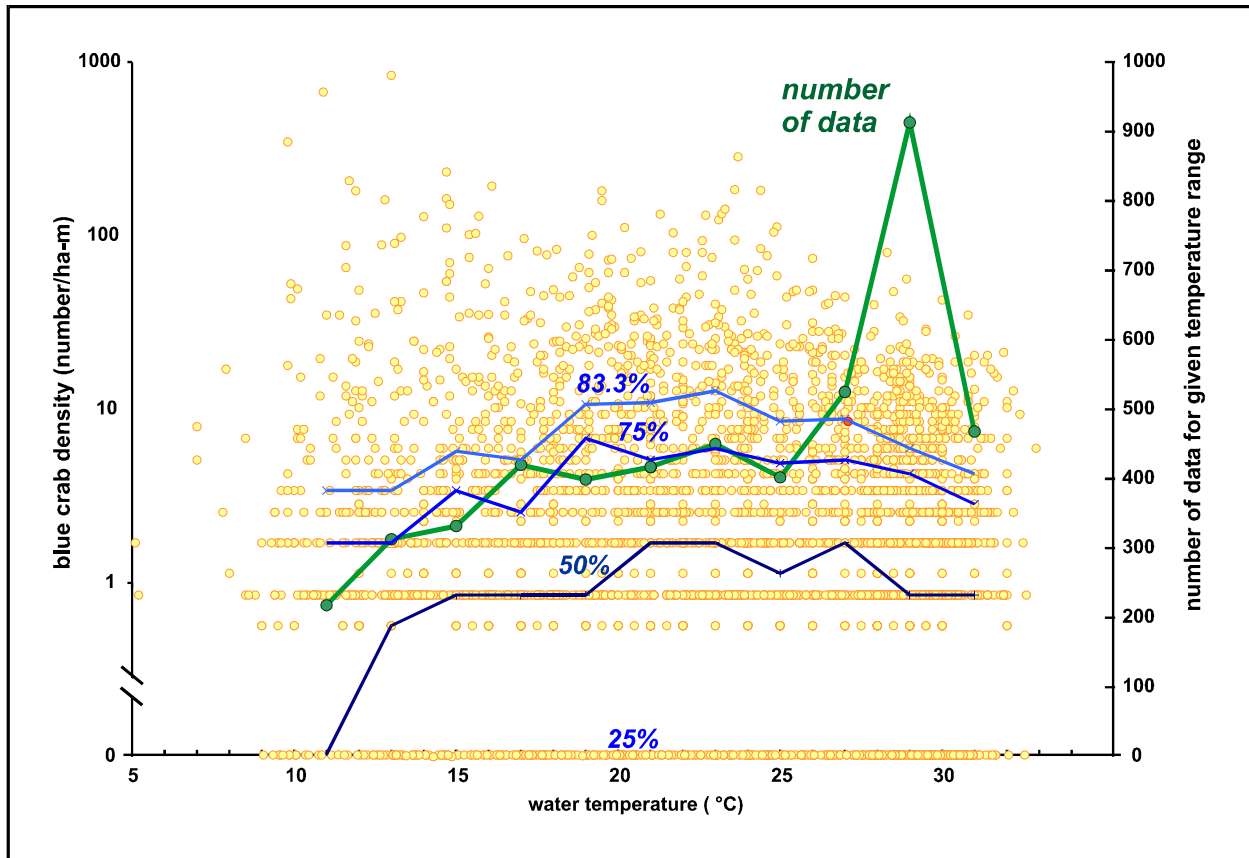


Figure 5-1 - Blue crab density for all 1982-2008 otter-trawl samples from San Antonio Bay vs concurrent water temperature (small filled circles), quantile values (lines) based on 2-degree bins, see text. Density values plotted on logarithmic axis, except for values below 0.5.

An inspection of Table 5-1 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.

The obvious first analysis is to examine the relation between crab abundance, as measured by volumetric density, and primary environmental parameters. Figures 5-1 and 5-2 display the

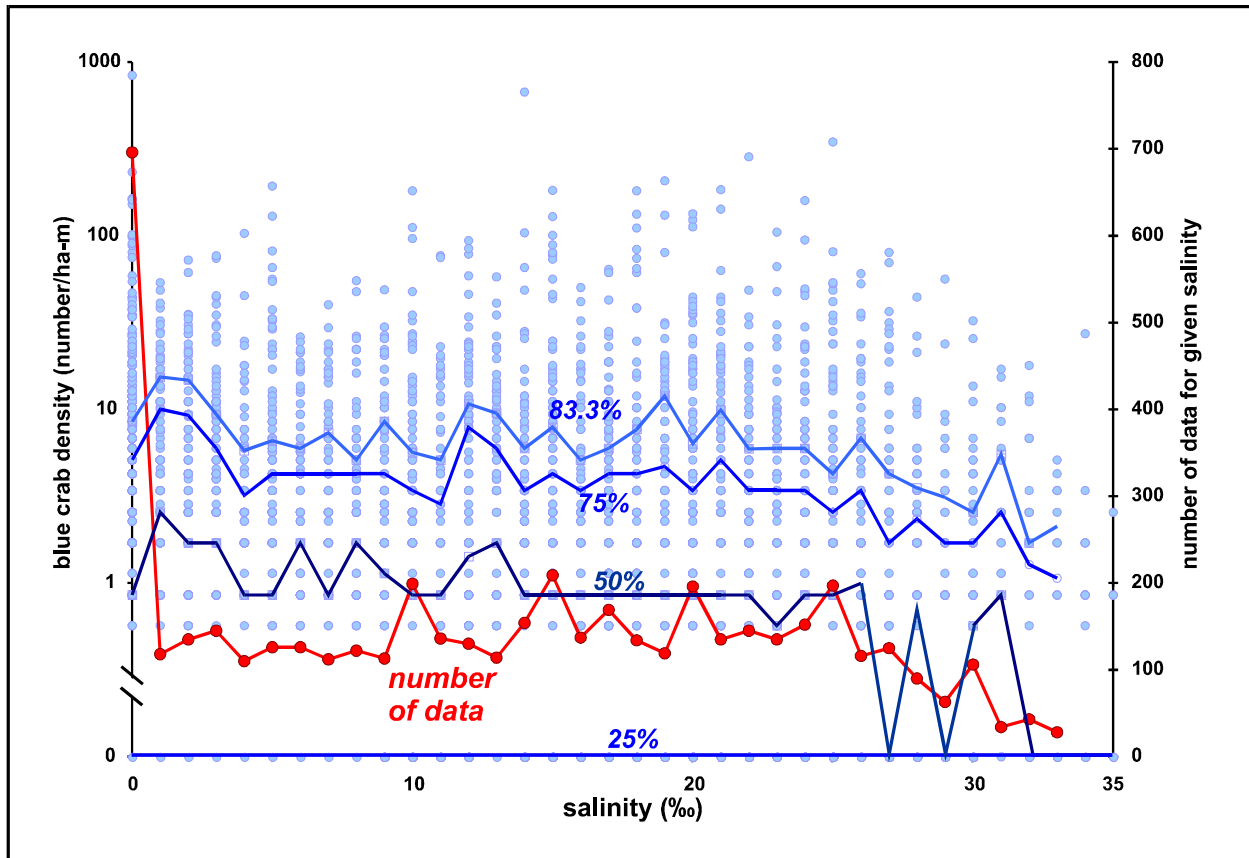


Figure 5-2 - Blue crab density for all 1982-2008 otter-trawl samples from San Antonio Bay vs concurrent salinity (small filled circles), quantile values (lines) based on 1-part-per-thousand bins, see text. Density values plotted on logarithmic axis, except for values below 0.5.

individual trawl values of blue-crab density from San Antonio Bay (the entire area depicted in Figure 5-4, 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 tows. The selected quantiles are 16.7% (lower hexile), 25% (lower quartile), 50% (median), 75% (upper quartile), 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 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

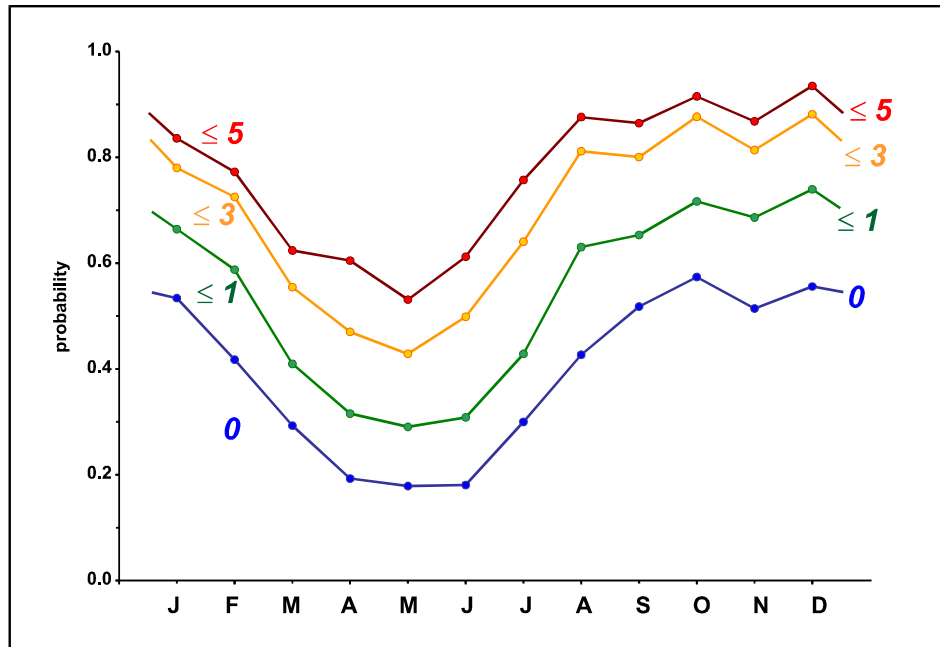


Figure 5-3 - Probability of catching the indicated number of blue crabs in the TPWD otter trawl, from data of 1982-2008

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 5-3, which plots the probability of catching a given number of crabs, from 0 to 5, in the TPWD otter trawl as a function of season. If the blue-crab density data are plotted on a linear ordinate in Figs. 5-1 and 5-2, 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.

5.3 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 5-4. The distribution by segment, and by temperature or salinity are tabulated in Tables 5-2 and 5-3, 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 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. 5-3. Although the peaks in abundance are not reflected, there is an increased probability of catching more than five crabs during the March - June period. A better depiction is Figure 5-5, 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

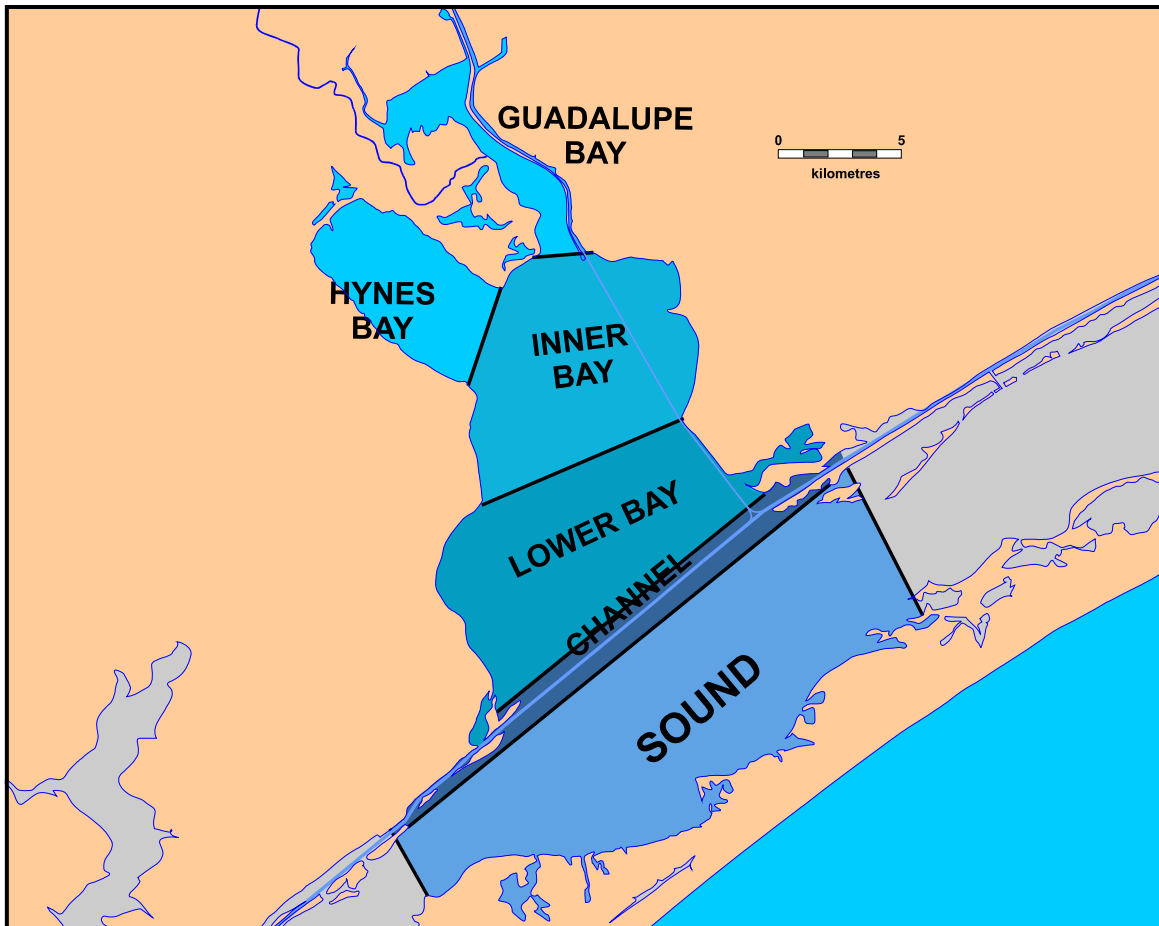


Figure 5-4 - Segmentation of San Antonio Bay for analysis of blue crab distribution. Channel segment is ± 1 km from axis of Gulf Intracoastal Waterway.

rather closely. More detail on seasonal variation in size statistics is shown in Figure 5-6, which includes means \pm standard deviation, and medians, quartiles and outer hexiles for each month. In Fig. 5-5, 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. 4-6. 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 4.4.5.2 above) where they could be trawled. Recruitment of a size range more or less evenly distributed about 60mm would be consistent with the increase in abundance with no alteration to

Table 5-2
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. 5-4.
Entry omitted when number of trawls < 20.

<i>temperature range (°C):</i>	<i>Guadalupe</i>	<i>Hynes</i>	<i>Inner</i>	<i>Lower</i>	<i>Channel</i>	<i>Sound</i>
	(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

the mean or median of the distribution, as indicated by Fig. 5-5. 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 90mm. 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 90mm. One scenario that would entail this result is a loss of crabs of sizes evenly distributed about 90mm. 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. 4-13). The loss of crabs smaller than median might be simply due to predation. The fourth period is September – December, during which abundance, though

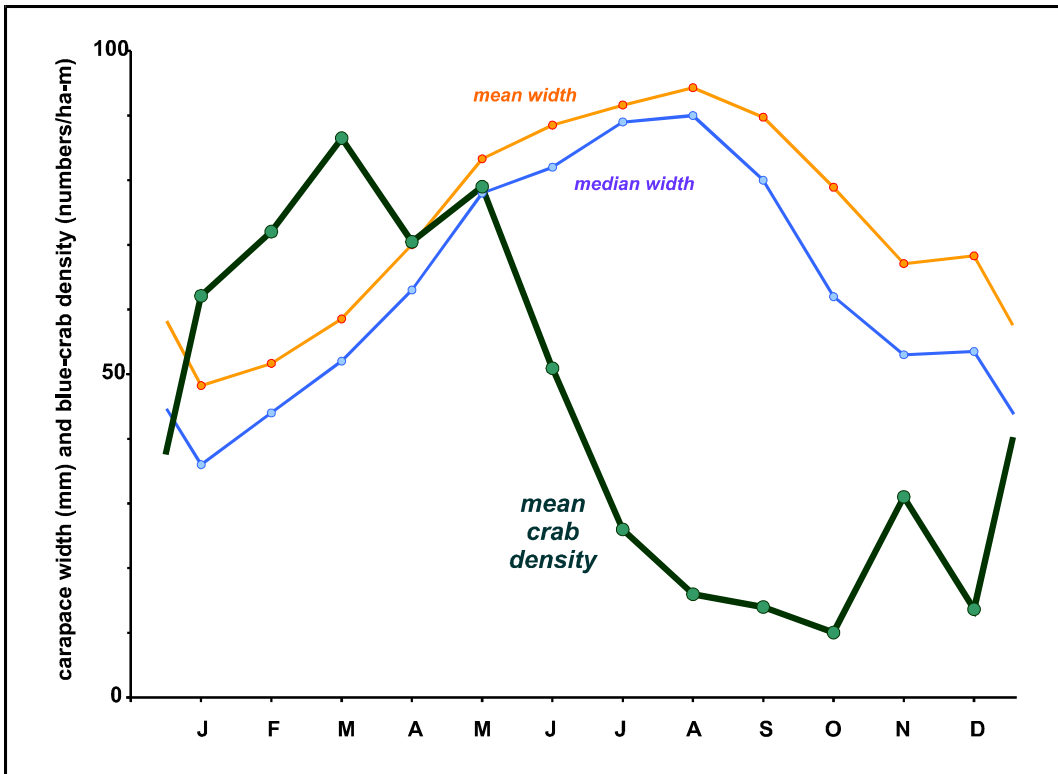


Figure 5-5 - Monthly mean variation of blue-crab density and carapace width, from TPWD 1982-2008 otter-trawl data

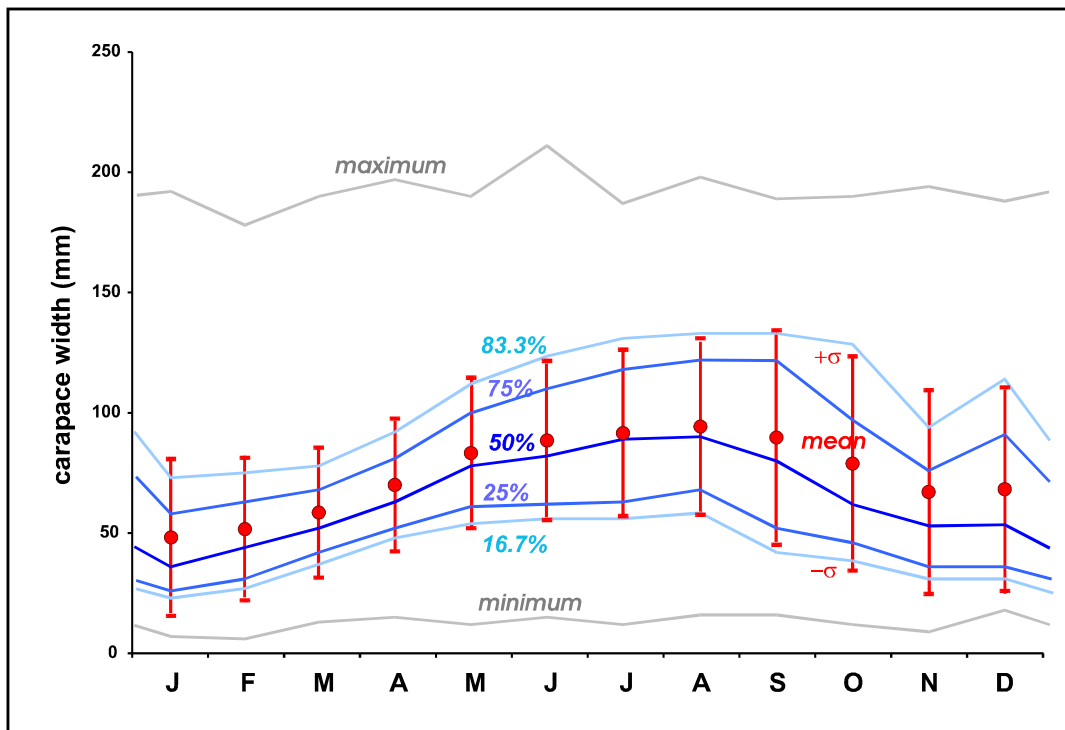


Figure 5-6 - Statistics of blue-crab size from TPWD 1982-2008 otter-trawl data

Table 5-3

Average densities of trawled blue-crab in number/ha-m, in incremental salinity ranges, and in San Antonio Bay segments shown in Fig. 5-4. Entry omitted when number of data < 20.

<i>salinity range (‰):</i>	<i>Guadalupe</i>	<i>Hynes</i>	<i>Inner</i>	<i>Lower</i>	<i>Channel</i>	<i>Sound</i>
(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

variable, exhibits no systematic decrease or increase, while the mean and median shift downward to smaller sizes. A 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. 4-6. 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. 5-5 and 5-6 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. 5-5 to identify the calendar periods associated with each feature of the pulse offers a basis for conjecturing the underlying processes.

Table 5-4

Mean monthly densities (nos/ha-m) of blue-crab, 1982-2008 trawl, by bay segment, see Fig. 5-4. Upper Bay aggregates Guadalupe, Hynes & Inner Bay. Outer Bay aggregates Channel & Sound.

	<i>Jan</i>	<i>Feb</i>	<i>Mar</i>	<i>Apr</i>	<i>May</i>	<i>Jun</i>
<i>Guadalupe</i>	7.4	4.1	22.0	20.7	23.7	27.6
<i>Hynes</i>	13.1	58.2	104.6	49.8	64.9	47.5
<i>Inner Bay</i>	33.6	65.2	102.0	84.8	111.9	65.0
<i>Upper Bay</i>	27.3	56.8	94.1	70.2	91.7	57.6
<i>Lower Bay</i>	149.0	66.3	96.0	97.9	101.2	61.1
<i>Channel</i>	178.3	260.3	120.1	154.0	130.2	80.1
<i>Sound</i>	18.7	35.7	62.5	37.3	36.2	28.2
<i>Outer Bay</i>	43.0	90.7	72.4	53.0	49.8	37.0
<i>San Antonio Bay</i>	62.1	72.0	86.5	70.5	79.0	50.9
	<i>Jul</i>	<i>Aug</i>	<i>Sep</i>	<i>Oct</i>	<i>Nov</i>	<i>Dec</i>
<i>Guadalupe</i>	19.9	24.6	7.7	10.4	8.4	6.9
<i>Hynes</i>	37.0	16.6	8.8	9.4	19.9	3.8
<i>Inner Bay</i>	29.1	22.3	18.8	8.8	10.7	15.5
<i>Upper Bay</i>	29.6	21.2	15.2	9.1	12.9	11.9
<i>Lower Bay</i>	30.1	16.0	13.6	10.9	10.9	21.5
<i>Channel</i>	29.2	23.1	22.0	24.9	128.5	17.0
<i>Sound</i>	17.1	6.7	11.0	6.8	36.6	7.9
<i>Outer Bay</i>	19.4	10.1	13.0	10.4	60.1	9.7
<i>San Antonio Bay</i>	26.0	16.0	14.0	10.0	31.0	13.6

The segmentation of Fig. 5-4 was used to display the spatial aspects of the monthly variation of blue-crab distribution in San Antonio Bay. Table 5-4 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. 5-7 for the six geographical segments and in Fig. 5-8 for the regional segments. (The averages over the entirety of San Antonio Bay listed in the last row of Table 5-4 are shown in Fig. 5-5.) While this data is noisy, it does not show a

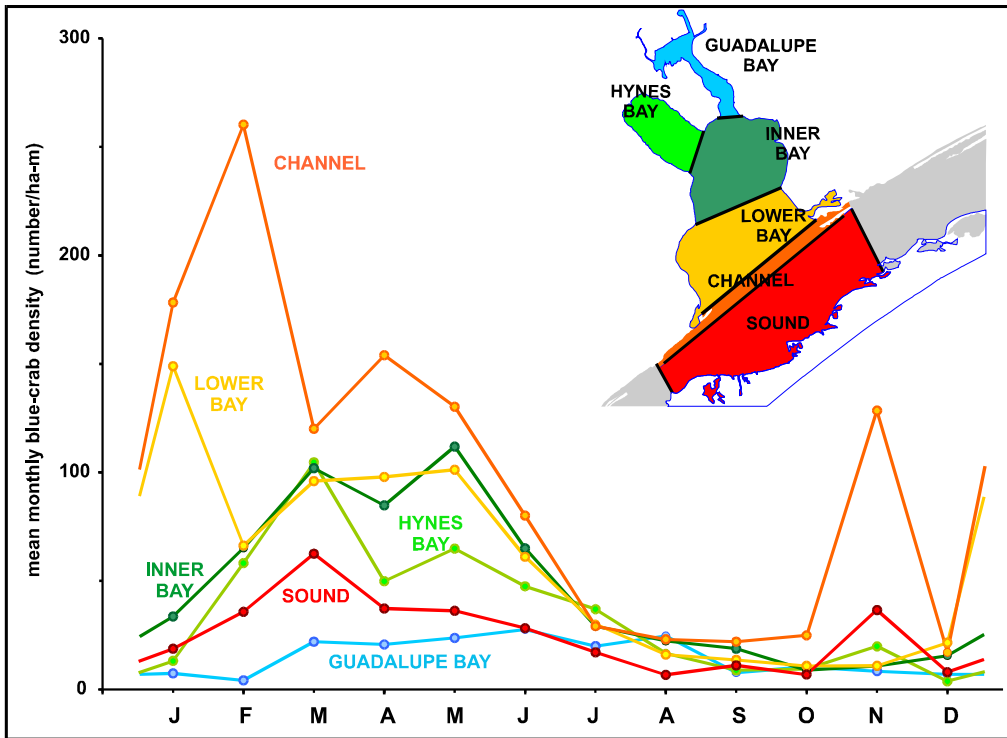


Figure 5-7 - Average monthly blue-crab density in 1982-2008 otter trawl, distributed into segments of Fig. 5-4, see also Table 5-4.

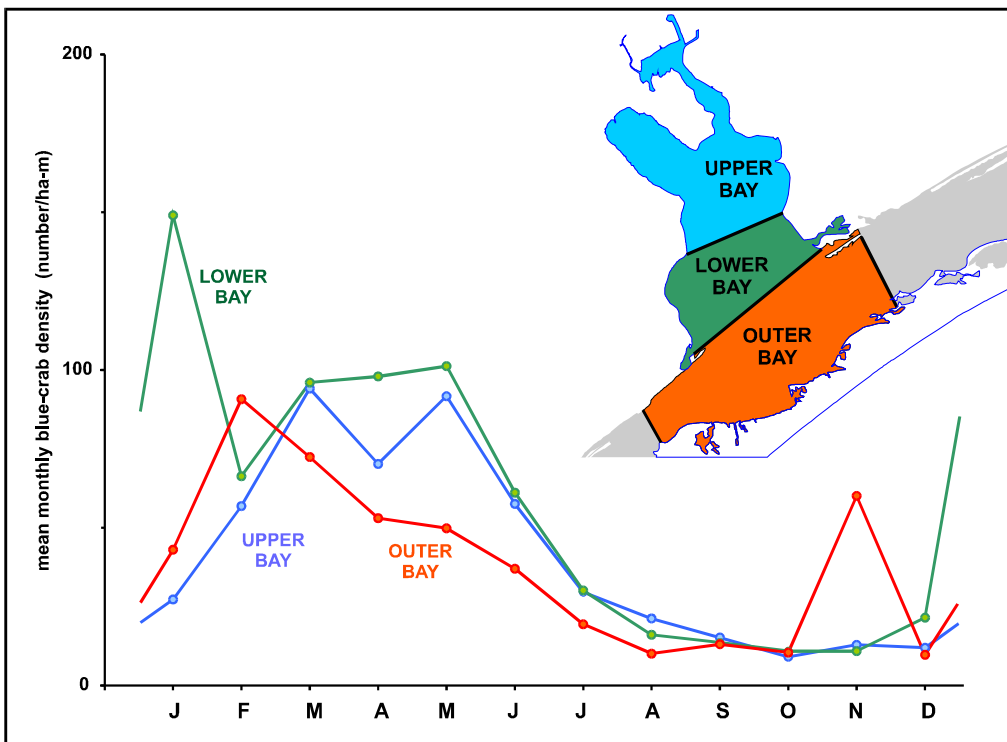


Figure 5-8 - Same as Figure 5-7, except aggregating data over larger “regional” segments. Upper Bay combines Guadalupe Bay, Hynes Bay and Inner Bay, and Outer Bay combines Channel and Sound.

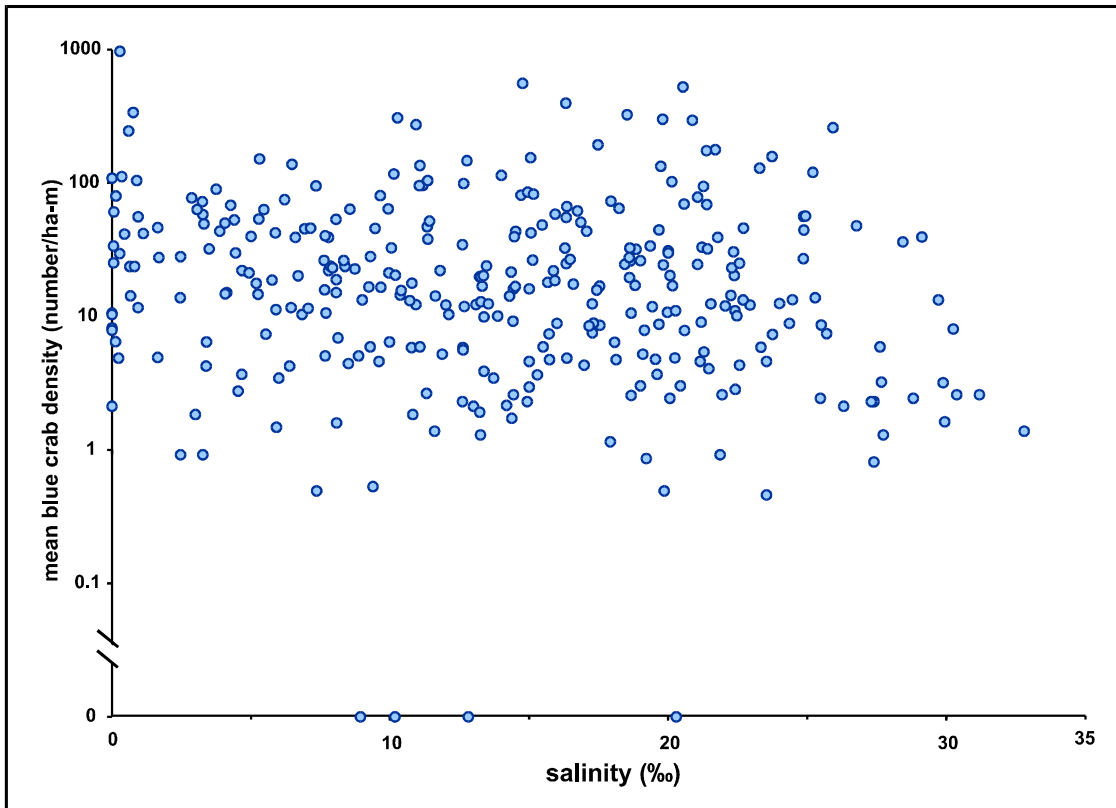


Figure 5-9 - Monthly-mean bay-average blue crab density versus corresponding averaged salinity, from 1982-2008 otter-trawl data. Densities greater than 0.1 no/ha-m logarithmically transformed.

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 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 5-7 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. 5-8 (see also Table 5-4) 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.

5.4 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. 5-5 *et seq.* above. The monthly density data are still skewed positive, dominated by small values, but, unlike the individual trawl-event data of Figs. 5-1 and 5-2, there are few months with exactly zero mean density. Re-examining the variation with salinity, displayed in Figure 5-9, 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 averaged inflow. As might be expected, the monthly mean inflow also proves to have high positive skew. To exhibit their direct correlation, Figure 5-10 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 is 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 5-5. (Salinity was included 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

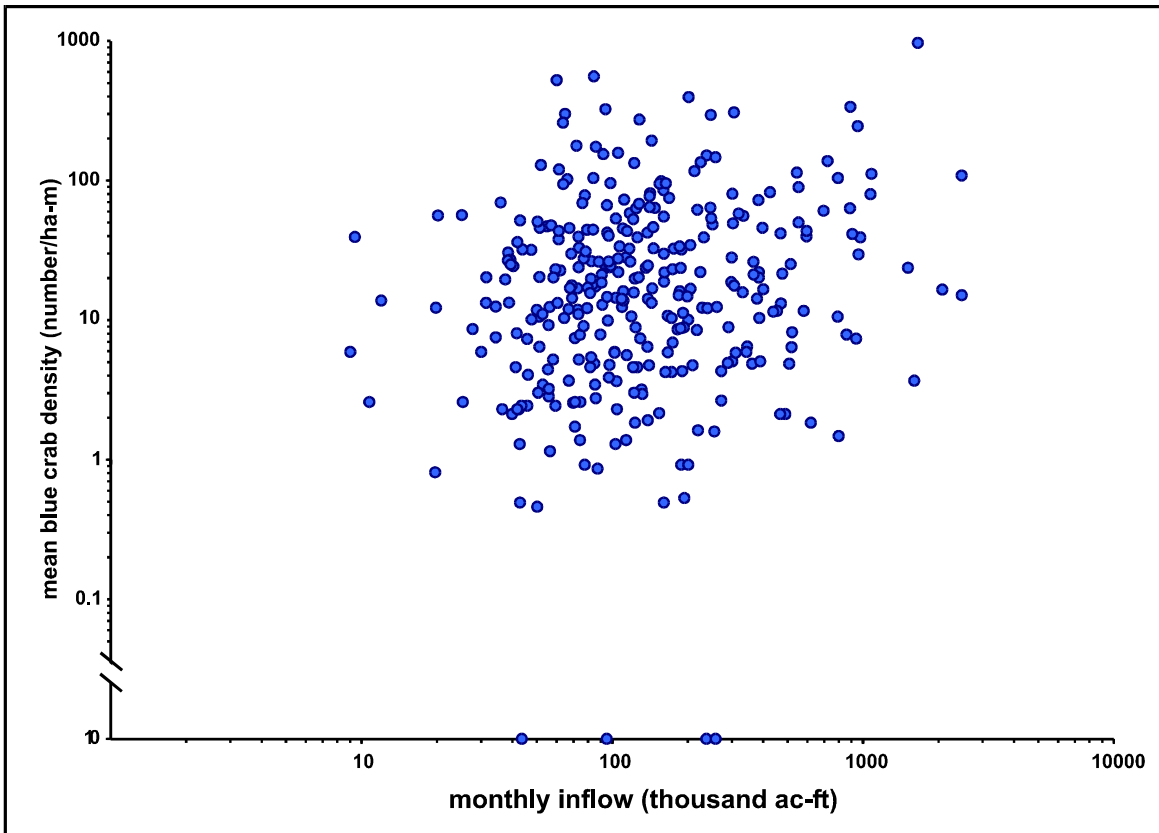


Figure 5-10 - Monthly-mean bay-average blue crab density versus corresponding mean inflow, from 1982-2008 otter-trawl data. Densities greater than 0.1 no/ha-m and flows logarithmically transformed.

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).

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 5-11. There is a clear seasonal pulse in abundance that varies in magnitude from year to year. However, the timing of the pulse

Table 5-5

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

<i>Lag</i> (mos)	<i>correlation with:</i>		<i>Lag</i> (mos)	<i>correlation with:</i>	
	<i>salinity</i>	<i>inflow</i>		<i>salinity</i>	<i>inflow</i>
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			

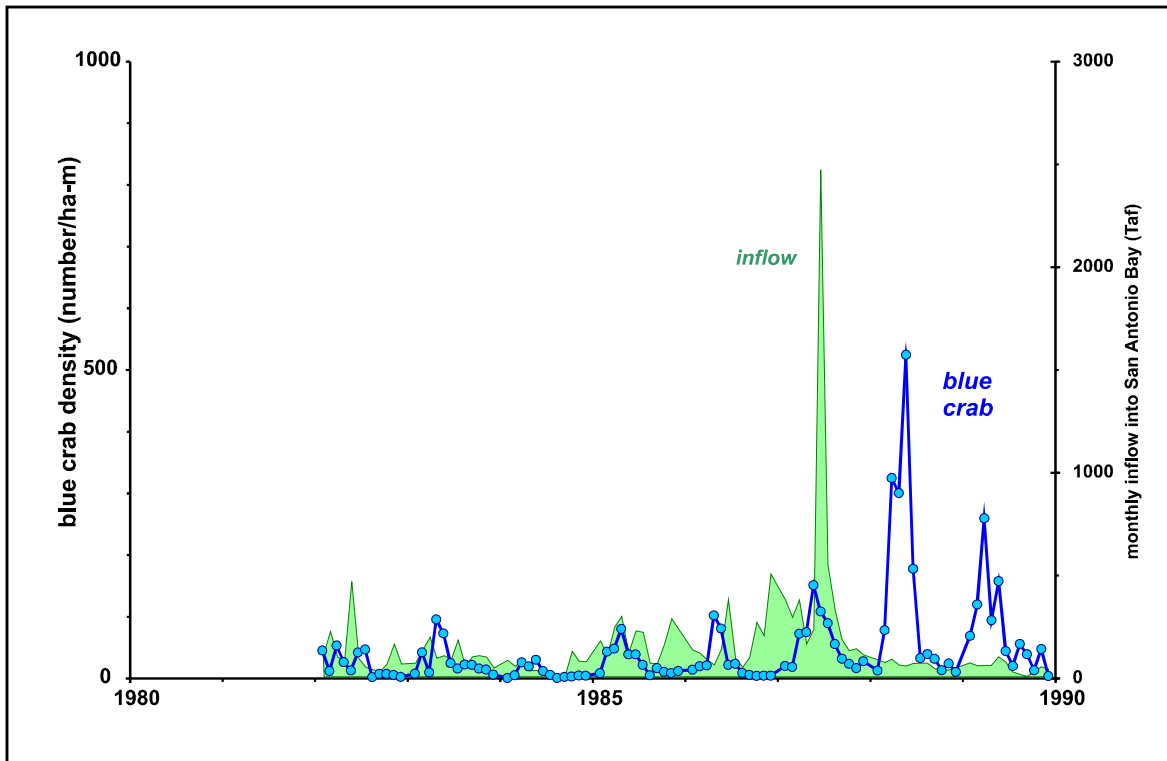


Figure 5-11a - Time series of blue crab density in San Antonio Bay, 1982-1989

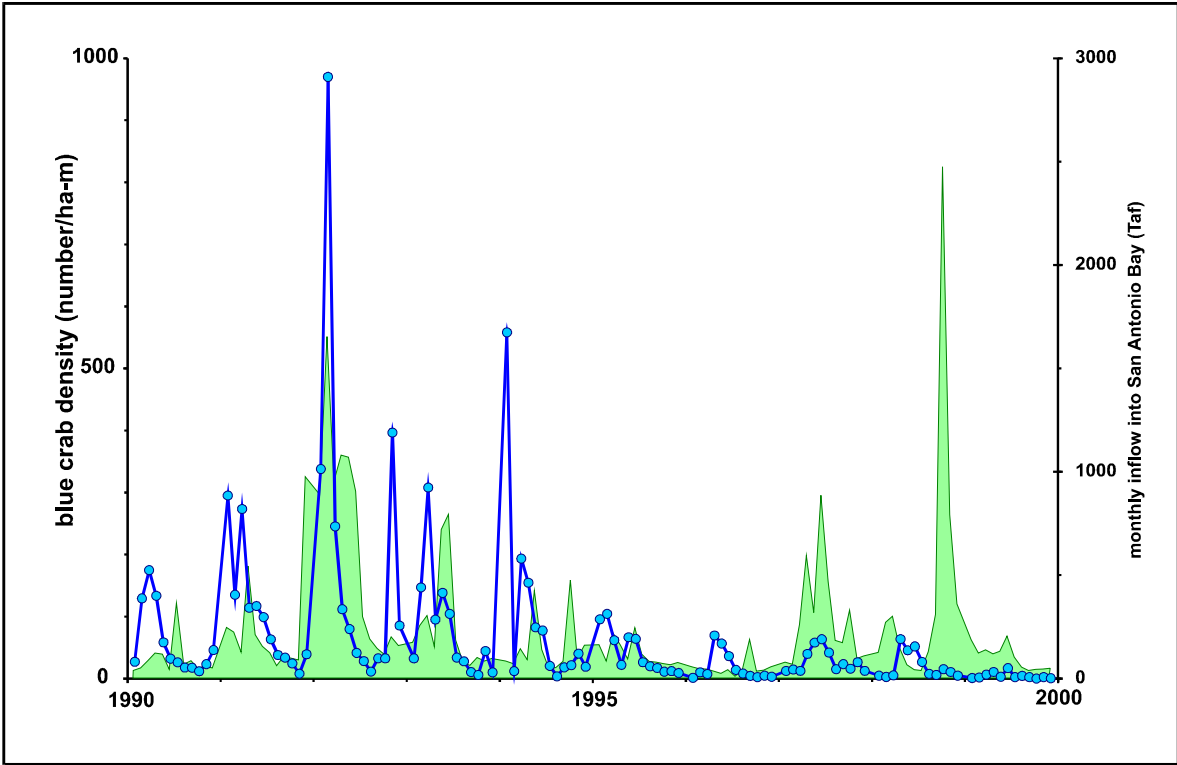


Figure 5-11b - Time series of blue crab density in San Antonio Bay, 1990-1999

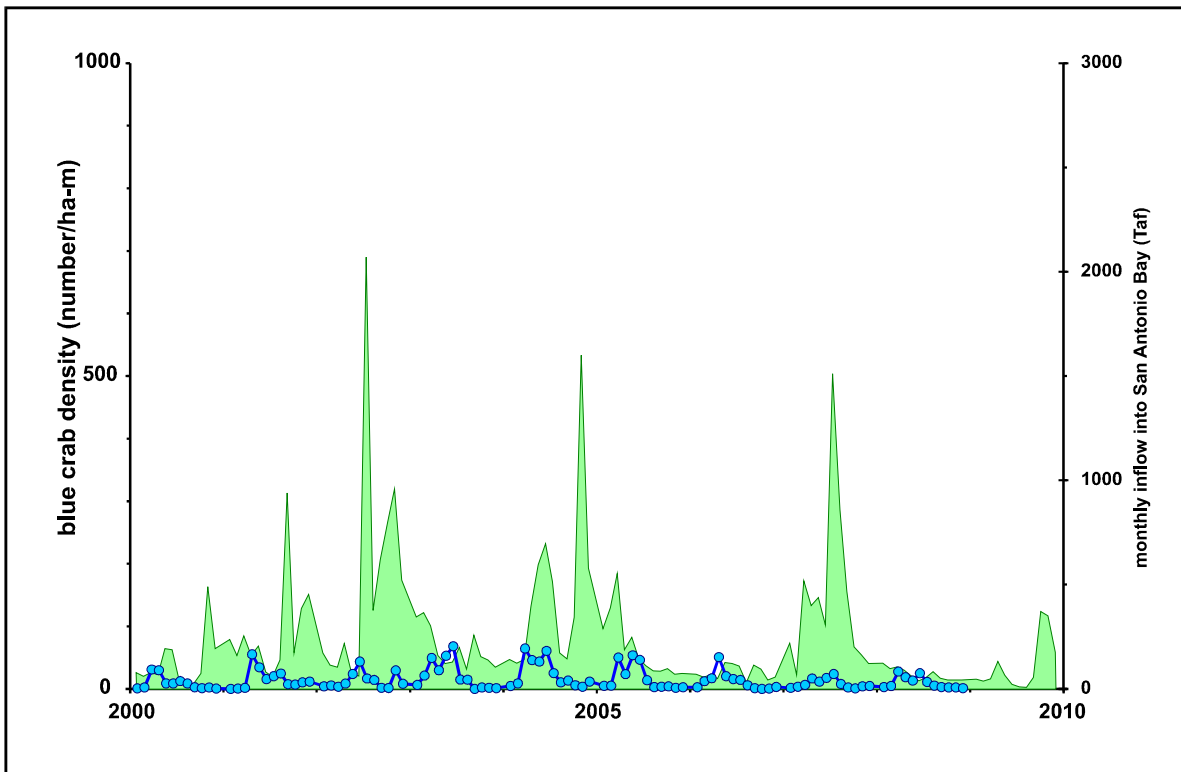


Figure 5-11c - Time series of blue crab density in San Antonio Bay, 2000-2008

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.

This kind of variability would certainly erode correlation with monthly salinity, e.g. Fig. 5-9, but this may be a result of applying linear methods to what is much more complex behavior. With respect to inflow (see Chapter 2), monthly values of which are also plotted in Fig. 5-11, 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.

5.5 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 averaged over the Texas bays versus year, shown in Figure 5-12. 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 5-13, 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.

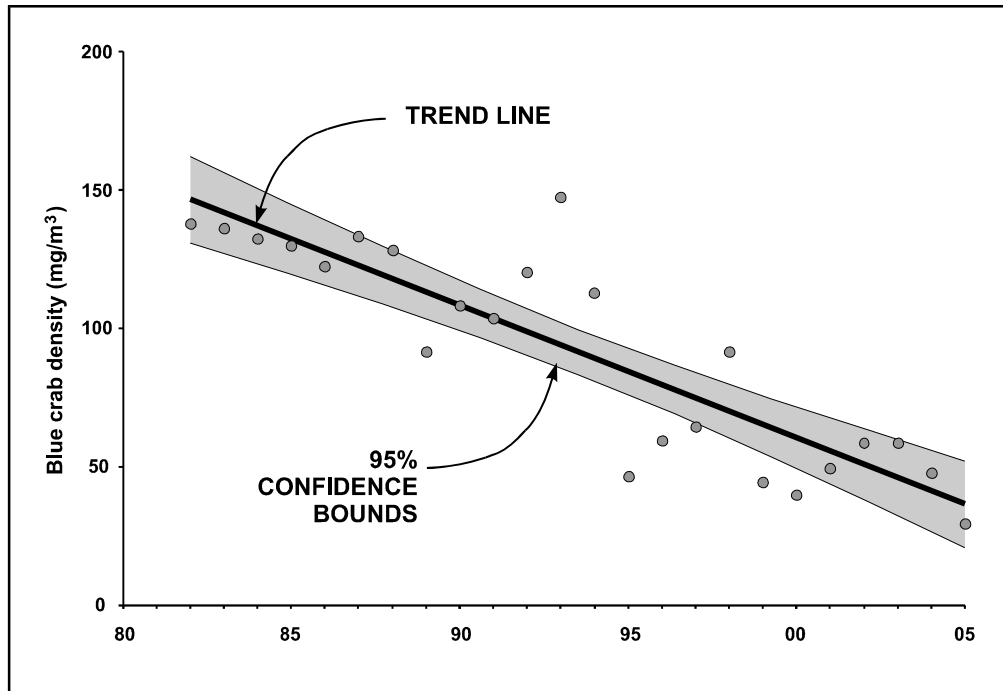


Figure 5-12 - Annual blue crab biomass, collected in TWPD otter trawl samples 1982-2005, averaged over all bays, showing regression line versus year with 95% confidence band on regression

The 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 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

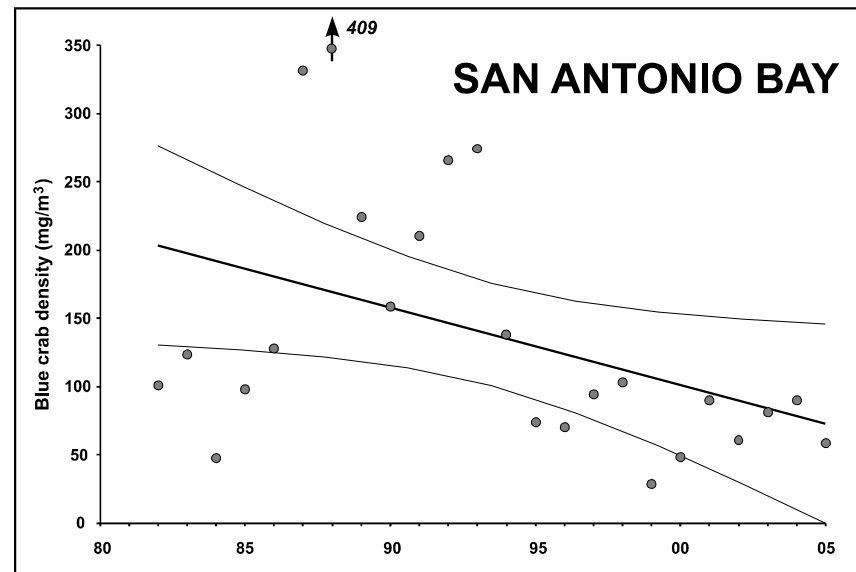
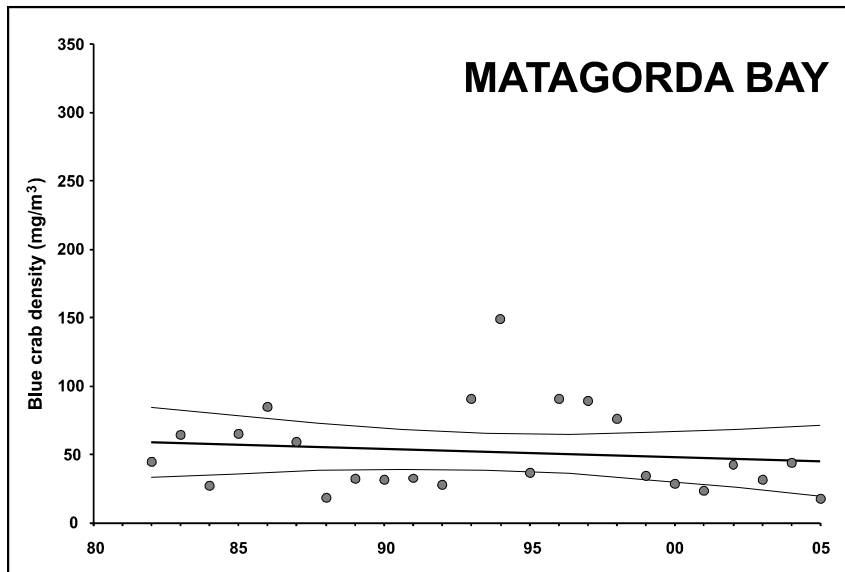
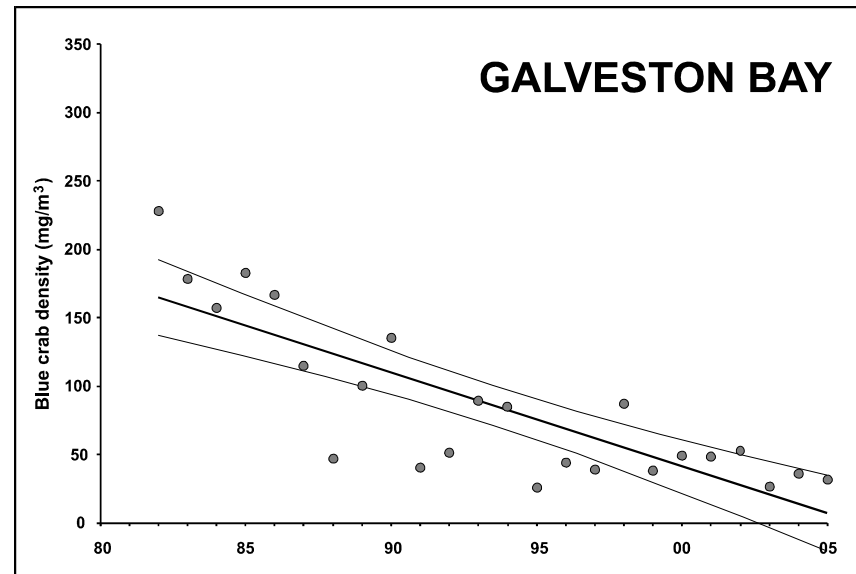
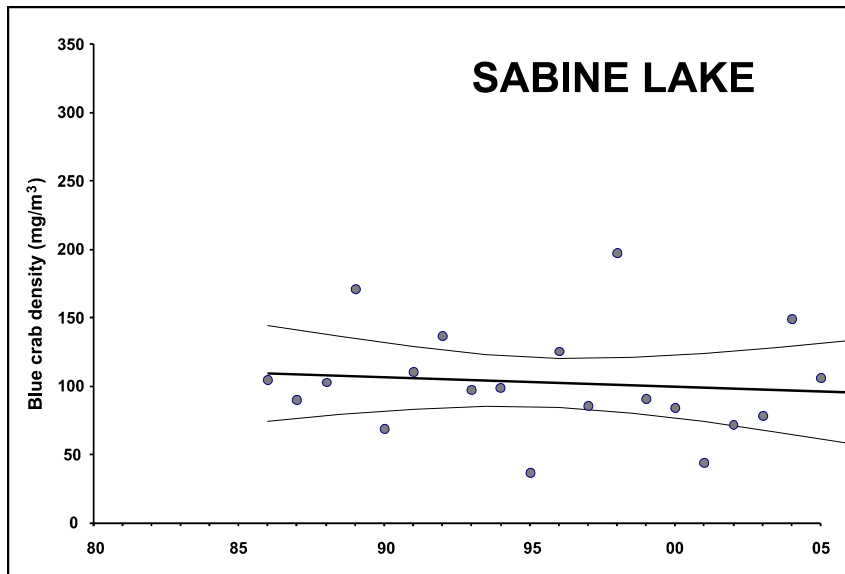


Figure 5-13 - Time trends in annual otter-trawl biomass for each major bay, 1982-2005, with 95% confidence bounds on regression

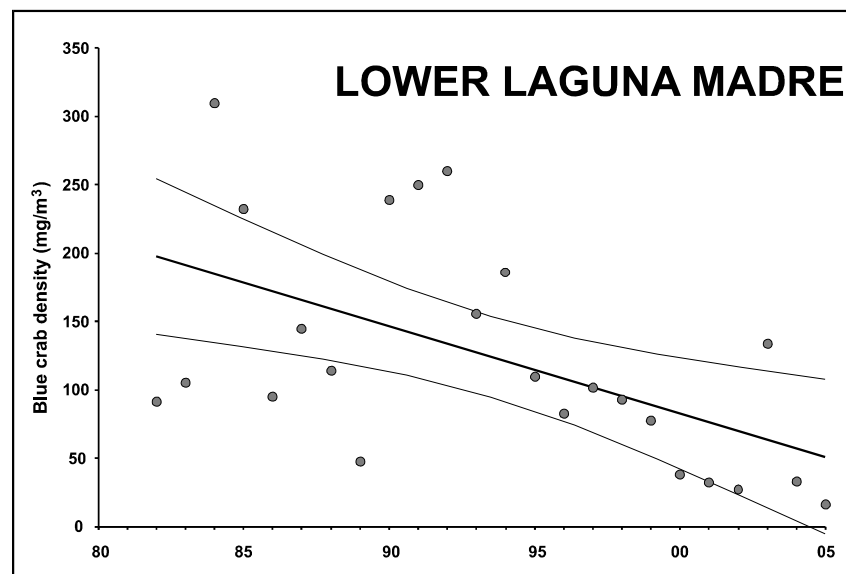
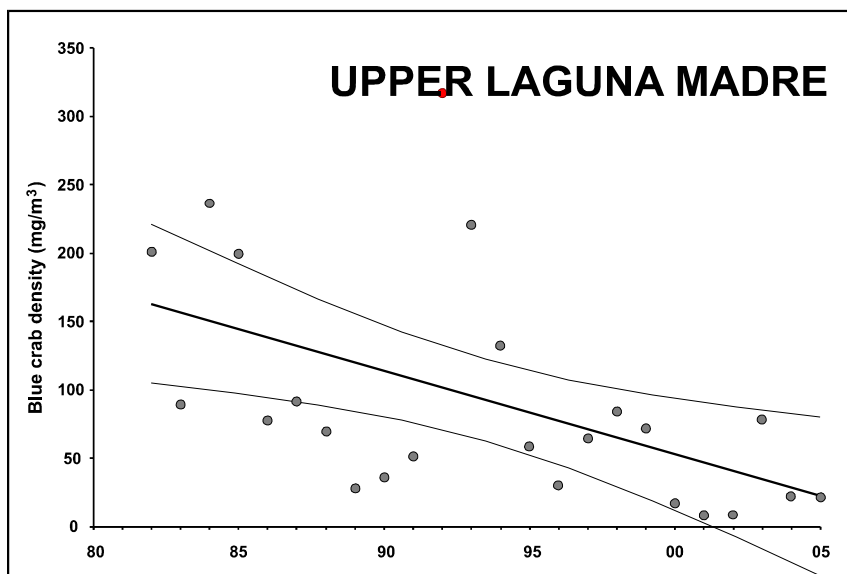
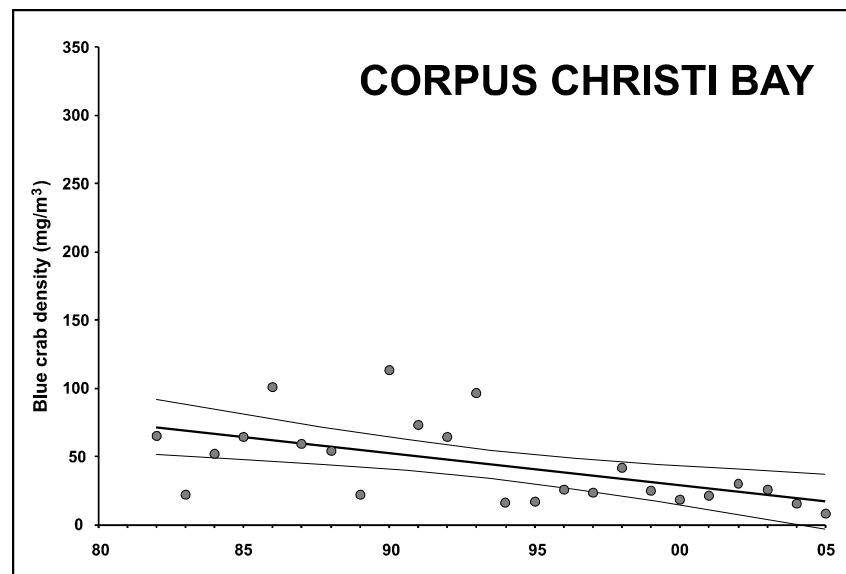
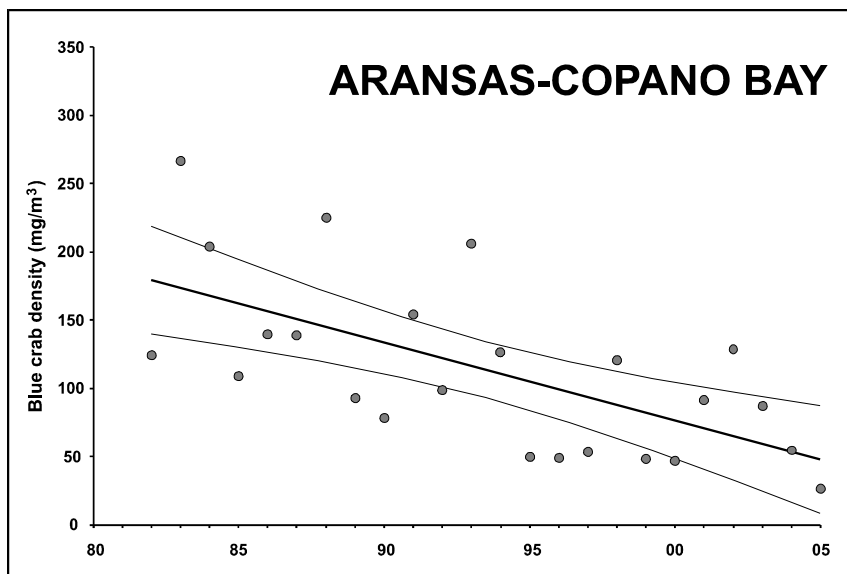


Figure 5-13 - Continued

project to determine the extent to which its status could be an explanatory variable for fluctuations in blue crab abundance. As reported in Chapter 3, 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 Section 3.4), and therefore unlikely to have significantly affected the abundance of crabs 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. 5-11a 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. 5-11b) 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. 5-13, 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. 5-11). 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.

5.6 The blue crab life cycle in San Antonio Bay

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. 4-6), 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 4.2.1). 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-postlarval (Section 4.2.3 and 4.3.2), *viz.* high salinity above 20‰ and warm temperatures 25-30°C. 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 5-1). 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 5.4). 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 the sudden reduction of salinity to zero during a major flood hydrograph (Section 4.3.2.2). The negative correlation of blue-crab density in San Antonio Bay with 2-3-month lag after inflow (Table 5-5) 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 4.1.3), 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 4.3.1.2). 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 4.4.4.3), and the time variation in salinity induced at any fixed point in the estuary by the current (Section 4.3.1.2).

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 4.3.1.2). 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 (Section 3.2, Ward, 1997), will be directed inland from the sea, and the associated salinity change may serve as a cue for selective current transport. 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 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 4.2.1, 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 4.2.2). 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 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). It may be that 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 4.3.2).

The domination of Chesapeake Bay in research on the blue crab life cycle (Sections 4.4.1 and 4.4.5) 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 suggested by the graphic of Figure 5-14. 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 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 4.4.1), consisting of the cold, winter period of crab inactivity. This biphasic 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

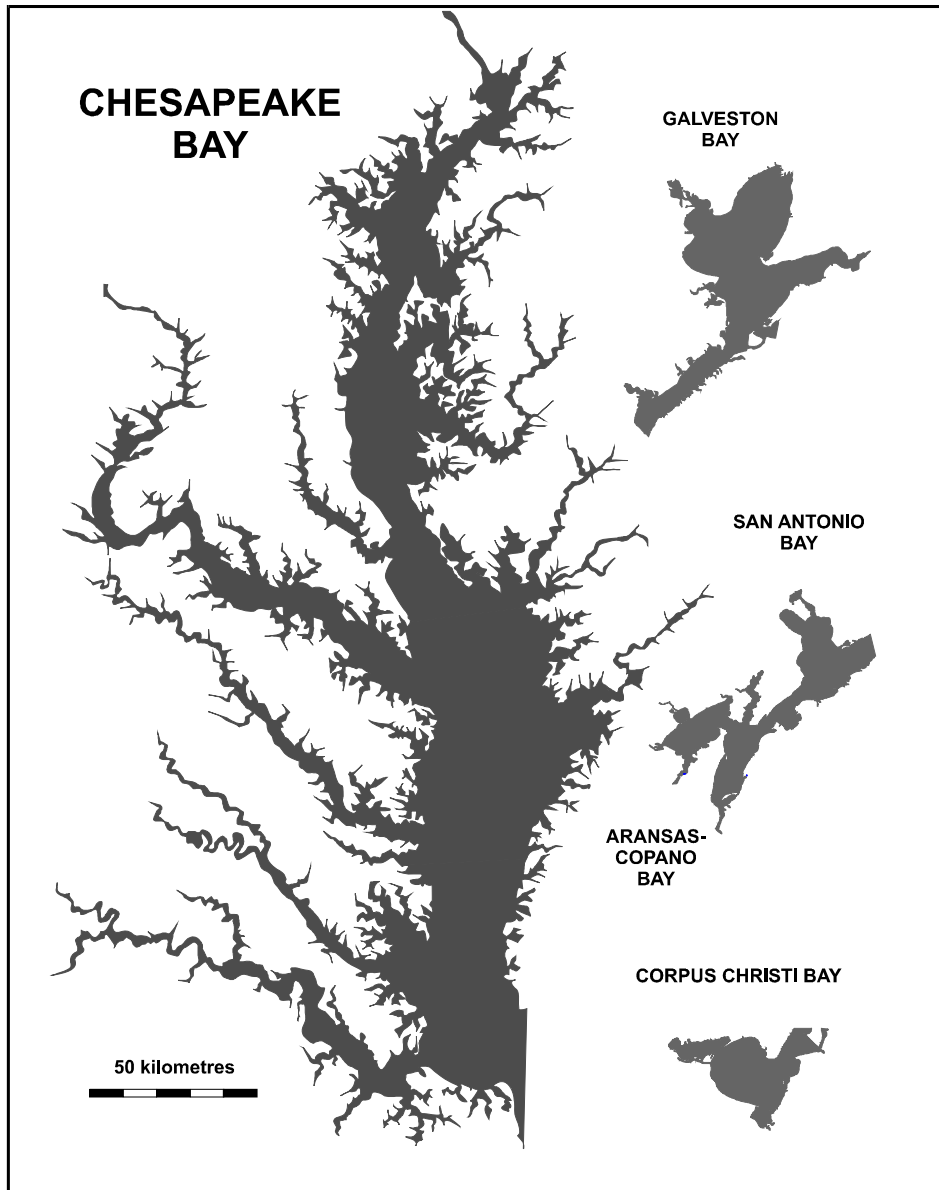


Figure 5-14 - Comparison of estuary scales, Chesapeake Bay versus Texas coast

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 5-15 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 M. 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. 5-15. 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. 5-15. 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 activities, 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 shorter development to maturity in San Antonio Bay, completed about a year sooner than in the Chesapeake (cf. Fig. 4-6).

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 4.4.3.1 and 4.4.3.2). 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

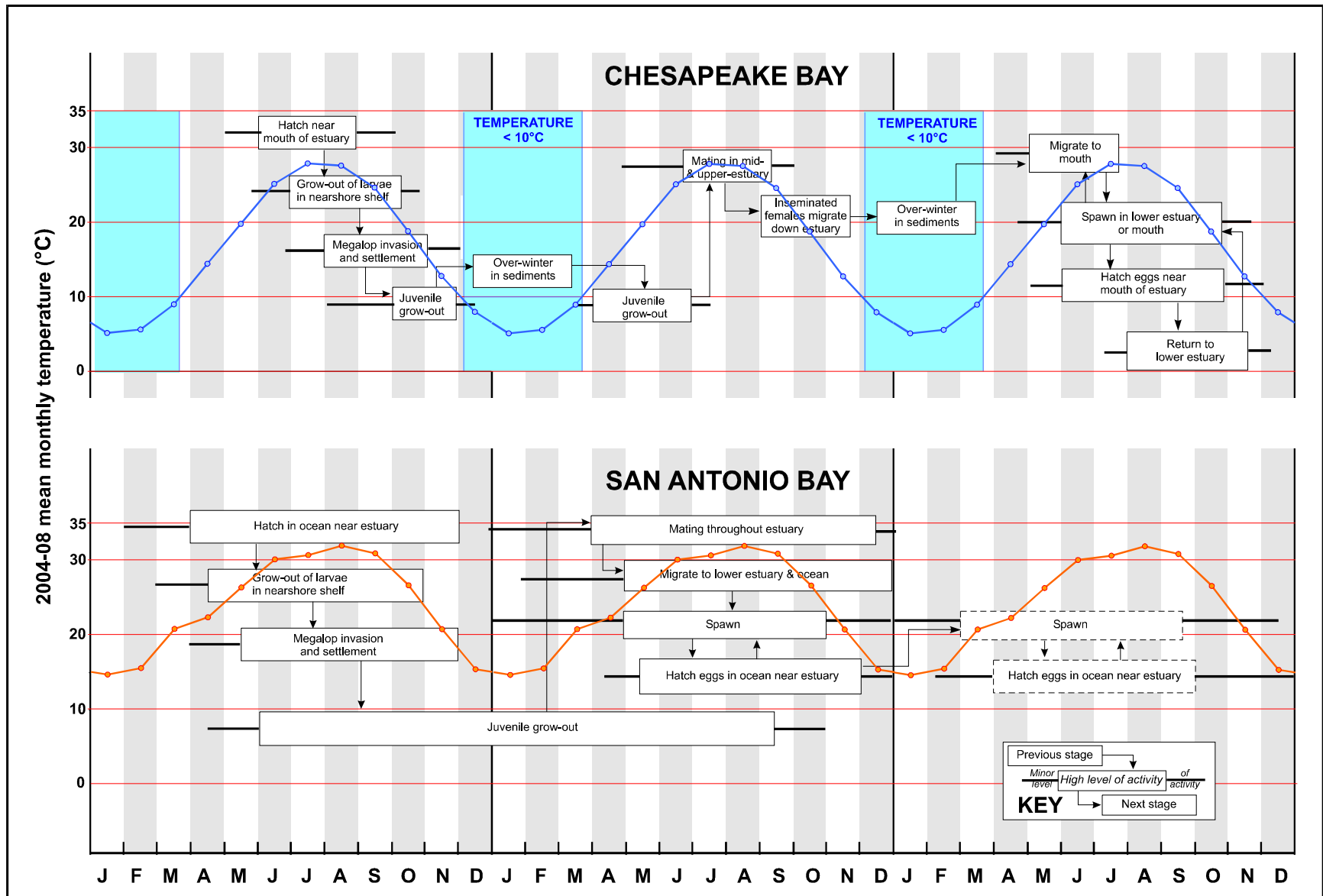


Figure 5-15 - Time line of life stages of a single year class of blue crab in two representative estuaries of mid-Atlantic (above), and Texas coast (below)

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 retention 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 4.4.3.2 that the reversals of the Louisiana-Texas coastal current would plausibly retain postlarvae from summer hatching on the Texas coast.

The plausibility of this mechanism for 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 4.4.4.4. 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. 4-21. 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. seem to be 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 4.4.3). 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 4.4.4.1). 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 4.4.4.4). It should be noted, however, that the data is very limited upon which the judgment of equivalent juvenile densities is based (Sections 4.4.4.4 and 4.4.5.1). (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 explicitly 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 in the analysis.

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 5.5). 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 (Section 3.4). As noted earlier (Sections 4.4.2 and 4.4.4.1), 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 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 5.5 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.

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APPENDIX A

Estimation of 1942-76 nongauged flows by component watershed

As noted in the text, some means of subdividing the 1942-76 TxRR monthly bay-total inflow into its component sources is needed. The method pursued here is to establish statistical regressions of monthly TxRR flow based upon monthly rainfall for each of the component watersheds for the 1977-2008 period, during which TxRR data are available for each watershed of Table 2. This in effect assumes that because local rainfall drives local runoff in the daily model of TxRR, monthly rainfall should likewise drive monthly runoff. This is, of course, imperfect. The TxRR monthly output is based upon a daily calculation, taking account of runoff when rainfall exceeds infiltration, storage of rainfall in the soil, and evapotranspiration and other losses during interstorm periods, all of which impart lag and memory into the watershed signal relative to the driver of rainfall. In addition, the partition of the monthly periods in this sequence of rainfall and runoff sorts rainfall and (longer-term) runoff into different monthly compartments.

The source of precipitation data was the National Climatic Data Center (NCDC) Summary of the Day file, made up primarily of records from the NOAA Cooperative Observer program. These data are plagued by missing entries, lost records, variable instrument reading times, and other aberrations. We require a substantially continuous record over the 1942-2009 period in the general geographical area of the watershed. This requirement reduced the available stations to four: Victoria (which, in fact is a first-order National Weather Service station), Goliad, Aransas National Wildlife Reserve (ANWR), continuing the earlier cooperative record from Austwell, and Port O'Connor. (Port O'Connor had some gaps in its record, which were filled from Port Lavaca or Point Comfort.)

Both linear and quadratic regressions forms were evaluated (the latter forced through the origin), and each rainfall location was tested as well as the various pairwise and tripwise averages of locations. The quadratic relation proved better in every instance, though not by a substantial amount, and no advantage was gained by averaging together rainfall gauges. The best regressions for each of the four watershed categories are summarized in Table A-1. The Guadalupe regressions are based on the entire data set, combining those data in which watershed 18014 is included in the runoff area with those in which it is not. A separate analysis was done in which these data were separated in the regressions, but the differences proved negligible. A representative graph of the data and the linear and quadratic best-fit regression forms are shown in Figure A-1.

With these regressions, the runoff components for each ungauged watershed for the 1942-76 period were estimated from the TxRR total by:

$$\text{Guad+Santone above barrier} = \max\{0, \text{TxRR total ungauged} - (\text{periphery} + \text{w/s 24608})\} \quad (\text{A-1})$$

The separation of the ungauged flow into components is sought while holding their total as close as possible to the TxRR total value. In (A-1), the Guad+Santone watershed flow is estimated as the difference between the TxRR total and the regression values for the bay periphery and 24608

Table A-1
 Summary of statistical regressions of ungauged watershed runoff versus rainfall

Regression form: $Q = ar^2 + br$
 Q = watershed runoff flow, taf / mo
 r = rainfall, ins/mo

versus rainfall at:	watershed (see Table 2-2)			
	Guadalupe Victoria	San Antonio Goliad	Periphery ANWR	w/s 24608 Port O'Connor
a	0.262	0.141	0.156	0.038
b	1.604	0.807	1.051	0.644
explained variance	0.57	0.52	0.84	0.70

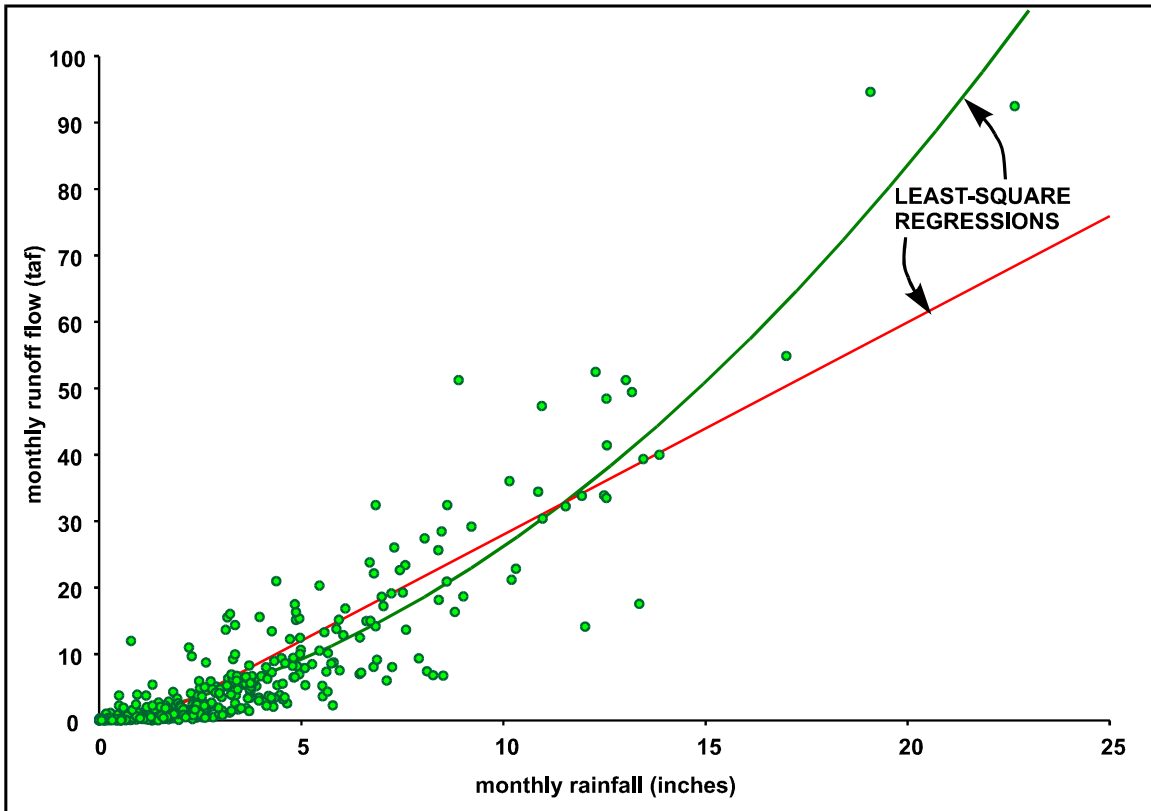


Figure A-1 – Monthly watershed inflow versus monthly rainfall, peripheral watershed (24601-34607), and best-fit regressions

watersheds. The need for the $\max\{ \}$ function arises because a large positive excursion in a data point above the (periphery + w/s 24608) regressions drives this difference negative. While the total of the three watersheds indeed exactly equals the TxRR total, this is only by dint of a negative flow from Guad+Santone. Physically this is unacceptable, so the $\max\{ \}$ operation assures that each value for this watershed is nonnegative. On average over the 1942-76 period, this results in about a 2% error in the computed total compared to the TxRR value.

It is messier to further separate the ungauged Guad+Santone flow into the separate contributions from the ungauged San Antonio (w/s 19011 + 19012) and the ungauged Guadalupe (w/s 18012 + 18020, plus the runoff from w/s 18014 whenever the Victoria gauge on Coleta Creek is unavailable). If the regressions from Table A-1 are employed to estimate each of these components, the 1942-76 average error in the computed total bay runoff inflow compared to the TxRR value is about 35%. An analogous equation to (A-1) that estimates the Guadalupe runoff from the regression of Table A-1 (which is slightly superior in explained variance to the San Antonio regression) and the San Antonio runoff by differencing:

$$\text{ungauged San Antonio} = \max\{0, \text{Guad+Santone} - \text{ungauged Guadalupe}\} \quad (\text{A-2})$$

encounters the same problem as (A-1) of occasional large positive residuals in the ungauged Guadalupe regression driving the answer negative, hence the need for the $\max\{ \}$ function. This effect is minimized by selecting the alternative equation

$$\text{ungauged Guadalupe} = \max\{0, \text{Guad+Santone} - \text{ungauged San Antonio}\} \quad (\text{A-3})$$

for any month when the (Guad+Santone – ungauged Guadalupe) term in (A-1) is negative but the (Guad+Santone – ungauged San Antonio) term in (A-2) is positive. On average over the 1942-76 period, this strategy results in an error of about 8% in the computed total bay inflow compared to the TxRR value.

APPENDIX B

Regression line through fixed point

A line through a fixed point (x_0, y_0) has equation:

$$y = m(x - x_0) + y_0$$

To pass this line through N data points (x, y) as a least-squares fit, the minimum of

$$\sum [y - m(x - x_0) - y_0]^2$$

where the sum is extended over N data points, is given at the value of m where its derivative with respect to m is zero, i.e.

$$\begin{aligned} m &= \frac{\sum yx - N\bar{x}y_0 - N\bar{y}x_0 + Nx_0y_0}{\sum x^2 - 2x_0\sum x + Nx_0^2} \\ &= \frac{\overline{yx} - \bar{x}y_0 - \bar{y}x_0 + x_0y_0}{\overline{x^2} - 2\bar{x}x_0 + x_0^2} \end{aligned}$$

APPENDIX C
Monthly component flows into San Antonio Bay

year/mo	component flows (Taf)				total bay (Taf)	year/mo	component flows (Taf)				total bay (Taf)		
	Guad	Santone	bay	ret-divs			Guad	Santone	bay	ret-divs			
1942	1	55.1	17.5	0.2	0.1	72.0	1946	1	86.7	21.0	5.9	0.2	105.3
1942	2	56.5	60.7	13.0	0.1	130.3	1946	2	113.8	53.2	4.0	0.1	171.1
1942	3	53.4	29.9	1.3	0.1	84.7	1946	3	193.1	50.6	5.7	0.1	249.5
1942	4	160.0	31.2	0.4	-0.1	191.5	1946	4	95.9	44.1	2.6	-0.2	140.0
1942	5	100.1	26.5	1.8	-0.2	127.0	1946	5	140.7	111.7	2.1	-0.3	254.3
1942	6	57.4	16.6	4.3	-0.3	75.4	1946	6	168.4	115.3	12.9	-0.5	296.2
1942	7	516.7	377.3	43.3	-0.4	936.9	1946	7	56.5	16.4	4.1	-0.5	75.2
1942	8	79.8	64.0	11.5	-0.3	155.1	1946	8	93.7	76.1	17.2	-0.4	186.6
1942	9	275.0	335.0	3.1	-0.2	612.9	1946	9	301.7	303.2	17.9	-0.2	622.5
1942	10	177.4	134.5	6.8	0.0	318.7	1946	10	390.5	439.4	6.7	0.0	836.6
1942	11	109.3	39.6	1.9	0.1	149.1	1946	11	229.1	64.0	4.1	0.2	297.4
1942	12	92.2	31.4	3.6	0.1	125.3	1946	12	141.8	34.5	1.4	0.2	176.2
1943	1	93.6	45.7	7.6	0.1	147.0	1947	1	232.9	48.9	3.2	0.2	279.7
1943	2	64.6	29.3	3.6	0.1	97.5	1947	2	121.3	28.6	0.7	-0.4	149.6
1943	3	81.4	52.2	2.7	0.1	136.4	1947	3	137.8	34.0	1.4	-1.2	168.7
1943	4	62.6	23.4	0.0	0.0	85.7	1947	4	138.0	35.4	8.6	-8.2	173.8
1943	5	72.2	29.5	5.9	-0.1	107.5	1947	5	179.7	126.9	7.6	-11.9	302.3
1943	6	96.3	72.7	0.3	-0.2	169.2	1947	6	77.1	22.2	6.7	-16.3	89.7
1943	7	64.0	36.2	3.1	-0.2	103.0	1947	7	68.7	18.8	0.7	-17.6	70.5
1943	8	43.1	15.5	0.4	-0.1	57.1	1947	8	96.4	21.4	25.7	-14.3	116.4
1943	9	66.6	20.2	5.6	-0.1	73.3	1947	9	43.0	16.2	0.9	-10.6	47.9
1943	10	41.4	15.8	0.5	0.1	57.1	1947	10	37.3	13.8	3.2	-4.2	50.0
1943	11	50.3	22.9	3.5	0.1	76.8	1947	11	44.2	20.0	11.2	0.0	75.3
1943	12	55.7	23.0	8.2	0.1	87.1	1947	12	52.4	17.5	3.8	0.2	67.4
1944	1	105.2	123.0	16.8	0.2	245.2	1948	1	46.8	24.3	6.5	0.2	77.7
1944	2	98.3	21.7	0.5	0.1	120.6	1948	2	56.7	38.4	4.7	-0.4	99.4
1944	3	211.4	90.0	6.7	0.1	308.3	1948	3	52.6	35.1	2.8	-1.4	89.0
1944	4	92.0	17.4	1.0	0.0	110.4	1948	4	37.0	14.2	2.9	-9.5	41.7
1944	5	272.7	186.2	16.3	-0.1	475.2	1948	5	107.1	34.3	1.4	-13.8	128.9
1944	6	185.7	31.0	1.2	-0.1	215.0	1948	6	34.6	9.0	0.1	-18.9	24.8
1944	7	76.7	17.0	2.6	-0.2	94.1	1948	7	50.0	24.5	0.7	-20.4	51.1
1944	8	65.1	28.3	7.2	-0.1	100.5	1948	8	45.8	46.9	17.7	-16.5	81.9
1944	9	118.1	47.2	16.2	0.0	181.5	1948	9	29.2	58.3	21.9	-12.3	97.1
1944	10	53.9	38.7	6.0	0.1	98.7	1948	10	29.2	20.3	1.7	-4.8	45.8
1944	11	78.8	18.7	1.7	0.1	99.3	1948	11	26.7	10.0	1.7	0.0	35.4
1944	12	144.3	52.3	4.3	0.2	201.1	1948	12	26.9	10.0	0.2	0.2	36.8
1945	1	201.6	43.9	1.2	0.2	245.1	1949	1	34.5	11.5	2.2	0.2	44.1
1945	2	182.0	49.4	1.5	0.1	233.0	1949	2	65.2	16.6	5.5	-0.1	78.1
1945	3	177.3	37.7	2.8	0.1	217.9	1949	3	102.1	16.3	1.9	-0.6	119.8
1945	4	349.4	101.6	6.0	-0.2	456.8	1949	4	274.0	258.8	31.4	-4.7	559.5
1945	5	94.8	25.6	0.6	-0.3	120.7	1949	5	175.0	44.1	0.1	-6.8	212.2
1945	6	93.3	44.8	9.4	-0.5	147.0	1949	6	76.3	60.1	1.6	-9.4	123.7
1945	7	63.9	20.7	8.8	-0.5	92.9	1949	7	61.6	55.3	11.6	-10.2	118.3
1945	8	65.5	96.1	64.7	-0.4	226.0	1949	8	45.0	18.2	1.3	-8.2	52.9
1945	9	41.3	12.8	1.0	-0.2	52.0	1949	9	39.0	12.5	6.3	-6.1	47.3
1945	10	82.4	29.7	6.5	0.0	118.6	1949	10	211.3	145.0	26.6	-2.3	380.5
1945	11	47.9	15.1	0.1	0.1	63.2	1949	11	52.6	19.0	0.7	0.1	72.4
1945	12	64.1	16.1	2.7	0.2	83.0	1949	12	74.9	26.8	2.9	0.2	104.8

(continued)

APPENDIX C (contined)
1950-1957

year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>	year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>
	<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>			<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>	
1950 1	45.8	17.2	1.5	0.0	64.4	1954 1	37.6	9.2	1.8	-1.3	45.8
1950 2	51.6	17.6	4.1	-0.4	72.9	1954 2	28.6	6.9	0.0	-2.1	33.0
1950 3	42.9	14.2	0.8	-1.0	56.0	1954 3	26.3	6.9	0.2	-3.3	29.3
1950 4	84.8	16.2	2.4	-5.6	94.4	1954 4	38.0	9.5	2.3	-11.0	29.8
1950 5	58.6	14.0	3.1	-7.9	65.5	1954 5	47.9	16.1	1.2	-14.6	47.2
1950 6	144.0	43.0	3.8	-10.8	180.0	1954 6	17.5	7.5	0.3	-19.6	2.9
1950 7	39.5	11.6	0.1	-11.7	36.3	1954 7	10.3	5.1	0.5	-21.2	-6.6
1950 8	25.6	13.1	1.9	-9.5	28.2	1954 8	8.7	3.1	1.1	-17.6	-6.8
1950 9	32.8	10.7	6.5	-7.2	32.8	1954 9	12.4	4.0	3.6	-13.8	0.2
1950 10	23.6	8.1	0.0	-2.9	27.0	1954 10	10.5	9.2	28.0	-6.4	41.3
1950 11	21.2	7.5	0.1	-0.2	28.5	1954 11	13.3	8.7	1.1	-1.8	21.4
1950 12	26.8	8.1	1.2	-0.1	34.5	1954 12	17.6	5.3	0.9	-1.8	19.3
1951 1	27.6	7.7	1.3	-0.7	32.5	1955 1	18.1	7.8	2.4	0.1	26.2
1951 2	24.2	11.0	0.5	-1.4	33.8	1955 2	63.1	20.7	1.3	-0.4	84.7
1951 3	33.5	10.7	5.5	-2.6	40.1	1955 3	21.6	10.9	0.1	-1.2	30.0
1951 4	28.1	11.6	1.0	-10.7	29.1	1955 4	18.8	5.3	0.7	-7.8	15.5
1951 5	63.3	40.7	4.8	-14.9	94.0	1955 5	55.6	19.3	4.1	-11.3	63.1
1951 6	149.1	75.3	0.8	-20.1	205.1	1955 6	51.9	9.9	0.4	-15.4	42.6
1951 7	20.2	7.5	0.8	-21.7	5.9	1955 7	19.4	4.2	4.2	-16.7	5.0
1951 8	11.7	5.5	0.0	-17.8	-0.9	1955 8	29.1	10.2	11.4	-13.5	25.6
1951 9	71.4	84.7	50.7	-13.7	193.2	1955 9	19.6	38.5	13.5	-10.1	61.5
1951 10	15.8	11.5	3.7	-5.9	25.1	1955 10	9.6	9.0	1.4	-4.0	16.0
1951 11	23.3	9.3	1.0	-1.0	30.4	1955 11	9.7	4.5	1.5	-0.1	12.3
1951 12	21.1	9.3	1.2	-1.0	29.8	1955 12	11.9	7.1	1.9	0.0	20.2
1952 1	21.2	8.4	0.5	-1.0	28.8	1956 1	14.2	6.4	1.8	0.1	20.3
1952 2	30.0	12.3	3.4	-1.8	37.7	1956 2	16.2	6.1	1.0	0.0	21.8
1952 3	26.1	11.8	0.7	-3.0	35.5	1956 3	10.9	5.2	3.4	-1.7	16.6
1952 4	45.4	38.1	8.8	-11.1	81.3	1956 4	13.2	5.2	4.9	-4.9	14.5
1952 5	117.0	77.8	6.0	-15.1	185.8	1956 5	20.2	20.9	1.7	-7.9	34.8
1952 6	89.5	18.4	0.5	-20.2	88.2	1956 6	5.8	1.6	1.2	-6.4	-0.1
1952 7	36.9	10.2	2.8	-21.9	20.4	1956 7	4.6	3.2	0.1	-7.3	-0.6
1952 8	14.0	4.8	2.4	-18.1	0.2	1956 8	3.0	3.7	8.4	-3.1	11.3
1952 9	290.0	218.7	7.1	-14.0	501.9	1956 9	7.7	11.9	1.2	-3.7	13.0
1952 10	44.0	9.2	0.0	-6.3	46.9	1956 10	24.1	22.6	4.3	-0.2	42.4
1952 11	72.7	23.7	8.2	-1.4	103.2	1956 11	7.7	9.3	1.1	0.0	17.6
1952 12	122.3	17.7	1.8	-1.4	140.4	1956 12	35.2	23.5	1.7	0.0	55.2
1953 1	102.7	16.7	0.6	-1.1	118.3	1957 1	8.5	6.8	0.5	-0.1	14.4
1953 2	52.1	11.9	3.4	-2.0	65.3	1957 2	30.8	9.3	3.1	-2.7	32.7
1953 3	40.8	10.5	0.4	-3.3	48.1	1957 3	106.3	139.7	10.3	0.0	256.4
1953 4	48.5	17.3	0.3	-12.0	54.1	1957 4	304.4	333.4	21.5	0.0	659.4
1953 5	182.4	74.3	9.7	-16.3	250.0	1957 5	463.2	276.2	12.3	-0.5	751.2
1953 6	21.9	5.1	1.6	-21.9	5.2	1957 6	345.0	205.7	6.5	-1.3	556.0
1953 7	21.0	7.6	1.0	-23.8	4.6	1957 7	41.9	10.1	0.0	-5.7	46.1
1953 8	68.3	74.7	52.0	-19.6	175.3	1957 8	24.0	6.7	0.4	-5.7	23.3
1953 9	112.7	98.2	1.2	-15.2	196.9	1957 9	249.4	122.5	11.3	-3.0	380.2
1953 10	114.5	14.4	7.7	-6.8	127.4	1957 10	505.5	70.9	1.6	-1.4	576.6
1953 11	42.0	9.3	1.4	-1.6	50.8	1957 11	302.5	134.8	7.2	-0.4	444.1
1953 12	58.1	12.0	3.4	-1.6	68.6	1957 12	124.9	18.2	0.6	0.1	142.3

(continued)

APPENDIX C (contined)
1958-1965

year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>	year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>
	<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>			<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>	
1958 1	278.5	186.8	13.3	0.1	478.8	1962 1	56.9	20.4	0.7	0.1	77.2
1958 2	558.1	322.3	8.0	0.1	888.5	1962 2	51.9	18.1	0.2	0.1	69.7
1958 3	247.1	40.4	1.9	-0.1	289.3	1962 3	50.0	15.0	0.8	0.0	64.3
1958 4	123.0	22.3	0.6	-1.9	144.0	1962 4	70.3	19.4	4.2	-1.8	86.8
1958 5	281.3	132.4	4.1	-5.2	412.6	1962 5	48.8	16.2	3.0	-6.0	61.9
1958 6	107.1	27.0	0.6	-5.2	128.1	1962 6	68.4	73.1	12.7	-6.1	148.2
1958 7	79.2	31.1	2.2	-7.1	103.7	1962 7	33.8	12.4	0.0	-6.7	39.5
1958 8	46.5	12.1	0.4	-7.2	51.0	1962 8	22.8	9.0	0.2	-7.1	22.6
1958 9	195.7	75.7	30.6	-1.0	301.0	1962 9	66.1	18.9	12.0	-3.6	87.4
1958 10	152.7	168.5	5.7	0.1	327.1	1962 10	43.2	9.4	6.4	-0.6	55.4
1958 11	136.1	98.5	4.1	0.1	238.7	1962 11	46.6	15.1	3.4	0.0	65.2
1958 12	100.8	75.3	10.6	0.1	186.8	1962 12	56.3	39.8	9.6	0.0	105.7
1959 1	79.6	28.6	1.5	0.2	109.3	1963 1	43.8	13.2	1.0	-0.1	57.5
1959 2	135.3	150.9	12.5	-0.1	298.6	1963 2	62.1	26.2	3.0	-0.2	91.1
1959 3	82.1	24.5	0.1	-0.6	105.5	1963 3	41.5	12.2	0.5	-0.3	53.6
1959 4	218.4	42.0	4.0	-3.8	260.6	1963 4	45.6	12.5	0.2	-3.6	53.2
1959 5	117.3	48.7	3.4	-5.4	164.0	1963 5	33.4	9.4	0.4	-11.9	28.0
1959 6	76.7	36.2	10.5	-7.4	116.0	1963 6	36.5	7.5	5.7	-17.2	18.7
1959 7	81.6	21.0	2.2	-8.0	94.9	1963 7	22.9	7.0	1.4	-14.9	13.5
1959 8	66.9	36.4	25.6	-6.5	122.5	1963 8	17.8	2.9	0.4	-15.0	-1.1
1959 9	46.5	14.5	2.0	-4.8	58.2	1963 9	14.3	8.9	3.8	-8.6	16.1
1959 10	177.7	155.5	23.4	-1.9	354.7	1963 10	15.6	18.1	3.9	-1.3	33.9
1959 11	79.7	26.6	1.2	0.0	107.6	1963 11	56.7	20.5	6.9	-0.2	77.7
1959 12	77.9	27.0	4.9	0.1	109.9	1963 12	34.1	15.1	1.1	-0.2	46.8
1960 1	89.5	24.2	1.3	0.1	114.2	1964 1	33.2	17.0	2.2	0.1	52.5
1960 2	93.0	48.7	6.9	0.1	148.7	1964 2	55.1	47.1	3.2	0.1	105.5
1960 3	76.8	44.4	4.5	0.1	125.7	1964 3	79.7	46.0	1.4	0.0	127.0
1960 4	79.1	20.8	1.4	-0.5	99.5	1964 4	41.4	11.5	0.1	-10.0	42.1
1960 5	152.0	22.5	3.7	-4.8	173.5	1964 5	35.2	9.4	1.9	-15.0	24.8
1960 6	190.5	100.7	18.7	-9.8	300.1	1964 6	43.0	20.3	4.2	-10.7	56.9
1960 7	177.4	37.5	1.3	-11.1	205.1	1964 7	19.8	5.5	1.2	-16.1	6.6
1960 8	144.4	97.6	28.1	-9.2	261.0	1964 8	45.3	40.9	2.5	-8.9	79.7
1960 9	67.0	15.3	2.2	-4.5	80.1	1964 9	73.3	35.3	14.9	-4.4	119.1
1960 10	727.5	432.8	35.8	0.1	1196.1	1964 10	51.9	19.4	2.1	-4.4	68.4
1960 11	485.8	169.7	7.3	0.1	663.0	1964 11	59.1	35.6	0.4	0.0	93.6
1960 12	223.6	160.9	20.4	0.1	405.0	1964 12	32.5	16.2	5.9	0.0	54.7
1961 1	246.0	105.9	7.1	0.1	359.2	1965 1	109.7	38.6	2.7	0.0	151.1
1961 2	271.7	165.6	11.2	0.1	448.5	1965 2	289.3	146.3	2.6	-0.1	438.2
1961 3	153.8	42.1	0.2	0.0	195.1	1965 3	80.5	19.9	0.6	-0.2	99.4
1961 4	102.8	28.3	1.9	-0.8	132.2	1965 4	74.6	27.5	0.7	-8.1	93.0
1961 5	73.2	16.4	1.0	-4.0	85.4	1965 5	293.0	202.8	4.6	-9.4	491.0
1961 6	436.2	117.8	32.8	-4.1	582.7	1965 6	271.8	77.8	3.8	-12.6	340.8
1961 7	187.4	131.1	7.2	-5.6	320.1	1965 7	69.5	14.2	1.3	-13.9	70.6
1961 8	77.4	23.5	4.6	-6.7	94.1	1965 8	43.7	10.6	2.4	-14.1	42.0
1961 9	135.7	95.7	17.3	-0.4	248.3	1965 9	54.0	10.5	6.2	-11.0	47.8
1961 10	65.4	34.1	0.3	0.0	98.3	1965 10	91.6	65.1	11.4	-4.9	163.2
1961 11	150.0	54.5	4.5	0.1	209.1	1965 11	122.0	37.5	5.1	-0.2	164.5
1961 12	62.7	21.1	1.6	0.1	84.4	1965 12	177.3	104.5	5.9	-0.2	287.6

(continued)

APPENDIX C (contined)
1966-1973

year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>	year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>
	<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>			<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>	
1966 1	86.4	56.1	4.5	0.0	147.0	1970 1	119.9	60.1	2.8	-0.8	182.0
1966 2	99.3	70.5	5.0	-0.1	174.7	1970 2	108.5	29.0	2.2	-0.6	139.1
1966 3	98.9	19.8	0.8	-0.2	118.6	1970 3	191.0	80.3	5.5	-2.2	274.5
1966 4	136.2	67.8	8.1	-2.5	209.6	1970 4	120.8	64.1	1.1	-3.8	182.2
1966 5	182.9	181.3	14.3	-2.6	375.9	1970 5	259.6	69.7	7.2	-5.6	289.0
1966 6	81.8	41.8	11.9	-2.6	132.9	1970 6	173.8	221.4	11.0	-9.9	396.2
1966 7	73.2	48.2	1.4	-9.6	113.2	1970 7	83.5	30.3	5.8	-10.2	109.4
1966 8	46.1	27.2	1.3	-7.6	67.1	1970 8	55.6	15.6	1.4	-8.5	64.1
1966 9	57.7	32.6	6.9	-5.4	91.7	1970 9	59.1	15.8	34.8	-4.9	104.7
1966 10	56.0	43.6	2.2	-1.9	99.9	1970 10	71.0	53.3	16.3	-3.8	136.7
1966 11	43.5	30.0	0.7	-0.4	73.8	1970 11	43.8	14.9	0.0	-1.8	57.0
1966 12	39.2	22.9	1.6	-0.2	63.5	1970 12	44.2	13.1	0.6	-1.2	56.7
1967 1	42.0	27.3	4.4	-1.3	72.4	1971 1	41.6	14.6	0.2	-2.1	54.3
1967 2	33.0	27.0	2.3	-1.1	61.2	1971 2	36.3	11.6	1.4	-1.1	46.2
1967 3	32.5	24.6	0.9	-4.0	54.1	1971 3	36.4	11.9	0.0	-5.1	42.9
1967 4	32.0	31.1	0.4	-7.8	55.7	1971 4	29.3	12.3	3.4	-10.2	34.7
1967 5	29.6	28.4	23.9	-9.9	72.0	1971 5	24.5	21.8	9.8	-10.2	45.8
1967 6	16.7	31.2	0.1	-14.4	33.6	1971 6	43.7	13.4	4.1	-14.1	31.5
1967 7	15.3	10.8	12.6	-11.0	25.2	1971 7	20.9	22.0	0.2	-10.5	32.7
1967 8	26.5	31.3	10.4	-9.7	58.6	1971 8	109.5	79.0	8.4	-8.7	177.5
1967 9	925.8	1195.4	86.8	-2.7	2205.2	1971 9	264.9	199.4	34.2	-6.5	492.0
1967 10	216.2	258.4	5.3	-2.0	478.0	1971 10	126.2	241.0	18.6	-3.5	382.2
1967 11	138.0	119.8	2.0	-1.1	258.6	1971 11	90.3	129.1	3.2	-2.0	220.6
1967 12	70.9	114.2	1.1	-0.8	185.5	1971 12	132.3	138.7	26.3	-2.4	294.9
1968 1	455.4	264.9	9.6	-0.7	721.2	1972 1	99.6	46.3	5.1	-2.0	149.0
1968 2	142.1	152.8	3.1	-0.4	297.5	1972 2	94.6	72.3	5.7	-1.3	171.4
1968 3	119.7	62.9	4.2	-1.3	185.5	1972 3	72.3	30.8	0.7	-2.7	101.1
1968 4	175.4	65.6	1.0	-4.9	237.1	1972 4	46.7	39.6	3.5	-7.1	82.6
1968 5	420.9	134.5	8.2	-7.1	556.5	1972 5	844.3	260.4	15.0	-9.2	1065.2
1968 6	415.5	59.7	82.8	-8.7	549.3	1972 6	176.8	119.1	4.7	-12.2	288.5
1968 7	115.1	161.0	7.3	-13.3	270.1	1972 7	128.0	31.8	9.4	-11.0	132.5
1968 8	63.9	40.8	2.0	-9.3	97.4	1972 8	95.8	36.9	7.0	-6.7	133.0
1968 9	130.6	50.8	10.8	-6.2	175.0	1972 9	79.8	30.8	14.4	-10.7	95.4
1968 10	56.6	97.3	2.6	-4.3	152.2	1972 10	67.1	91.2	2.4	-6.3	154.4
1968 11	68.4	39.0	3.3	-2.0	108.6	1972 11	57.7	117.7	6.7	-1.8	180.2
1968 12	129.1	54.7	1.6	-1.9	183.6	1972 12	52.6	24.3	0.4	-1.8	74.9
1969 1	58.8	84.7	1.4	-1.7	143.2	1973 1	75.7	27.2	2.6	-1.5	98.6
1969 2	207.3	62.0	6.0	-0.5	274.8	1973 2	99.4	34.3	2.4	-2.4	130.3
1969 3	193.2	99.4	3.4	-1.0	295.0	1973 3	161.0	32.1	0.5	-3.4	189.4
1969 4	294.7	87.0	16.5	-4.8	393.4	1973 4	353.1	106.6	9.1	-4.1	451.3
1969 5	236.6	110.4	5.6	-8.4	344.2	1973 5	142.9	58.2	0.6	-10.3	191.4
1969 6	114.3	50.6	1.5	-13.8	152.6	1973 6	585.8	253.1	27.0	-9.8	793.6
1969 7	57.6	10.5	0.0	-15.3	49.2	1973 7	273.0	290.4	0.5	-15.5	541.6
1969 8	53.0	14.3	5.6	-9.4	54.6	1973 8	176.0	163.8	11.1	-11.6	339.4
1969 9	73.4	19.9	2.4	-10.3	62.8	1973 9	164.9	142.6	29.0	-5.0	331.6
1969 10	93.1	23.6	10.5	-4.5	113.5	1973 10	770.0	464.6	18.3	-5.3	1247.7
1969 11	80.8	25.4	8.1	-1.7	112.6	1973 11	208.1	177.2	2.0	-2.4	384.9
1969 12	104.0	44.4	8.1	-1.8	154.8	1973 12	136.5	99.7	0.3	-2.8	233.8

(continued)

APPENDIX C (contined)
1974-1981

year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>	year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>
	<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>			<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>	
1974 1	239.0	50.7	3.2	-1.8	284.2	1978 1	63.2	32.3	1.8	-1.9	95.4
1974 2	108.0	98.8	0.0	-2.6	204.2	1978 2	67.9	37.3	8.1	-1.8	111.5
1974 3	96.0	65.0	4.6	-2.8	162.8	1978 3	58.0	32.8	0.2	-3.3	87.8
1974 4	74.0	35.1	0.6	-8.0	101.6	1978 4	60.9	41.7	1.5	-7.0	97.1
1974 5	186.2	57.2	39.2	-10.0	272.6	1978 5	48.7	27.9	0.1	-13.2	63.5
1974 6	111.9	33.5	4.8	-15.0	135.1	1978 6	105.4	64.5	5.3	-12.8	162.4
1974 7	55.5	15.6	0.4	-14.9	54.8	1978 7	40.5	12.5	0.5	-12.2	41.4
1974 8	87.8	64.0	10.6	-12.0	124.7	1978 8	230.8	107.6	0.7	-10.1	329.0
1974 9	252.0	104.5	13.4	-12.0	357.8	1978 9	374.9	128.9	14.1	-8.0	510.0
1974 10	95.7	94.3	5.5	-7.2	188.3	1978 10	96.7	39.4	3.8	-4.2	135.6
1974 11	289.3	64.7	64.6	-2.7	407.3	1978 11	120.6	63.1	3.2	-1.2	185.7
1974 12	182.4	176.5	2.9	-3.8	358.1	1978 12	64.6	35.3	1.8	-2.1	99.6
1975 1	132.6	81.7	2.2	-3.3	213.3	1979 1	334.3	102.9	18.7	-1.8	454.1
1975 2	258.0	116.8	0.9	-4.3	371.5	1979 2	229.5	64.4	8.7	-2.0	300.7
1975 3	139.8	110.2	0.1	-6.8	243.4	1979 3	243.9	81.3	6.7	-2.8	329.0
1975 4	135.9	79.5	0.3	-9.7	206.0	1979 4	327.5	173.0	5.8	-4.6	501.7
1975 5	578.9	154.8	8.2	-10.8	708.5	1979 5	542.2	158.1	15.0	-7.9	707.3
1975 6	413.2	230.0	5.1	-14.6	633.8	1979 6	387.9	173.0	4.1	-15.2	549.7
1975 7	214.7	92.8	3.8	-12.4	298.9	1979 7	176.0	77.2	33.8	-12.2	274.7
1975 8	128.6	37.6	13.9	-9.1	171.1	1979 8	127.2	46.2	4.8	-12.1	166.1
1975 9	91.9	82.9	7.1	-11.2	170.6	1979 9	199.7	76.0	94.6	-7.3	363.0
1975 10	81.4	27.8	4.2	-5.5	97.7	1979 10	60.4	23.3	0.8	-6.2	78.3
1975 11	61.4	59.0	2.0	-2.9	119.4	1979 11	55.7	25.2	1.4	-2.0	80.2
1975 12	103.2	31.8	2.8	-3.8	110.1	1979 12	54.9	30.4	1.2	-1.7	84.9
1976 1	59.5	50.8	0.5	-3.4	107.4	1980 1	91.1	39.7	5.4	-2.2	134.1
1976 2	52.0	20.2	0.1	-3.3	68.3	1980 2	57.8	28.1	0.4	-1.8	84.5
1976 3	59.9	22.7	0.7	-3.1	77.3	1980 3	50.2	20.5	1.2	-6.2	65.7
1976 4	351.0	172.6	8.1	-6.9	524.8	1980 4	44.1	22.9	0.2	-7.8	59.4
1976 5	406.7	165.2	13.3	-7.6	577.7	1980 5	189.1	86.0	5.2	-8.9	271.5
1976 6	203.8	119.0	4.4	-11.0	316.2	1980 6	66.5	21.5	0.1	-16.1	72.0
1976 7	163.8	85.6	29.6	-6.9	272.2	1980 7	38.1	13.3	0.5	-14.9	37.0
1976 8	112.3	35.2	1.5	-8.7	133.9	1980 8	44.9	62.7	7.9	-8.4	107.1
1976 9	127.2	51.5	5.8	-11.4	145.6	1980 9	81.7	65.3	7.5	-12.8	141.7
1976 10	296.1	113.6	10.6	-3.2	397.1	1980 10	64.2	22.2	1.4	-2.7	85.2
1976 11	317.0	255.8	7.6	-1.0	579.4	1980 11	50.8	25.6	0.5	-2.3	74.6
1976 12	457.1	284.8	18.4	-1.6	758.6	1980 12	51.7	25.5	0.4	-2.4	75.3
1977 1	200.5	94.5	5.1	-0.6	299.6	1981 1	56.6	30.5	2.9	-2.6	87.4
1977 2	289.5	89.5	2.1	-0.3	380.7	1981 2	51.6	23.5	0.8	-1.5	74.4
1977 3	146.0	61.7	0.7	-2.6	205.8	1981 3	78.3	26.1	0.3	-1.5	103.1
1977 4	649.0	266.1	9.4	-4.5	919.9	1981 4	100.2	28.1	2.3	-5.8	124.9
1977 5	318.2	165.2	20.9	-8.8	495.6	1981 5	184.3	79.4	33.9	-7.2	290.4
1977 6	291.7	132.7	21.0	-12.8	432.5	1981 6	727.6	326.0	49.4	-9.1	1093.9
1977 7	109.6	42.9	0.3	-12.0	140.8	1981 7	257.5	120.0	14.4	-9.0	382.8
1977 8	76.5	29.1	0.8	-13.0	93.4	1981 8	130.0	49.1	8.1	-9.3	177.9
1977 9	71.0	49.7	7.2	-11.6	116.4	1981 9	697.2	154.1	5.1	-10.2	846.2
1977 10	68.3	34.7	6.3	-4.0	105.3	1981 10	186.8	115.7	14.2	-4.9	311.8
1977 11	109.5	85.9	20.3	-1.9	213.7	1981 11	312.3	106.4	12.0	-1.6	429.1
1977 12	59.6	35.2	0.3	-2.1	93.0	1981 12	109.7	38.1	5.5	-2.5	150.8

(continued)

APPENDIX C (contined)
1982-1989

year/mo	component flows (Taf)				total bay (Taf)	year/mo	component flows (Taf)				total bay (Taf)
	Guad	Santone	bay	ret-divs			Guad	Santone	bay	ret-divs	
1982 1	78.5	31.6	0.2	-0.1	110.2	1986 1	112.3	26.5	1.4	-1.5	138.7
1982 2	137.7	62.8	28.5	-0.8	228.3	1986 2	98.3	25.7	0.1	-1.2	123.0
1982 3	69.2	34.3	0.3	-0.5	103.3	1986 3	77.0	17.2	0.0	-3.4	90.8
1982 4	59.6	26.0	1.2	-4.2	82.6	1986 4	58.6	14.7	0.2	-7.3	66.2
1982 5	393.8	72.2	9.2	-4.6	470.5	1986 5	108.7	33.0	6.8	-6.9	141.6
1982 6	81.2	25.2	0.3	-11.4	95.4	1986 6	208.9	176.3	5.3	-6.4	384.1
1982 7	47.9	17.7	0.2	-10.9	54.9	1986 7	74.2	31.6	0.2	-8.5	97.5
1982 8	31.2	18.2	0.8	-7.7	42.4	1986 8	45.9	16.9	1.4	-8.5	55.7
1982 9	28.8	15.2	1.2	-10.9	34.3	1986 9	75.0	33.0	1.0	-6.9	102.0
1982 10	39.4	33.9	0.3	-2.7	70.9	1986 10	175.6	68.5	30.4	-2.5	272.0
1982 11	116.8	41.7	8.7	-0.6	166.6	1986 11	157.7	36.7	16.0	-1.5	209.0
1982 12	42.5	27.2	0.3	-0.2	69.7	1986 12	367.8	135.3	5.9	-1.2	507.8
1983 1	46.0	26.2	3.8	-1.7	74.3	1987 1	286.7	93.8	5.0	-1.6	384.0
1983 2	99.6	31.3	8.3	-1.1	138.1	1987 2	204.4	82.9	12.4	-1.7	298.1
1983 3	153.4	43.1	4.8	-0.7	200.6	1987 3	284.5	98.4	1.2	-1.7	382.4
1983 4	82.5	19.7	0.1	-4.0	98.3	1987 4	128.0	47.0	0.1	-6.7	168.5
1983 5	91.0	26.5	0.1	-6.1	111.4	1987 5	142.2	98.9	1.7	-4.8	237.9
1983 6	77.1	23.1	1.9	-8.4	93.7	1987 6	1535.5	935.1	9.4	-6.3	2473.7
1983 7	138.6	30.4	23.8	-7.0	185.8	1987 7	438.0	113.5	10.6	-9.6	552.5
1983 8	43.3	21.9	1.2	-4.4	62.0	1987 8	283.9	52.3	3.4	-6.2	333.3
1983 9	54.8	50.7	7.4	-7.1	105.7	1987 9	152.5	43.9	2.8	-10.4	188.8
1983 10	82.0	28.7	4.7	-4.8	110.6	1987 10	108.8	32.1	3.4	-8.4	136.0
1983 11	69.3	29.7	5.4	-1.0	103.3	1987 11	103.3	39.9	3.4	-2.4	144.2
1983 12	33.7	18.2	0.2	-0.9	51.2	1987 12	77.0	39.0	0.2	-2.7	113.5
1984 1	55.8	26.1	7.0	-1.5	87.4	1988 1	59.2	35.0	0.1	-3.1	91.2
1984 2	39.8	19.6	0.2	-1.5	58.1	1988 2	51.3	29.0	0.0	-2.6	77.7
1984 3	62.9	24.7	2.2	-1.4	88.4	1988 3	65.3	32.1	0.0	-3.5	93.9
1984 4	27.6	15.2	0.0	-5.4	37.4	1988 4	47.7	25.8	0.2	-8.9	64.8
1984 5	28.2	16.8	1.7	-8.2	38.4	1988 5	50.0	21.4	0.0	-11.4	60.0
1984 6	18.9	12.1	0.1	-11.3	19.8	1988 6	60.6	24.0	1.9	-14.5	72.0
1984 7	7.9	10.3	0.5	-9.7	9.0	1988 7	60.0	25.2	1.9	-13.5	73.7
1984 8	11.0	11.6	2.7	-5.6	19.7	1988 8	66.8	15.7	0.3	-9.4	73.3
1984 9	8.4	8.7	1.0	-7.4	10.7	1988 9	36.3	18.6	2.1	-9.5	47.5
1984 10	53.3	66.5	15.0	-3.9	130.9	1988 10	34.4	15.4	0.8	-12.0	38.7
1984 11	44.9	36.5	4.3	-1.0	84.7	1988 11	29.3	15.5	0.0	-4.5	40.3
1984 12	56.3	26.8	0.4	-1.8	81.7	1988 12	36.9	18.3	0.1	-4.2	51.0
1985 1	136.1	42.3	4.2	-0.7	181.9	1989 1	48.0	25.5	6.0	-3.5	76.0
1985 2	89.5	24.5	1.7	-1.1	114.6	1989 2	42.9	21.0	0.1	-2.7	61.3
1985 3	182.8	53.4	15.5	-0.8	251.0	1989 3	47.5	20.3	0.0	-4.1	63.6
1985 4	230.7	58.5	13.3	-1.3	301.1	1989 4	46.3	24.8	0.1	-7.5	63.8
1985 5	103.8	27.4	0.5	-5.7	126.0	1989 5	93.0	22.3	0.1	-10.1	105.4
1985 6	181.8	56.4	1.0	-7.4	231.7	1989 6	47.4	25.4	17.5	-11.1	79.3
1985 7	165.9	66.2	2.4	-10.0	224.6	1989 7	19.9	9.9	11.0	-9.4	31.4
1985 8	65.8	15.7	0.4	-8.4	73.5	1989 8	11.7	14.7	2.2	-8.4	20.2
1985 9	45.8	29.3	1.5	-4.0	72.6	1989 9	11.1	8.7	0.3	-10.7	9.4
1985 10	104.7	62.3	1.9	-2.6	166.3	1989 10	25.3	14.2	1.0	-9.1	31.4
1985 11	211.5	79.4	1.2	-1.5	290.5	1989 11	24.5	25.8	10.1	-3.4	57.0
1985 12	203.3	35.4	2.1	-1.2	239.6	1989 12	28.3	19.6	0.5	-2.2	46.2

(continued)

APPENDIX C (contined)
1990-1997

year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>	year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>
	<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>			<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>	
1990 1	26.5	14.9	0.2	-2.3	39.3	1994 1	53.8	28.0	3.2	-0.5	84.4
1990 2	25.6	20.9	6.7	-1.2	51.9	1994 2	46.8	26.4	0.3	-0.7	72.8
1990 3	43.6	33.3	10.5	-1.4	86.0	1994 3	82.9	57.2	4.2	-0.7	143.5
1990 4	71.9	47.7	3.9	-1.1	122.3	1994 4	57.6	37.6	0.7	-3.8	92.1
1990 5	85.9	32.1	4.7	-5.3	117.5	1994 5	286.6	142.4	2.4	-5.6	425.7
1990 6	44.8	8.4	0.2	-9.6	43.8	1994 6	110.8	34.7	3.7	-8.4	140.8
1990 7	148.5	182.7	41.4	-6.8	365.8	1994 7	44.8	16.7	0.2	-10.5	51.2
1990 8	52.1	24.7	0.9	-8.8	68.9	1994 8	39.4	16.8	0.8	-4.1	52.8
1990 9	61.0	27.8	1.5	-4.3	86.0	1994 9	54.4	28.6	7.0	-6.6	83.4
1990 10	34.6	20.7	0.1	-5.5	50.0	1994 10	355.3	113.5	12.2	-4.6	476.5
1990 11	40.1	22.2	0.4	-3.4	59.4	1994 11	70.7	27.2	0.2	-1.5	96.7
1990 12	35.2	17.2	0.2	-1.3	51.4	1994 12	124.4	32.8	5.5	-1.9	160.8
1991 1	196.7	47.8	2.6	0.0	247.1	1995 1	132.8	31.1	0.5	-0.8	163.6
1991 2	164.6	59.7	1.1	-0.3	225.2	1995 2	62.0	22.4	0.8	-1.2	84.1
1991 3	96.3	27.4	4.8	-0.3	128.2	1995 3	169.3	41.4	8.2	-0.6	218.3
1991 4	400.6	126.7	17.5	-0.6	544.1	1995 4	126.6	33.7	2.6	-1.5	161.4
1991 5	162.5	51.1	2.6	-3.5	212.7	1995 5	66.2	27.7	6.5	-5.2	95.2
1991 6	103.2	36.5	22.8	-5.9	156.6	1995 6	196.8	47.8	8.6	-7.1	246.2
1991 7	100.2	31.4	1.1	-8.3	124.4	1995 7	78.0	46.5	1.9	-8.4	118.0
1991 8	44.1	17.9	5.2	-6.2	61.1	1995 8	67.6	19.1	1.0	-5.5	82.2
1991 9	68.2	23.4	19.2	-4.0	106.9	1995 9	56.1	28.3	0.3	-4.9	79.8
1991 10	60.7	19.0	22.1	-3.4	98.5	1995 10	41.2	17.4	18.2	-3.6	73.2
1991 11	55.4	21.0	13.4	-0.1	89.7	1995 11	45.3	16.2	6.2	-0.7	67.0
1991 12	650.2	310.9	15.2	-0.3	975.9	1995 12	52.0	21.7	3.7	-0.6	76.8
1992 1	693.2	181.3	15.1	0.2	889.9	1996 1	39.7	17.8	0.1	-1.2	56.5
1992 2	1154.4	466.1	32.4	1.5	1654.5	1996 2	34.3	14.3	0.0	-0.9	47.7
1992 3	657.1	280.3	15.4	-0.2	952.5	1996 3	32.8	15.4	0.0	-2.5	45.8
1992 4	753.5	310.9	13.6	2.1	1080.1	1996 4	28.4	12.2	0.9	-5.7	35.9
1992 5	655.3	394.0	23.4	-2.3	1070.4	1996 5	23.7	11.3	0.0	-9.9	25.1
1992 6	546.8	353.4	9.7	-3.9	906.0	1996 6	36.6	14.9	1.0	-10.6	41.8
1992 7	208.3	94.8	4.7	-8.4	299.5	1996 7	10.6	9.9	0.0	-8.5	12.0
1992 8	133.0	58.9	6.3	-6.8	191.4	1996 8	28.1	14.3	2.3	-3.1	41.6
1992 9	102.6	43.6	3.0	-3.2	146.0	1996 9	141.1	45.6	6.5	-3.3	189.9
1992 10	85.2	33.7	0.7	-2.6	117.0	1996 10	26.4	11.7	0.3	-2.0	36.4
1992 11	113.4	75.7	12.5	0.1	201.7	1996 11	27.1	14.4	0.8	-1.1	41.2
1992 12	103.7	54.7	1.4	0.3	160.1	1996 12	37.7	18.1	0.5	-0.5	55.8
1993 1	123.2	50.3	2.5	-0.2	175.8	1997 1	61.9	16.0	1.6	-0.3	79.3
1993 2	150.3	59.3	48.5	-0.2	257.9	1997 2	52.5	16.9	0.3	-0.6	69.1
1993 3	212.6	66.0	27.4	-0.3	305.7	1997 3	190.3	30.6	40.0	0.3	261.2
1993 4	111.1	41.3	3.3	-1.3	154.4	1997 4	506.1	82.9	6.3	0.1	595.4
1993 5	484.0	220.7	19.1	-2.0	721.8	1997 5	240.2	62.1	18.6	-1.8	319.2
1993 6	581.3	201.7	15.6	-4.1	794.5	1997 6	668.4	222.6	0.6	-4.7	887.0
1993 7	121.2	73.2	0.3	-9.1	185.6	1997 7	388.0	88.1	0.2	-7.2	469.0
1993 8	57.2	26.1	0.1	-6.5	76.9	1997 8	167.7	19.9	1.1	-4.8	183.9
1993 9	46.3	21.4	0.2	-3.7	64.3	1997 9	112.8	31.5	33.5	-3.8	173.9
1993 10	71.2	29.5	3.8	-2.5	102.1	1997 10	223.5	56.0	52.5	-0.7	331.2
1993 11	56.0	28.6	0.5	-1.2	83.9	1997 11	68.7	25.2	3.9	-0.9	96.8
1993 12	62.2	25.4	8.6	-0.2	96.0	1997 12	78.2	31.4	0.5	-0.7	109.4

(continued)

APPENDIX C (contined)
1998-2005

year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>	year/mo	<i>component flows (Taf)</i>				<i>total bay (Taf)</i>
	<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>			<i>Guad</i>	<i>Santone</i>	<i>bay</i>	<i>ret-divs</i>	
1998 1	93.3	33.7	0.3	-1.5	125.8	2002 1	126.3	44.5	2.7	-1.0	172.6
1998 2	201.8	67.3	3.1	-0.1	272.2	2002 2	85.0	29.8	0.2	-0.9	114.1
1998 3	232.6	67.2	2.3	-1.0	301.0	2002 3	76.8	29.6	0.1	-2.6	103.9
1998 4	121.7	30.9	0.2	-5.0	147.9	2002 4	160.3	59.8	1.0	-3.8	217.3
1998 5	61.7	15.0	0.0	-9.3	67.5	2002 5	55.2	23.6	0.8	-6.2	73.4
1998 6	44.5	10.0	0.0	-11.6	42.9	2002 6	47.9	16.9	3.8	-7.4	61.2
1998 7	36.5	10.1	0.3	-8.6	38.3	2002 7	1102.6	957.1	13.8	-2.7	2070.8
1998 8	80.7	46.5	6.7	-4.6	129.3	2002 8	292.2	85.9	6.0	-6.7	377.3
1998 9	239.0	56.6	16.3	-1.2	310.7	2002 9	375.8	220.8	27.0	-4.2	619.4
1998 10	1952.5	494.7	29.2	-1.1	2475.3	2002 10	434.7	318.3	47.3	-1.0	799.3
1998 11	620.9	144.9	26.0	0.3	792.2	2002 11	653.4	254.1	51.2	0.6	959.3
1998 12	294.8	66.3	0.8	-0.7	361.2	2002 12	375.4	138.2	8.0	-0.2	521.4
1999 1	137.4	50.0	1.7	-0.7	188.3	2003 1	248.4	90.7	6.7	-0.5	345.3
1999 2	89.3	33.2	2.0	-1.3	123.2	2003 2	275.5	87.2	3.6	-0.4	365.9
1999 3	95.1	45.0	0.1	-2.2	138.1	2003 3	219.9	77.5	6.6	-1.1	302.9
1999 4	78.9	43.9	0.9	-4.5	119.2	2003 4	113.2	49.2	0.2	-2.1	160.5
1999 5	99.3	39.4	0.2	-7.2	131.7	2003 5	94.1	32.6	0.1	-5.5	121.3
1999 6	151.2	61.1	0.3	-7.5	205.0	2003 6	86.0	40.4	7.2	-5.6	127.9
1999 7	77.2	31.6	2.2	-6.7	104.3	2003 7	99.8	67.9	36.0	-4.6	199.1
1999 8	44.8	16.1	0.1	-5.6	55.4	2003 8	68.0	28.8	2.4	-3.7	95.4
1999 9	32.7	14.2	0.1	-7.2	39.8	2003 9	119.5	107.2	34.4	-3.1	258.1
1999 10	32.1	14.6	0.3	-3.4	43.6	2003 10	98.8	51.2	5.9	-2.0	153.9
1999 11	33.6	16.6	0.0	-4.3	45.9	2003 11	101.2	37.7	0.9	-1.3	138.5
1999 12	35.0	17.6	0.0	-2.5	50.2	2003 12	70.0	34.4	0.4	-1.8	103.0
2000 1	47.6	29.1	3.5	-2.5	77.6	2004 1	99.8	38.2	3.3	-1.4	140.0
2000 2	38.1	22.7	0.1	-1.6	59.3	2004 2	86.2	37.6	0.5	-0.4	123.8
2000 3	51.6	22.8	6.4	-2.5	78.3	2004 3	97.6	44.4	0.3	-1.3	141.0
2000 4	43.4	26.3	1.7	-2.8	68.6	2004 4	241.1	153.6	3.0	-0.6	397.1
2000 5	89.5	53.3	54.9	-4.5	193.1	2004 5	374.3	171.5	51.2	-1.5	595.5
2000 6	105.6	54.5	32.4	-5.5	187.0	2004 6	492.7	184.5	22.6	-3.8	696.0
2000 7	27.1	12.6	0.3	-5.8	34.3	2004 7	351.8	165.1	3.9	-6.4	514.4
2000 8	19.8	8.6	3.4	-4.1	27.7	2004 8	117.1	60.4	0.5	-5.7	172.4
2000 9	16.4	12.6	0.9	-4.6	25.3	2004 9	95.4	49.4	0.5	-1.9	143.4
2000 10	31.2	45.6	0.6	-3.0	74.4	2004 10	234.7	87.9	21.2	-1.2	342.6
2000 11	322.8	165.0	3.6	-1.3	490.0	2004 11	1218.4	362.9	16.9	0.8	1598.9
2000 12	150.2	42.0	2.5	-1.0	193.8	2004 12	461.4	118.7	0.7	-0.7	580.0
2001 1	174.5	54.8	8.9	-1.1	237.1	2005 1	208.2	82.6	0.6	-2.6	288.8
2001 2	126.1	35.6	0.2	-1.5	160.5	2005 2	299.4	89.4	1.5	-1.1	389.2
2001 3	209.9	46.9	0.5	-2.3	255.1	2005 3	414.4	133.2	5.1	0.0	552.7
2001 4	111.0	53.0	0.1	-3.7	160.3	2005 4	135.0	54.3	0.4	-2.2	187.5
2001 5	139.2	67.9	1.2	-3.6	204.7	2005 5	188.3	58.4	3.4	-2.3	247.8
2001 6	62.7	27.0	0.4	-8.5	81.6	2005 6	102.0	46.5	1.7	-4.6	145.6
2001 7	49.9	12.4	0.8	-4.8	58.2	2005 7	80.7	32.3	4.3	-6.5	110.9
2001 8	82.4	53.5	8.0	-5.3	138.7	2005 8	67.8	26.0	0.3	-8.1	85.9
2001 9	538.6	396.5	6.9	-3.0	939.0	2005 9	59.2	29.6	1.8	-5.2	85.4
2001 10	117.3	52.1	6.7	-2.0	174.0	2005 10	63.8	25.5	9.4	-1.9	96.9
2001 11	248.1	120.5	17.2	-0.2	385.6	2005 11	46.4	19.6	7.3	-2.4	70.9
2001 12	357.0	95.6	2.0	-0.5	454.1	2005 12	48.1	25.9	1.8	-1.2	74.6

(continued)

APPENDIX C (continued)
2006-2009

year/mo	component flows (Taf)				total bay (Taf)	year/mo	component flows (Taf)				total bay (Taf)
	Guad	Santone	bay	ret-divs			Guad	Santone	bay	ret-divs	
2006 1	47.6	24.4	0.2	-1.3	71.0	2008 1	71.0	43.9	8.5	-1.1	122.2
2006 2	42.7	15.2	0.1	-1.7	56.3	2008 2	60.3	35.5	2.7	-1.0	97.5
2006 3	46.3	23.1	0.3	-1.9	67.8	2008 3	69.5	34.4	1.9	-0.4	105.4
2006 4	39.1	15.6	0.0	-4.4	50.4	2008 4	57.1	34.6	1.6	-2.7	90.6
2006 5	88.9	30.4	13.6	-5.6	127.4	2008 5	44.0	22.8	0.1	-6.4	60.5
2006 6	82.2	31.2	12.9	-4.4	121.8	2008 6	35.2	12.9	0.0	-8.7	39.4
2006 7	56.7	17.9	39.4	-5.1	108.9	2008 7	37.0	23.0	0.4	-7.7	52.7
2006 8	19.9	8.7	3.5	-2.0	30.0	2008 8	39.6	37.7	9.1	-4.0	82.3
2006 9	42.4	47.6	25.6	-2.0	113.5	2008 9	32.7	21.1	0.3	-3.4	50.6
2006 10	56.7	29.4	10.0	-1.1	95.0	2008 10	28.2	17.5	2.2	-4.5	43.4
2006 11	24.9	17.7	1.6	-1.4	42.8	2008 11	25.8	15.3	2.4	-1.8	41.8
2006 12	32.4	23.3	2.0	-1.8	55.9	2008 12	28.9	15.9	0.0	-2.1	42.7
2007 1	125.9	61.5	32.2	0.1	219.7	2009 1	29.3	18.2	0.0	-1.7	45.7
2007 2	48.0	19.4	0.4	-0.7	67.1	2009 2	25.0	14.5	0.0	-2.5	37.1
2007 3	343.6	169.2	5.9	0.0	518.7	2009 3	30.5	19.1	0.5	-2.4	47.8
2007 4	269.6	119.9	10.0	0.4	399.8	2009 4	111.1	21.9	0.6	-2.4	131.3
2007 5	327.3	108.2	5.3	-2.4	438.4	2009 5	33.6	27.6	9.8	-5.4	65.6
2007 6	235.9	69.0	5.6	-4.3	306.2	2009 6	16.9	12.5	0.2	-7.4	22.2
2007 7	936.7	480.4	92.5	0.3	1509.9	2009 7	10.7	7.5	0.0	-8.0	10.2
2007 8	477.5	367.1	16.3	-1.8	859.2	2009 8	9.3	7.6	0.3	-9.9	7.3
2007 9	315.4	147.0	5.6	-0.6	467.5	2009 9	22.8	31.1	4.0	-3.8	54.1
2007 10	120.2	79.6	2.2	-1.1	201.0	2009 10	235.4	132.8	2.9	-0.3	370.7
2007 11	108.8	51.9	4.1	-2.0	162.8	2009 11	246.0	89.6	14.5	0.5	350.6
2007 12	77.1	44.3	0.7	-1.0	121.1	2009 12	124.9	43.3	8.8	-1.6	175.4

Key:

- Guad* - Inflow from Guadalupe basin
- Santone* - Inflow from San Antonio basin
- bay* - Inflow from peripheral drainage around San Antonio Bay
- ret - divs* - Return flows net of diversions, total above salt barrier and directly into bay
- total bay* - Total inflows into San Antonio Bay

All units: thousands of acre feet per month

Note - Prior to 1977, the component flows were estimated from rainfall, using the methods of Appendix A, and will not total exactly to the "total bay" value. See Section 2,2.1.

APPENDIX D

Points (Taf/mo) on 1942-2009 cumulative frequency distribution by frequency of occurrence

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	annual
max	889.9	1654.5	952.5	1080.1	1070.4	2473.7	2070.8	859.2	2205.2	2475.3	1598.9	975.9	2475.3
0.99	776.9	1141.3	684.6	972.8	1066.9	1549.2	1695.0	536.3	1356.9	1652.8	1170.4	830.3	1180.8
0.98	638.8	738.9	541.1	831.3	958.4	1030.0	1315.1	364.4	907.4	1230.1	902.5	697.9	938.4
0.95	429.6	421.0	363.7	582.8	717.2	854.6	548.7	331.8	621.4	823.5	633.7	516.7	620.2
0.90	313.3	367.5	303.7	508.7	583.0	652.4	408.7	201.8	504.3	476.9	433.6	374.4	449.9
0.85	278.1	298.0	288.5	399.7	490.2	549.6	299.4	177.9	379.3	380.0	383.2	285.2	343.8
0.83	246.8	293.7	272.3	396.5	474.4	529.9	294.9	177.1	362.1	368.1	341.7	238.6	312.5
0.80	241.9	266.5	255.8	284.9	433.3	391.4	271.3	171.8	323.2	338.0	277.8	198.2	288.5
0.75	194.6	226.0	244.9	211.5	352.1	308.7	200.6	142.8	250.8	313.5	215.5	184.0	226.6
0.70	175.4	171.3	205.3	186.9	290.3	284.3	140.0	128.8	189.8	186.9	200.1	160.7	187.9
0.65	150.1	149.2	187.7	165.3	263.7	210.5	118.1	112.2	174.5	159.2	165.6	147.0	166.3
0.60	144.0	131.9	147.4	155.5	239.9	181.4	109.7	95.8	145.7	139.8	145.2	121.9	143.2
0.55	132.8	123.1	135.2	138.9	203.0	156.0	103.6	85.4	118.7	130.4	112.0	109.8	126.2
0.50	116.3	114.3	122.7	123.6	179.6	146.3	94.5	80.8	106.3	115.2	103.3	103.9	112.1
0.45	107.7	100.3	105.4	102.9	133.2	133.2	73.9	73.4	97.8	102.6	96.7	93.5	100.9
0.40	94.6	89.8	102.7	96.5	126.8	123.3	57.6	63.7	87.1	98.4	84.6	84.1	92.9
0.35	85.7	80.8	92.2	91.3	118.9	94.5	51.9	57.8	81.6	95.9	77.2	76.0	81.8
0.30	77.6	73.1	87.8	82.9	105.6	82.3	46.4	54.7	72.7	74.8	73.9	70.2	72.7
0.25	73.8	68.9	78.0	68.0	82.4	72.0	38.0	48.8	60.6	65.6	66.5	61.8	63.4
0.20	67.0	62.9	64.9	61.1	66.3	49.1	33.3	34.6	51.2	50.0	58.0	55.5	54.3
0.17	56.6	59.7	57.2	54.3	63.8	42.7	26.2	27.8	47.8	46.0	51.8	51.9	47.8
0.15	54.4	58.1	54.2	53.2	63.1	41.9	20.7	25.7	47.5	43.7	46.1	51.2	45.8
0.10	45.2	47.2	47.2	40.4	56.2	29.5	9.8	20.0	33.8	40.5	40.9	46.6	35.5
0.05	30.1	34.9	37.2	31.5	36.1	19.1	5.3	2.7	14.1	32.2	29.2	35.3	22.1
0.02	22.3	32.8	29.6	20.1	26.1	3.7	1.1	-1.0	9.9	25.7	18.9	23.5	9.6
0.01	18.4	29.1	25.1	15.2	25.0	2.0	-2.6	-3.0	6.4	22.1	15.9	19.9	3.2
min	14.4	21.8	16.6	14.5	24.8	-0.1	-6.6	-6.8	0.2	16.0	12.3	19.3	-6.8
means	163.6	180.4	169.3	200.4	258.7	270.4	190.4	113.2	219.0	240.9	199.9	165.2	197.6

APPENDIX E
Chronology of Cedar Bayou

The following extended table is a compilation of observations on the status of Cedar Bayou, or the occurrence of major hydrographic or engineering events that could potentially affect the inlet, drawn from a variety of sources. Each set of entries is given on a pair of pages, each page beginning with the date of observation. Remote imagery (aircraft or satellite photos) obtained from official sources further detailed in Appendix G.

APPENDIX E
Chronology of Cedar Bayou

<u>date</u>			<i>status</i>	<i>event</i>	<u>BEACH REACH</u>					<u>BACKBAY REACH</u>		
					<i>least depth</i>	<i>associated width</i>	<i>least depth over bar</i>	<i>aperture width</i>	<i>throat width</i>	<i>controlling cross section estimated</i>	<i>typical talweg depth</i>	<i>least width</i>
<i>day</i>	<i>mon</i>	<i>year</i>										
					(ft)	(ft)	(ft)	(ft)	(ft)	(ft ²)	(ft)	(ft)
	ca	1900	open		4.5	600	1.5	600	600	1800	5.5	300
18	Aug	1916		major hurricane, landfall Baffin Bay								
	ca	1917	open		4.5	600	1.5	600	600	1800	5.5	300
14	Sep	1919		major hurricane, landfall Baffin Bay								
22	Jun	1921		hurricane, Matagorda Bay								
	Feb	1926	open									
	Feb	1927	marginal									
29	Jun	1929		hurricane, San Antonio Bay								
28	Jun	1931		tropical storm, Baffin Bay								
25	Jul	1934		hurricane, Aransas Bay								
	ca	1934	open		4	750	3	600	500	1042	5	300
		1935	closed					0		0		
27	Jun	1936		hurricane, Aransas Bay								
	ca	1936	closed					0		0		
	ca	1937	closed					0		0		
	Jun	1938	closed					0		0		
	Mar	1939	closed	dredging begun				0		0		
	Nov	1939	open	dredging complete								
29	Aug	1942		hurricane, Matagorda Bay								
21	Jul	1945		tropical storm, Baffin Bay								
27	Aug	1945		major hurricane, Matagorda Bay								
30	Aug	1949	open									
	ca	1950	open									
	ca	1951	open									
	ca	1952	open		3							
	ca	1952	open					300	350	225		300
31	Dec	1953	marginal					200	200	67		
15	Feb	1954	open		2.5	600	1.1	610	495	600	5	250
31	Mar	1955	open									

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>source</i>	<i>citation or reference</i>	<i>comment</i>
<i>day</i>	<i>mon</i>	<i>year</i>			
	ca	1900	navigation chart	C&GS 209	3 ft on the bar
18	Aug	1916	NCDC	McAdie et al. (2009)	
	ca	1917	navigation chart	C&GS 209	same shoreline& depths as 1900 ed.
14	Sep	1919	NCDC	McAdie et al. (2009)	considerable damage Corpus Christi & Port Aransas, passes opened on St Joseph Is (Shepard & Moore, 1955)
22	Jun	1921	NCDC	McAdie et al. (2009)	
	Feb	1926	observation	Galtsoff (1931)	12 visits to Mesquite Bay, majority in Jun-Sep 26
	Feb	1927	observation	Galtsoff (1931)	water over the Gulf bar at high tide, no measurements
29	Jun	1929	NCDC	McAdie et al. (2009)	
28	Jun	1931	NCDC	McAdie et al. (2009)	
25	Jul	1934	NCDC	McAdie et al. (2009)	
	ca	1934	navigation chart	USC&GS 1285	3 ft on the bar, same shoreline as 1917
		1935	coastal pilot	USC&GS (1936)	least depth back bay reach 2 ft
27	Jun	1936	NCDC	McAdie et al. (2009)	
	ca	1936	observation	Collier and Hedgpeth (1950)	
	ca	1937	observation	Collier and Hedgpeth (1950)	Collier's notes on his 1936-38 surveys
	Jun	1938	TGFOC annual reports	Ward (1997)	
	Mar	1939	TGFOC annual reports	Ward (1997)	TGFOC dredging operations Mar - May, Jul - Nov
	Nov	1939	TGFOC annual reports	Ward (1997)	
29	Aug	1942	NCDC	McAdie et al. (2009)	closed Murdocks Pass according to TGFOC (Ward, 1997)
21	Jul	1945	NCDC	McAdie et al. (2009)	
27	Aug	1945	NCDC	McAdie et al. (2009)	tracked along Texas coast from Baffin Bay, until making landfall
30	Aug	1949	report, aerial photograph	Simmons and Hoese (1959)	reported aerial photograph by Naval Air Station on this date
	ca	1950	observation	Simmons and Hoese (1959)	
	ca	1951	observation	Simmons and Hoese (1959)	
	ca	1952	observation	Shepard & Moore (1955)	
	ca	1952	USGS topo map	St Charles Is SE	
31	Dec	1953	report, aerial photograph	Shepsis & Carter (2007)	aerial photo, dubious
15	Feb	1954	field survey	Lockwood & Andrews (1954)	cross-section area measured from field data on depths across section
31	Mar	1955	report, aerial photograph	Simmons and Hoese (1959)	referenced TGFOC photo, see their Fig. 6

(continued)

APPENDIX E
(continued)

<u>date</u>			<u>status</u>	<u>event</u>	<u>BEACH REACH</u>					<u>BACKBAY REACH</u>	
					<u>least depth</u>	<u>associated width</u>	<u>least depth over bar</u>	<u>aperture width</u>	<u>throat width</u>	<u>controlling cross section estimated</u>	<u>typical talweg depth</u>
<u>day</u>	<u>mon</u>	<u>year</u>									
				(ft)	(ft)	(ft)	(ft)	(ft)	(ft ²)	(ft)	(ft)
31	May	1955	closed				0		0		
ca	Nov	1955	closed				0		0		
	ca	1956	closed				0		0		
22	Nov	1956	open	opened with dragline							
17	Dec	1956	open								
11	Feb	1957	marginal	1							
22	Mar	1957	closed				0		0		
	ca	1957	closed				0		0		
27	Jun	1957	marginal	high water, temporary opening							
18	Sep	1957	marginal	high water, temporary opening							
22	Oct	1957	marginal								
	Jan	1958	marginal	high water, temporary opening							
5	Sep	1958		tropical storm Ella, Corpus Christi							
5	Sep	1958		high water, temporary opening							
1	Apr	1959	closed	just before dredging begins			0		0		
	Sep	1959	open	dredging complete		15	200	15			
24	Jun	1960		tropical storm, Corpus Christi							
		1961	closed ?								
11	Sep	1961		major hurricane Carla, Matagorda Bay							
		1963	open								
7	Aug	1964		tropical storm Abby, Matagorda Bay							
3	Oct	1964		major hurricane Hilda, SE LA							
		1965	open								
20	Sep	1967		major hurricane Beulah, Tampico							
	Sep	1967		3rd highest inflow for San Antonio Bay							
	Jan	1968	open			9				14	290
23	Jun	1968		tropical storm Candy, Aransas Bay							
22	Apr	1969	open				1350	400	533		
	Jun	1970	open			3					

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>source</i>	<i>citation or reference</i>	<i>comment</i>
<i>day</i>	<i>mon</i>	<i>year</i>			
31	May	1955	observation	Simmons and Hoese (1959)	
ca	Nov	1955	observation	Simmons and Hoese (1959)	
	ca	1956	observation	Simmons and Hoese (1959)	
22	Nov	1956	observation	Simmons and Hoese (1959)	local fishermen's actions
17	Dec	1956	report, aerial photograph	Simmons and Hoese (1959)	
11	Feb	1957	observation	Simmons and Hoese (1959)	channel had shifted to south and shoaled
22	Mar	1957	observation	Simmons and Hoese (1959)	completely closed, no evidence of channel
	ca	1957	coastal pilot	USC&GS (1958)	
27	Jun	1957	observation	Simmons and Hoese (1959)	Inundated 3 ft 27 Jun - 1 Jul, attributed to Hurricane Audrey
18	Sep	1957	observation	Simmons and Hoese (1959)	attributed to high river discharge
22	Oct	1957	oblique aerial photo	Leary (1959)	TGFC photo
	Jan	1958	observation	Simmons and Hoese (1959)	attributed to high river discharge
5	Sep	1958	NCDC	McAdie et al. (2009)	
5	Sep	1958	observation	Simmons and Hoese (1959)	attributed to TS Ella
1	Apr	1959	oblique aerial photo	Leary (1959)	TGFC photo
	Sep	1959	report	King (1971)	dredged by TGFC
24	Jun	1960	NCDC	McAdie et al. (2009)	Dwelted over watershed of San Antonio and Guadalupe
		1961	coastal pilot	USC&GS (1962)	Inspection cruise in 1961 of Key West to Rio Grande by USCGS <i>Scott</i>
11	Sep	1961	NCDC	McAdie et al. (2009)	
		1963	report	More (1969)	sampled semi-monthly Jan 63 - Nov 65
7	Aug	1964	NCDC	McAdie et al. (2009)	drifted W over lower watershed of San Antonio Bay
3	Oct	1964	report	Andrews (1970)	water level 2-2.5 ft above normal, extensive erosion from beach & deposition on back bay, attributed to Hilda
		1965	report	More (1969)	
20	Sep	1967	NCDC	McAdie et al. (2009)	drifted northward slowly, delivering heavy rainfalls, then tracked into Mexico
	Sep	1967			
	Jan	1968	observation	King (1971)	beginning of data collection
23	Jun	1968	NCDC	McAdie et al. (2009)	tracked N over lower watershed of San Antonio Bay
22	Apr	1969	USGS B&W vert aerial	AR1VCFI00010053	
	Jun	1970	observation	King (1971)	end of data collection

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>status</i>	<i>event</i>	<u>BEACH REACH</u>					<u>BACKBAY REACH</u>		
<i>day</i>	<i>mon</i>	<i>year</i>			<i>least depth</i>	<i>associated width</i>	<i>least depth over bar</i>	<i>aperture width</i>	<i>throat width</i>	<i>controlling cross section estimated</i>	<i>typical talweg depth</i>	<i>least width</i>
					(ft)	(ft)	(ft)	(ft)	(ft)	(ft ²)	(ft)	(ft)
3	Aug	1970		major hurricane Celia, Aransas Pass								
10	Sep	1971		hurricane Fern, Aransas Bay								
	Sep	1972	open					1380	520	1172		
15	Feb	1973	open					1200	600	1800		
	ca	1973	open					1500	650	2289		290
30	Jul	1978		tropical storm Amelia, Rio Grande								
1	Feb	1979	open					250	350	130		300
	Jun	1979	open					300	500	225		
ca	Jul	1979	closed	deliberate closure by sand berm				0		0		
11	Nov	1979	closed	berm still in place				0	350	0		
9	Aug	1980		major Hurricane Allen, Brownsville								
5	Sep	1980		tropical storm Danielle, Galveston								
12	Feb	1981	marginal					150	190	28		300
21	Sep	1982	marginal					200	190	57		
5	Nov	1982	marginal					130	220	18		320
6	Mar	1983	marginal					280	200	67		390
	Dec	1983		killer freeze thru early Jan								
	Jan	1984		massive kills of fish & shellfish								
7	Dec	1984	marginal					150	150	28		
	Jun	1987	open	2nd highest inflow for San Antonio Bay								
		1988	open	dredging complete								
2-9	Feb	1989		extreme low temperature event on coast								
6	Mar	1989	marginal					200	120	14		380
10	Dec	1989	marginal					100	80	4		300
	Feb	1992		5th highest inflow for San Antonio Bay								
18	Mar	1995	marginal					120	150	14		380
		1995	open	dredging complete								
		1996	open									
		1997	open									
22	Aug	1998		tropical storm Charley, Corpus Christi								

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>source</i>	<i>citation or reference</i>	<i>comment</i>
<i>day</i>	<i>mon</i>	<i>year</i>			
3	Aug	1970	NCDC	McAdie et al. (2009)	Eroded dunes but deposited sand on beaches of Mat Is (Wilkinson, 1973)
10	Sep	1971	NCDC	McAdie et al. (2009)	3-5 ft surge, substantial deposition on Mat Is beaches (Wilkinson, 1973)
	Sep	1972	NASA/MSC CIR vert aerial	AR6216000200119	both Bayou & Vincent merged & wide open
15	Feb	1973	report, aerial photograph	Shepsis & Carter (2007)	aerial photo
	ca	1973	USGS topo map	St Charles Is SE	photorevised
30	Jul	1978	NCDC	McAdie et al. (2009)	drifted NW into San Antonio Bay watershed
1	Feb	1979	USGS B&W vert aerial	AR1VEOC00040056	
	Jun	1979	NASA/Ames CIR vert aerial	Nov 79 aerial	widths from post-berm photograph (see below)
ca	Jul	1979	report	IXTOC websites below	to prevent pollution from Ixtoc blow-out (June 79)
11	Nov	1979	NASA/Ames CIR vert aerial	AR5790028428336	aperture measured behind berm
9	Aug	1980	NCDC	McAdie et al. (2009)	
5	Sep	1980	NCDC	McAdie et al. (2009)	drifted W over lower watershed of San Antonio Bay
12	Feb	1981	USGS NHAP CIR vert aerial	NC1NHAP810273026	Ixtoc berm gone
21	Sep	1982	NPW CIR vert aerial	ARL820510131978	
5	Nov	1982	USGS NHAP CIR vert aerial	NC1NHAP810377096	
6	Mar	1983	USGS NHAP CIR vert aerial	NC1NHAP810703176	
	Dec	1983			
	Jan	1984			
7	Dec	1984	report, aerial photograph	Shepsis & Carter (2007)	aerial photo
	Jun	1987			
		1988	report	Bengston et al. (ca 2004)	dredged by TPWD
2-9	Feb	1989			Mesquite Bay at 0 on 6 Feb
6	Mar	1989	USGS NAPP CIR vert aerial	NP0NAPP001506112	
10	Dec	1989	NASA/Ames CIR vert aerial	AR5890039814074	throat reduced due to bar structures
	Feb	1992			high flows throughout Dec 91 - Jun 92 period
18	Mar	1995	USGS NAPP CIR vert aerial	NP0NAPP008669010	throat reduced due to bar structures
		1995	report	Hagen (2003)	300,000 cu yds dredged by TPWD
		1996	oblique aerial photo	Watson (2010)	
		1997	oblique aerial photo	Watson (2010)	narrower than 1996
22	Aug	1998	NCDC	McAdie et al. (2009)	

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>status</i>	<i>event</i>	<u>BEACH REACH</u>					<u>BACKBAY REACH</u>		
					<i>least depth</i>	<i>associated width</i>	<i>least depth over bar</i>	<i>aperture width</i>	<i>throat width</i>	<i>controlling cross section estimated</i>	<i>typical talweg depth</i>	<i>least width</i>
<i>day</i>	<i>mon</i>	<i>year</i>										
					(ft)	(ft)	(ft)	(ft)	(ft)	(ft ²)	(ft)	(ft)
10	Sep	1998		tropical storm Frances, San Antonio Bay								
	Oct	1998		highest inflow for San Antonio Bay								
	ca	1999	closed					0		0		
22	Aug	1999		major hurricane Brett, Baffin Bay								
	Nov	2001	closed					0	100	0		
14	Dec	2001	closed					0				
7	Feb	2002	closed					0	220	0		380
	Jul	2002		4th highest flood for San Antonio Bay								
22	Aug	2002	closed					0		0		
6	Sep	2002		tropical storm Fay, Matagorda Bay								
15	Jul	2003		hurricane Claudette, Matagorda Bay								
	Nov	2003	marginal						50			
18	Dec	2003	marginal					200	100	8		
4	Nov	2004	marginal					110	60	2		
20	Jul	2005		major hurricane Emily, Tampico								
22	Jul	2005	marginal									
	Aug	2005	marginal					100	100	8		
9	Oct	2005	marginal					300	200	67		300
22	Nov	2005	marginal									
11	Dec	2005	marginal									
	May	2006	marginal					80	100	4		
16	May	2006	marginal									
17	Jul	2006	marginal									
31	Aug	2006	marginal									
28	Oct	2006	marginal									
17	Nov	2006	marginal									
8	Jan	2007	marginal									
16	Aug	2007		tropical storm Erin, Aransas Bay								
21	Sep	2007	marginal									
	Oct	2007	marginal					50	100	1		

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>source</i>	<i>citation or reference</i>	<i>comment</i>
<i>day</i>	<i>mon</i>	<i>year</i>			
10	Sep	1998	NCDC report	McAdie et al. (2009)	stalled offshore for several days before landfall, then tracked N into N Texas sustained through November reported shoaled
	Oct	1998			
	ca	1999			
22	Aug	1999	NCDC	McAdie et al. (2009)	
	Nov	2001	report, aerial photograph	Shepsis & Carter (2007)	aerial photo
14	Dec	2001	GLO CIR vert aerial	GLO 201PT 9-04	
7	Feb	2002	USGS NAPP CIR vert aerial	NP0NAPP012817064	
	Jul	2002			
22	Aug	2002	report	Sikes (2002)	
6	Sep	2002	NCDC	McAdie et al. (2009)	drifted W into lower watershed of San Antonio Bay
15	Jul	2003	NCDC	McAdie et al. (2009)	
	Nov	2003	oblique aerial photo	Watson (2010)	narrow channel through beach & dune line, width estimated
18	Dec	2003	report, aerial photograph	Shepsis & Carter (2007)	aerial photo
4	Nov	2004	USDA-FSA-APFO CIR vert aerial		water level low, lots of exposed bars
20	Jul	2005	NCDC	McAdie et al. (2009)	tracked W into N Mexico, opened Packery Channel
22	Jul	2005	oblique aerial photo	Watson (2010)	stated to be opened by Emily
	Aug	2005	TGLO CIR vert aerial		
9	Oct	2005	USDA-FSA-APFO NC vert aerial		shoreline indistinct, looks like high water event
22	Nov	2005	oblique aerial photo	Watson (2010)	looks same as 22Jul except lower water level
11	Dec	2005	oblique aerial photo	Watson (2010)	
	May	2006	TGLO CIR vert aerial		water level low
16	May	2006	oblique aerial photo	Watson (2010)	
17	Jul	2006	oblique aerial photo	Watson (2010)	
31	Aug	2006	oblique aerial photo	Watson (2010)	
28	Oct	2006	oblique aerial photo	Watson (2010)	stated to be "nearly closed at low tide"
17	Nov	2006	oblique aerial photo	Watson (2010)	
8	Jan	2007	oblique aerial photo	Watson (2010)	
16	Aug	2007	NCDC	McAdie et al. (2009)	
21	Sep	2007	oblique aerial photo	Watson (2010)	higher water level than photos of 06 & early 07
	Oct	2007	TGLO CIR vert aerial		water levels dropping

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>status</i>	<i>event</i>	<u>BEACH REACH</u>					<u>BACKBAY REACH</u>	
<i>day</i>	<i>mon</i>	<i>year</i>			<i>least depth</i>	<i>associated width</i>	<i>least depth over bar</i>	<i>aperture width</i>	<i>throat width</i>	<i>controlling cross section estimated</i>	<i>typical talweg depth</i>
					(ft)	(ft)	(ft)	(ft)	(ft ²)	(ft)	(ft)
20	Oct	2007	marginal								
5	Nov	2007	marginal								
16	Dec	2007	marginal								
6	Feb	2008	closed				0		0		
27	Feb	2008	closed				0		0		
28	Apr	2008	closed				0	50	0		330
28	Jun	2008	closed				0		0		
23	Jul	2008		hurricane Dolly, Port Mansfield							
28	Jul	2008	closed				0		0		
12	Sep	2008		major hurricane Ike, Galveston Bay							
17	Sep	2008	closed				0		0		
18	Oct	2008	closed				0		0		
8	Jan	2009	closed				0	70	0		330
16	Mar	2009	closed				0		0		
8	Aug	2009	closed				0		0		
14	Sep	2009	closed				0		0		

(continued)

APPENDIX E
(continued)

<u>date</u>			<i>source</i>	<i>citation or reference</i>	<i>comment</i>
<i>day</i>	<i>mon</i>	<i>year</i>			
20	Oct	2007	oblique aerial photo	Watson (2010)	stated to be "closed at low tide"
5	Nov	2007	oblique aerial photo	Watson (2010)	
16	Dec	2007	oblique aerial photo	Watson (2010)	
6	Feb	2008	oblique aerial photo	Watson (2010)	
27	Feb	2008	oblique aerial photo	Watson (2010)	moistened channel visible
28	Apr	2008	TOP-NAIP CIR vert aerial	TNRIS I2896_58_1	drainage channels visible, after high-water event?
28	Jun	2008	oblique aerial photo	Watson (2010)	
23	Jul	2008	NCDC	McAdie et al. (2009)	
28	Jul	2008	oblique aerial photo	Watson (2010)	wave wrack on beach, including former entrance location
12	Sep	2008	NCDC	McAdie et al. (2009)	into N Texas
17	Sep	2008	oblique aerial photo	Watson (2010)	
18	Oct	2008	oblique aerial photo	Watson (2010)	moistend region in vicinity of old mouth, effect of high water?
8	Jan	2009	TOP-NAIP CIR vert aerial	TNRIS I2896_58_1	
16	Mar	2009	oblique aerial photo	Watson (2010)	
8	Aug	2009	oblique aerial photo	Watson (2010)	
14	Sep	2009	oblique aerial photo	Watson (2010)	

APPENDIX F
Chronology of tropical cyclones since 1900 making landfall in Texas
or potentially affecting the Cedar Bayou region

<i>landfall date</i>		<i>status</i>	<i>name</i>	<i>landfall</i>	<i>comment</i>
<i>yr</i>	<i>mo da</i>				
1901	Jul 10	tropical storm		Matagorda Bay	
1902	Jun 26	hurricane		Aransas Bay	minimal hurricane
1909	Jun 29	hurricane		Brownsville	
1909	Jul 21	major hurricane		Freeport	
1909	Aug 28	major hurricane		Tampico	
1910	Aug 30	tropical storm		Brownsville	
1910	Sep 14	hurricane		Port Mansfield	
1912	Oct 16	hurricane		Baffin Bay	Moved N into Corpus Christi area
1913	Jun 27	hurricane		Baffin Bay	
1914	Sep 19	tropical storm		Sabine Lake	Moved W into Houston area
1915	Aug 17	major hurricane		Freeport	Recurved NE into midwest and Miss-Ohio Valley
1916	Aug 5	tropical storm		Tampico	
1916	Aug 18	major hurricane		Baffin Bay	continued into Rio Grande Valley
1918	Aug 8	major hurricane		Sabine Lake	
1919	Sep 14	major hurricane		Baffin Bay	
1921	Jun 22	hurricane		Matagorda Bay	continued N into Oklahoma
1921	Sep 6	hurricane		Vera Cruz	curved N into Rio Grande Valley
1925	Sep 6	tropical storm		Brownsville	Rio Grande Valley
1929	Jun 29	hurricane		San Antonio Bay	
1931	Jun 28	tropical storm		Baffin Bay	
1932	Aug 13	major hurricane		Galveston Bay	
1933	Jul 6	hurricane		Tampico	
1933	Jul 22	tropical storm		Freeport	
1933	Sep 4	hurricane		Brownsville	
1934	Jul 25	hurricane		Rockport	
1934	Aug 26	tropical storm		Freeport	neared Freeport, curved back to SE, then landfalled at Tampico
1936	Jun 27	hurricane		Aransas Pass	
1936	Sep 13	tropical storm		Brownsville	Rio Grande Valley
1938	Oct 17	tropical storm		Freeport	minimal storm
1940	Sep 23	tropical storm		Galveston Bay	minimal storm
1941	Sep 15	tropical storm		Galveston Bay	drifted SW over San Antonio Bay watershed
1941	Sep 23	hurricane		Freeport	
1942	Aug 29	hurricane		Matagorda Bay	Closed Murdocks Pass according to TGFOC (Ward, 1997)
1943	Jul 27	hurricane		Galveston Bay	drifted into N Texas
1943	Sep16-18	hurricane		W Louisiana	looped off coast of Texas for 16-18 Sep before drifting N to Louisiana
1945	Jul 21	tropical storm		Baffin Bay	drifted SW into Mexico
1945	Aug 27	major hurricane		Matagorda Bay	tracked along Texas coast from Baffin Bay, until making landfall
1947	Aug 1	tropical storm		Brownsville	minimal
1947	Aug 24	hurricane		Galveston Bay	

(continued)

APPENDIX F
(continued)

<i>landfall date</i>		<i>status</i>	<i>name</i>	<i>landfall</i>	<i>comment</i>
<i>yr</i>	<i>mo da</i>				
1949	Oct 3	hurricane		Freeport	N trajectory
1953	Sep 26	hurricane	Florence	Pensacola	Shepard & Moore report this flooded beaches on N end of Padre Island
1954	Jun 25	tropical storm		Tampico	drifted NW up Rio Grande Valley
1957	Jun 27	major hurricane	Audrey	Sabine Lake	
1958	Sep 5	tropical storm	Ella	Corpus Christi	hurricane strength in Cuba, but weakened when it reached W Gulf
1959	Jul 25	tropical storm	Debra	Galveston Bay	
1960	Jun 24	tropical storm		Corpus Christi	Dwelted over watershed of San Antonio and Guadalupe
1961	Sep 11	major hurricane	Carla	Pass Cavallo	tracked NE into Canada
1963	Sep 17	hurricane	Cindy	Galveston Bay	after landfall drifted SW just inside coast down to Laredo
1964	Aug 7	tropical storm	Abby	Matagorda Bay	drifted W over lower watershed of San Antonio Bay
1967	Sep 20	major hurricane	Beulah	Tampico	drifted northward slowly, delivering heavy rainfalls, then tracked into Mexico
1968	Jun 23	tropical storm	Candy	Aransas Pass	tracked N over lower watershed of San Antonio Bay
1970	Aug 3	major hurricane	Celia	Corpus Christi	drifted WNW into Rio Grande Valley
1970	Sep 15	tropical storm	Felice	Galveston Bay	curved N into N Texas
1971	Sep 16	hurricane	Edith	W Louisiana	paralleled Texas coast 15-16 Sep just offshore
1971	Sep 10	hurricane	Fern	Aransas	SW track into Mexico
1973	Sep 5	tropical storm	Delia	Freeport	dwelled offshore 4-5 Sep, then SW over lower San Antonio Bay watershed
1974	Sep 7	tropical storm	Carmen	Barataria	tracked W into Texas dissipating over upper Guadalupe watershed
1977	Sep 2	major hurricane	Anita	Tampico	
1978	Jul 30	tropical storm	Amelia	Rio Grande	drifted NW into San Antonio Bay watershed
1979	Aug 31	tropical storm	Elena	Matagorda Bay	minimal, drifted into NE Texas
1979	Sep 12	major hurricane	Frederick	Mobile Bay	extreme high tides in 2nd week of Sep, according to Chapman (1981)
1979	Sep n/a	tropical storm	Henri		high wave action off Padre, Farrington (1985), This storm never made landfall, but drifted from Campeche into NE GOM
1980	Aug 9	major hurricane	Allen	Brownsville	WNW into N Mexico
1980	Sep 5	tropical storm	Danielle	Galveston	drifted W over lower watershed of San Antonio Bay
1983	Aug 17	major hurricane	Alicia	Galveston Bay	tracked N into Oklahoma
1983	Aug 28	hurricane	Barry	Brownsville	moved W into N Mexico
1988	Sep 16	hurricane	Gilbert	Tampico	moved N into N Mexico
1993	Jun 20	tropical storm	Arlene	Baffin Bay	minimal
1995	Jul 30	tropical storm	Dean	Freeport	minimal, moved NW into N Texas

(continued)

APPENDIX F
(continued)

<i>landfall date</i>			<i>status</i>	<i>name</i>	<i>landfall</i>	<i>comment</i>
<i>yr</i>	<i>mo</i>	<i>da</i>				
1998	Aug	22	tropical storm	Charley	Corpus Christi	drifted W into Rio Grande Valley
1998	Sep	10	tropical storm	Frances	San Antonio Bay	stalled offshore for several days before landfall, then tracked N into N Texas
1999	Aug	22	major hurricane	Bret	Baffin Bay	tracked W into N Mexico
2001	Jun	5	tropical storm	Allison	Freeport	reversed, moved back offshore then into Louisiana
2002	Sep	6	tropical storm	Fay	Matagorda Bay	drifted W into lower watershed of San Antonio Bay
2003	Jul	15	hurricane	Claudette	Matagorda Bay	Rio Grande Valley
2003	Aug	16	hurricane	Erika	Brownsville	N Mexico
2003	Aug	31	tropical storm	Grace	Galveston Bay	minimal
2005	Sep	23	major hurricane	Rita	Sabine Lake	
2007	Aug	16	tropical storm	Erin	Aransas Bay	
2007	Sep	12	hurricane	Humberto	Galveston Bay	tracked N
2008	Jul	23	hurricane	Dolly	Port Mansfield	W into Mexico
2008	Aug	6	tropical storm	Edouard	Galveston Bay	into N Texas
2008	Sep	12	major hurricane	Ike	Galveston Bay	into N Texas

Appendix G
Aerial photography employed in study
obtained from state or federal agencies

<i>File ID</i>	<i>EROS Entity ID Project</i>	<i>Acquisition Date</i>		<i>Image Type</i>	<i>Flying Height in Feet</i>	<i>Agency</i>		
		<i>Roll Nbr</i>	<i>Frame Nbr</i>					
5SGY03011_062	AR1VCFI00010053	4/22/1969	BW	15600	U.S. Geological Survey	VCFI00	1	53
7OTQ02042_121	AR6216000200119	9/0/1972	CIR	9863	NASA Johnson Space Center	216	2	119
5WWT02011_056	AR1VEOC00040056	2/1/1979	BW	40000	U.S. Geological Survey	VEOC00	4	56
5RTQ10031_474	AR5790028428336	11/11/1979	CIR	65003	NASA - Ames Research Center		2842	8336
5MRD02052_027	NC1NHAP810273026	12/2/1981	CIR	40000	USGS NHAP	NHAP81	273	26
8EWT05011_075	ARL820510131978	9/21/1982	CIR	12005	National Park Service	82051	13	1978
5MRD04041_097	NC1NHAP810377096	11/5/1982	CIR	40000	USGS NHAP	NHAP81	377	96
5MBL05032_177	NC1NHAP810703176	3/6/1983	CIR	40000	USGS NHAP	NHAP81	703	176
7DYL09032_112	NP0NAPP001506112	3/6/1989	CIR	40000	USGS NAPP	NAPP	1506	112
8PWT10041_064	AR5890039814074	12/10/1989	CIR	63700	NASA - Ames Research Center		3981	4074
1BBL04052_010	NP0NAPP008669010	3/18/1995	CIR	40000	USGS NAPP	NAPP	8669	10
GLO 201PT 9-04	n/a	12/14/2001	CIR		TGLO			
1DWT28042_064	NP0NAPP012817064	2/7/2002	CIR	40000	USGS NAPP	NAPP	12817	64
TNRIS d289658_1	n/a	11/4/2004	CIR		USDA-FSA-APFO	TOP		
TGLO 4699 229-234	n/a	8/0/2005	CIR		TGLO			
TNRIS e2896_58_1	n/a	10/9/2005	NC		USDA-FSA-APFO	TOP		
TGLO 4743 232-233	n/a	5/0/2006	CIR		TGLO			
TGLO 4812-UTM14-157	n/a	10/0/2007	CIR		TGLO			
TNRIS l2896_58_1_cir_28042008	n/a	4/28/2008	CIR & NC		NAIP	TOP		
TNRIS l2896_58_1_cir_08012009	n/a	1/8/2009	CIR & NC		NAIP	TOP		

NAPP	National Aerial Photography Program
NHAP	National High Altitude Program
TOP	Texas Orthoimagery Program
NAIP	National Agricultural Imagery Program

Appendix H Estimation of inlet cross-section area

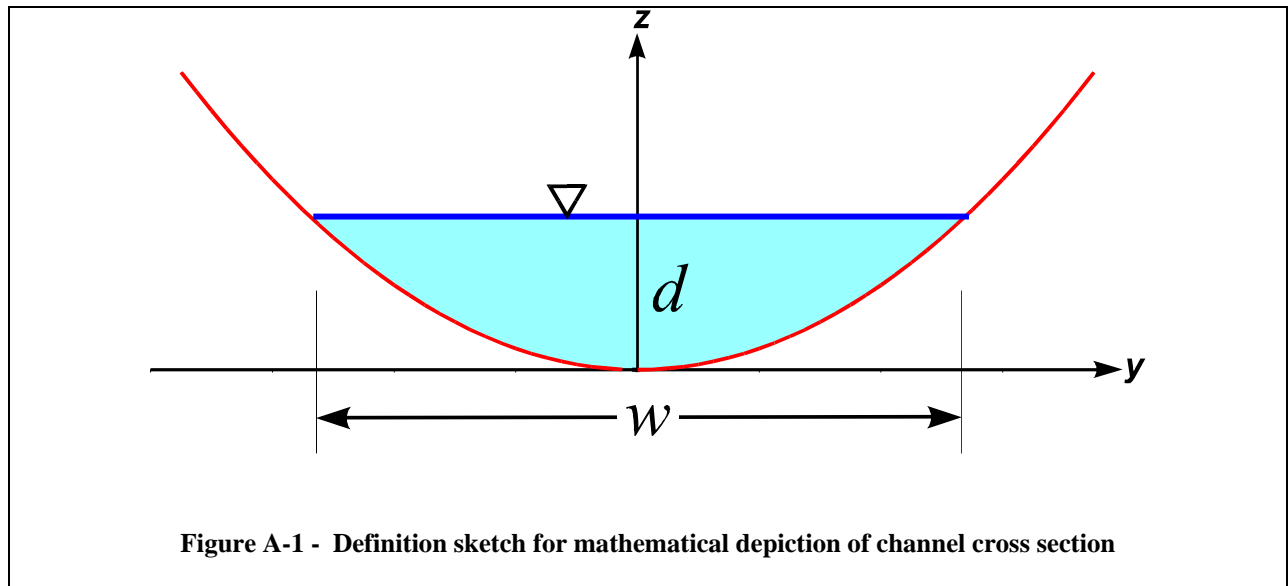
Assume the cross section profile of the channel to be symmetric about the central axis. We postulate a parabolic variation of bed elevation $z(y)$, measured positive upward from the low-point datum, across the lateral distance of the cross section y , with origin in the center of the channel, as sketched in Figure A-1. The equation for the bed elevation is:

$$z(y) = m y^2 \quad (1)$$

The coefficient m governs the shape of the cross section. The water level, or stage d , is then related to stream width w by:

$$d = m w^2 / 4 \quad (2)$$

the mean depth is:



$$D = h - \frac{1}{w} \int_{-w/2}^{w/2} z(y) dy = d - m w^2 / 12 \quad (3)$$

and cross section area is:

$$A = d w - m w^3 / 12 \quad (4)$$

or, as a function of width alone,

$$A(w) = m w^3 / 6 \quad (5)$$

From data on width and depth (observed simultaneously), m can be evaluated from:

$$m = 4 d / w^2 \quad (6)$$

Four surveys were utilized from the historical record of Cedar Bayou (see Appendix E), namely:

date	least depth (ft)	associated width (ft)	computed m (1/ft)	source
1917	4.5	600	5.000E-05	navigation chart
1934	4	750	2.844E-05	navigation chart
1952	3	350	9.796E-05	observation + topo map
1954	2.5	600	2.778E-05	field survey

The average of the individual computed values of m is 5.11×10^{-5} . First averaging the least depths and associated widths then computing m from these values using (6) gives 5.10×10^{-5} .

For the estimated cross section relation we adopt a value of $m = 5 \times 10^{-5}$.

APPENDIX I

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

$$y = A x^b \tag{1}$$

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

$$\log y = \log A + b \log x \tag{2}$$

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 (1).

By differentiating (1) with respect to time, substituting (1) into the resulting derivative, and rearranging terms, one exposes the physical meaning of the exponential b :

$$b = \frac{\frac{1}{y} \frac{dy}{dt}}{\frac{1}{x} \frac{dx}{dt}} \tag{3}$$

As noted in Chapter 4 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 (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 (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

$$[A] = [y] [x]^{-b} \quad (4)$$

and (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 $\text{g} (\text{mm})^{-b}$. 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 $\text{s}/\text{m}^{1/3}$. As a corollary, if Y and X are measurements reported in units different from those native to (1), from which the corresponding exponential multiplier is \mathcal{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

$$Y = \mathcal{A} X^b$$

$$\Rightarrow Q_y Y = Q_y Q_x^{-b} \mathcal{A} (Q_x X)^b$$

$$\Rightarrow y = (Q_y Q_x^{-b} \mathcal{A}) x^b$$

$$\text{whence } A = Q_y Q_x^{-b} \mathcal{A} \quad (5)$$

We note that if y and x are in exactly the same units then (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 4-1 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 4-1 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 4-1 was computed from the reported \mathcal{A} as:

$$A = 10^{-b} \mathcal{A}$$

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 (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

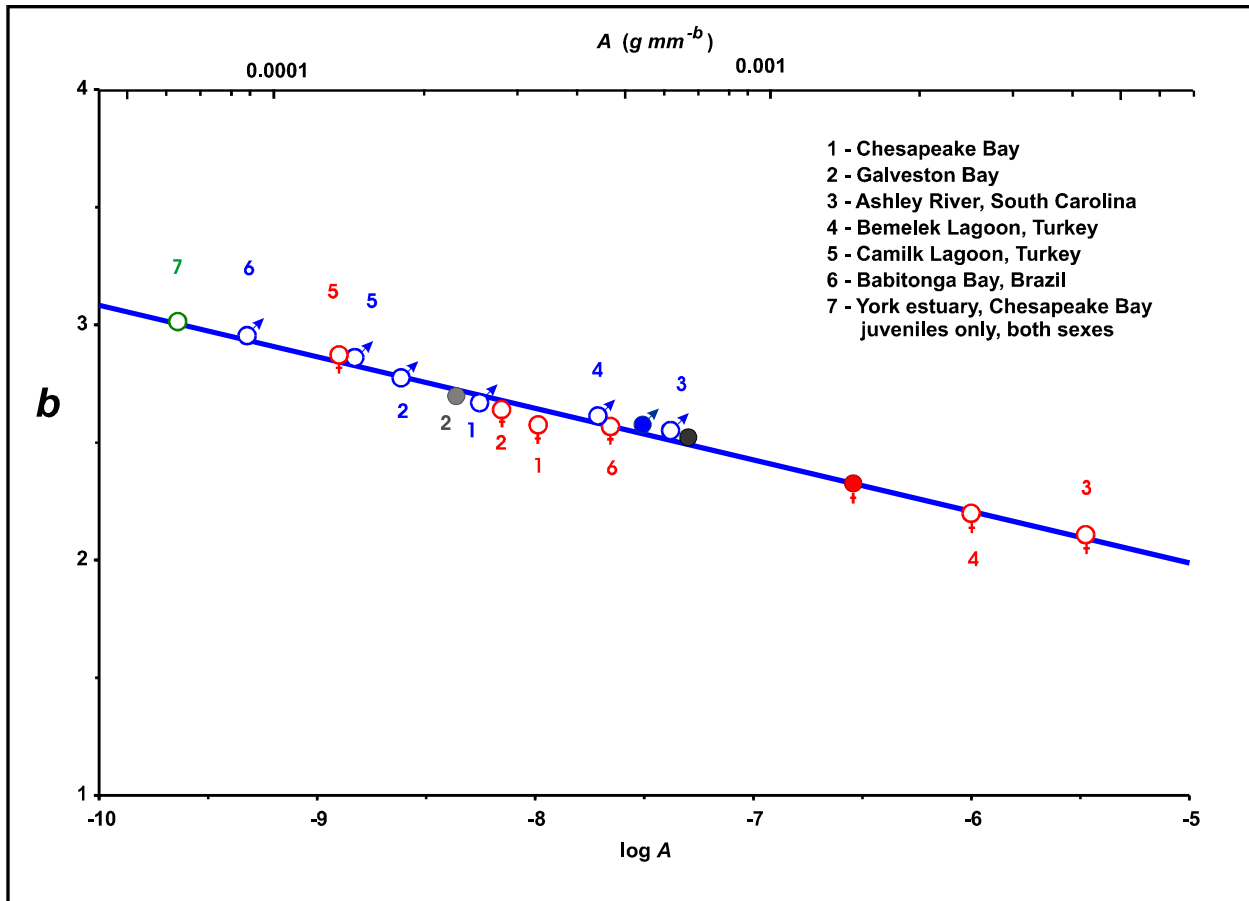


Figure A-1 - Regressed allometric equation parameters b (exponent) versus A (multiplier) from Table 4-1 as open circles, and least-squares regression line. Count-weighted pooled equations added for males, females and combined sexes (filled circles). Galveston Bay equation for combined sexes shown as 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 4-1* 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 (2), is fitted to a set of (\log) measurement pairs of carapace width (W) and body mass (M). In Table 4-1, 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.

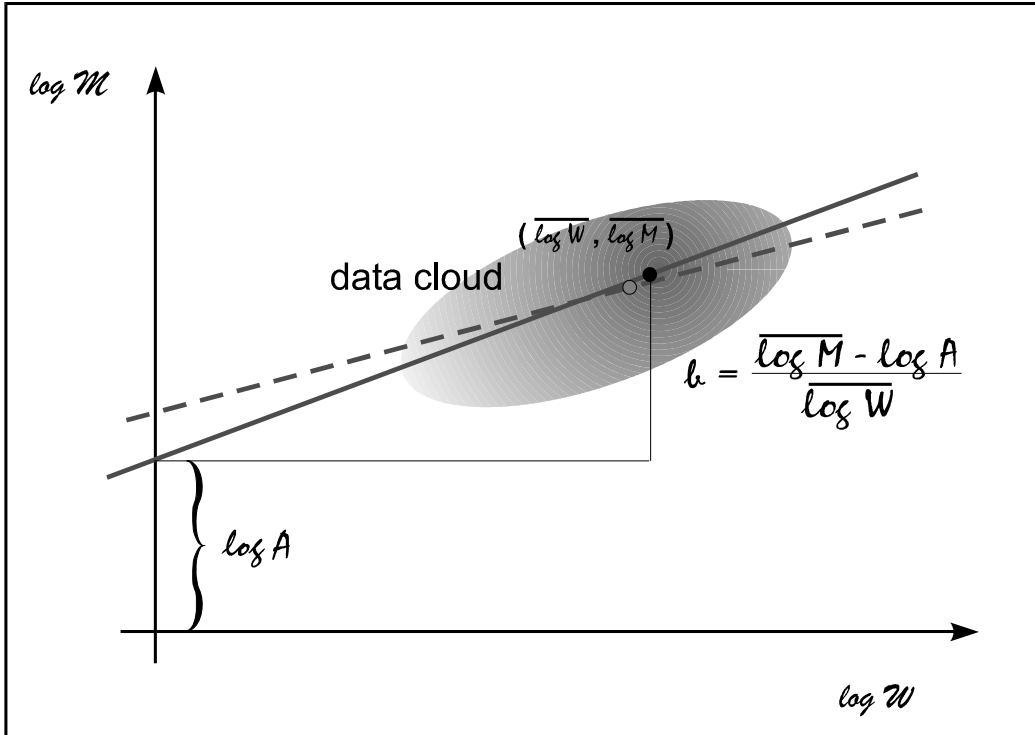


Figure A-2 - Sketch of regression line passing through cloud of log-transformed crab data.

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 4-1 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 4-1. In order to do this, we need either the raw data (which is obviously inaccessible) or the values of each of N , \bar{x} , \bar{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:

$$\bar{b} = \frac{\sum_i N_i b_i}{\sum_i N_i}, \quad \bar{A} = \frac{\sum_i N_i A_i}{\sum_i N_i} \quad (6)$$

where A_i, b_i are the regression parameters for the i th 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 4-1 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 (2) does not correspond to the best-fit power law (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 (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 J
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 here in Table J-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 J-1. These data are the source for Figure 4-12 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:

$$\int_{-\infty}^b n(w; \mu, \sigma) dw \qquad 1 - \int_{-\infty}^a n(w; \mu, \sigma) dw \qquad (1)$$

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 J-1
Data from Newcombe et al. (1949) on early juvenile instar carapace widths (CW, mm),
with best-guess at reconciliation, see text.

<i>Table 1</i>					<i>Tables 2 & 5</i>				
<i>Group</i>	<i>CW interval</i>		<i>number</i>	<i>mean CW</i>	<i>Group</i>	<i>CW interval</i>		<i>number</i>	<i>mean CW</i>
	<i>(range)</i>					<i>(range)</i>			
I	2.2	3.0	50	2.47	I	2.2	3.0	50	2.47
II	3.0	4.2	50	3.68	II	3.0	4.2	50	3.68
III	4.1	6.0	50	5.10	III	4.1	6.0	50	5.10
IV	5.5	7.4	50	6.64	IV	5.5	7.4	50	6.64
V	7.2	10.0	50	8.60	V	7.2	10.0	50	8.60
VI	8.7	12.4	50	10.19	VI	8.7	12.4	50	10.19
VII	9.7	13.0	35	11.00	VII	9.7	13.0	35	11.00
					VIII	13.5	16.5	6	14.50

<i>Table 6</i>					<i>Best guess corrected</i>					
<i>Group</i>	<i>CW interval</i>		<i>number</i>	<i>mean CW</i>	<i>Group</i>	<i>CW interval</i>		<i>number</i>	<i>mean CW</i>	<i>st dev CW</i>
	<i>(range)</i>					<i>(range)</i>				
I	2.2	3.0	50	2.5	I	2.2	3.0	50	2.47	0.14
II	3.0	4.2	50	3.7	II	3.0	4.2	50	3.68	0.25
III	4.1	6.0	50	5.1	III	4.1	6.0	50	5.10	0.42
IV	5.5	7.4	50	6.6	IV	5.5	7.4	50	6.64	0.46
V	7.2	10.0	50	8.6	V	7.2	10.0	50	8.60	0.66
VI	8.7	12.4	35	10.2	VI	8.7	12.4	50	10.19	0.85
VII	9.7	13.0	6	11.0	VII	9.7	13.0	35	11.00	0.81
					VIII	13.5	16.5	6	14.50	1.04

Table J-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. 4-12 of the text

<i>Instar</i>	<i>Newcombe et al. ranges</i>				<i>Pile et al. categories</i>			
	<i>lower</i>	<i>frac (%)</i>	<i>upper</i>	<i>frac (%)</i>	<i>lower</i>	<i>frac (%)</i>	<i>upper</i>	<i>frac(%)</i>
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 J-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. 4-12 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 J-1 have been compiled in Table J-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 J-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:

$$y = x + Rx = (1+R)x \quad (2)$$

Table J-3
Data from Gray and Newcombe (1938b) and Newcombe et al. (1949) on carapace-width increment on molting

<i>Early juveniles, sexes combined</i>												
<i>Instar</i>	<i>CW interval</i>		<i>number</i>	<i>initial final</i>		<i>increment</i>						
	<i>(range, mm)</i>			<i>(mm)</i>		<i>(mm)</i>	<i>(%)</i>					
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					
<i>juveniles, female</i>												
<i>Group</i>	<i>CW interval</i>		<i>number</i>	<i>mean CW (mm)</i>		<i>increment</i>						
	<i>(range, mm)</i>			<i>initial</i>	<i>final</i>	<i>(mm)</i>	<i>(%)</i>					
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
<i>juveniles, male</i>												
<i>Group</i>	<i>CW interval</i>		<i>number</i>	<i>mean CW (mm)</i>		<i>increment</i>						
	<i>(range, mm)</i>			<i>initial</i>	<i>final</i>	<i>(mm)</i>	<i>(%)</i>					

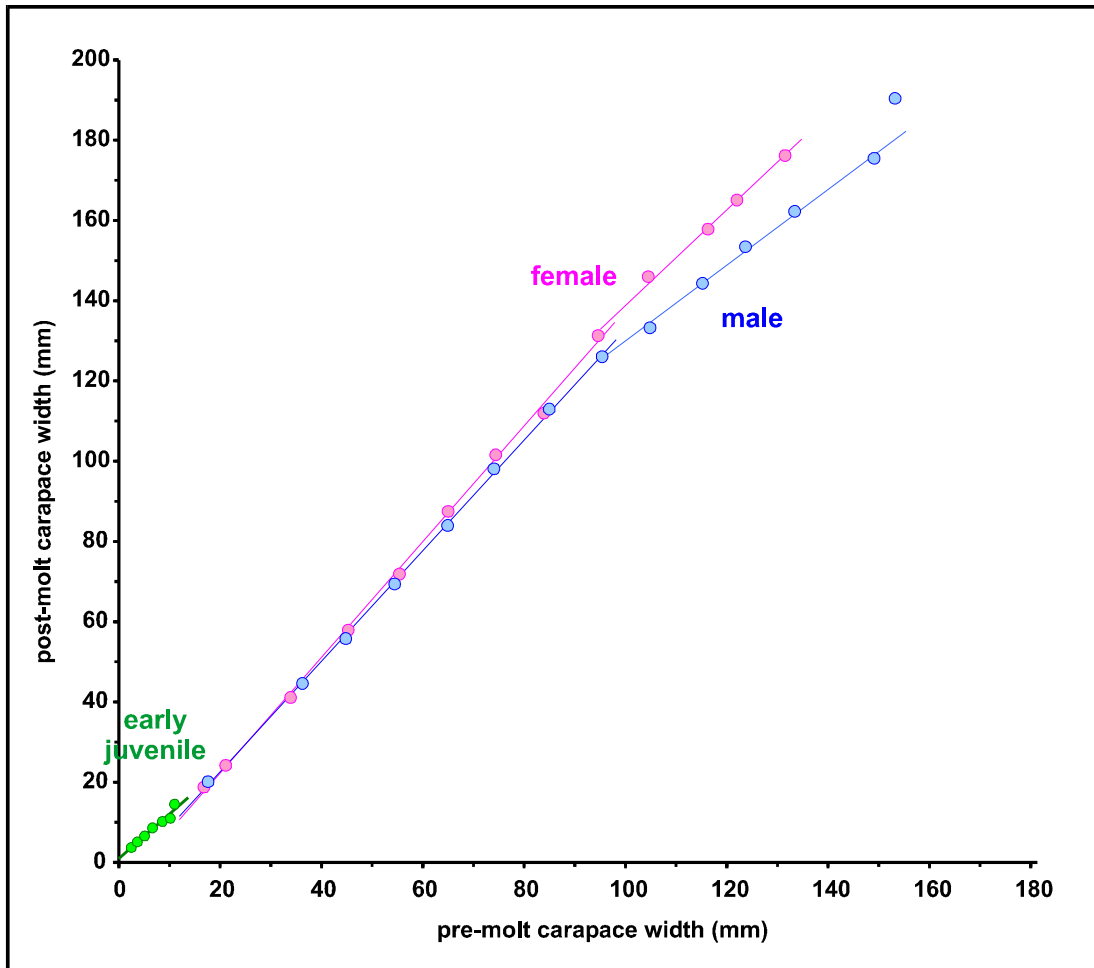


Figure J-1 - Post-molt carapace width regressed against pre-molt carapace width, data from Gray and Newcombe (1938b) and Newcombe et al. (1949)

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 J-3 yields a regression line $y = 1.285x + 0.36$, 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 J-1 above, which shows a different regression for the early juveniles and a break in slope at about 100 mm.

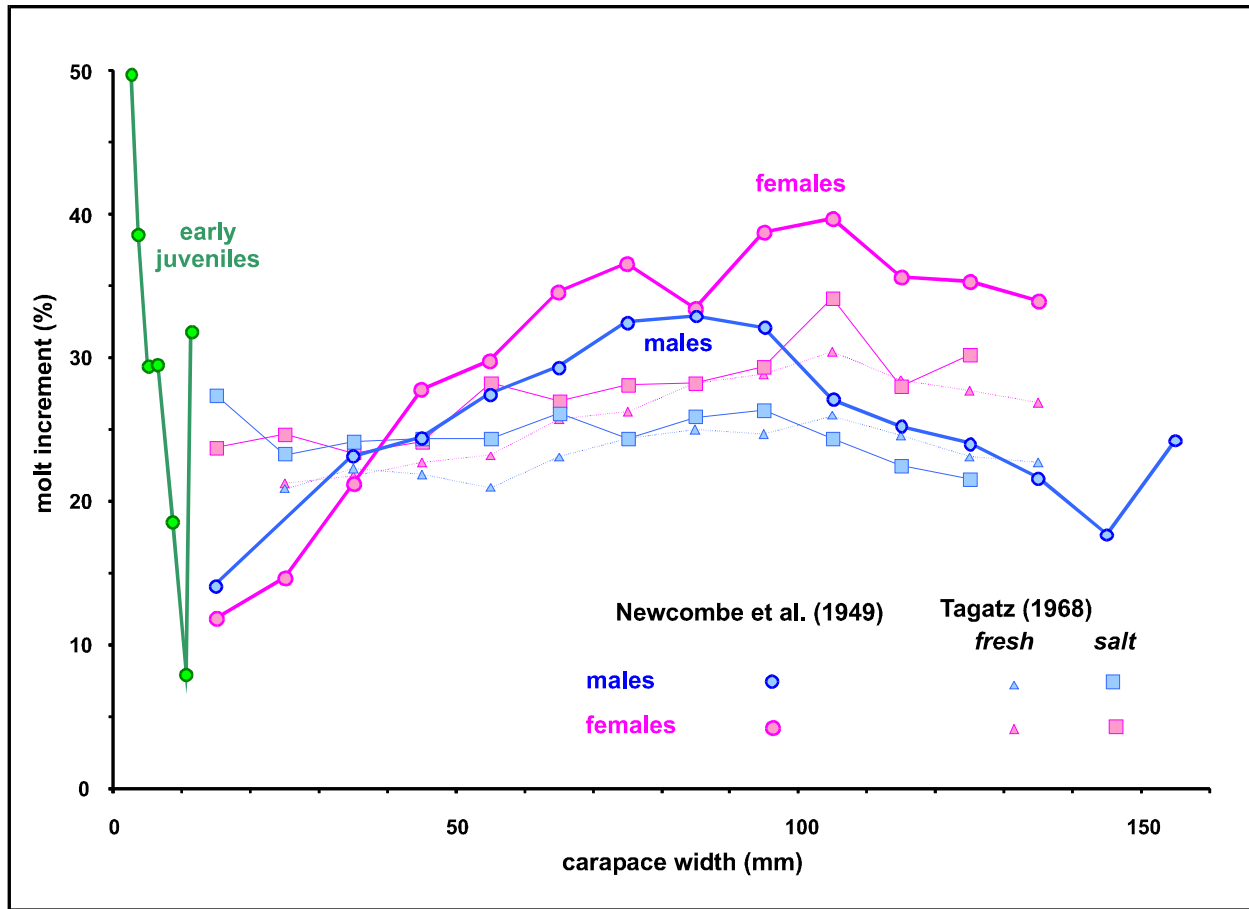


Figure J-2 - Apparent post-molt increment as fraction (%) of pre-molt carapace width as function of size of crab, data of Newcombe et al. (1949) and Tagatz (1968b)

This leads to an apparent variation in molt increment, as plotted in Fig. J-2. Much concern was indulged in by Newcombe et al. (1949) in explaining the variation in increment with carapace 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

$$\Delta w = (mx + b - x) / x = m - 1 + b / x \quad (3)$$

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. J-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),

Table J-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)

<i>Instar</i>	<i>Pile et al. (1996) category</i>		<i>Probability (%) of instar (Column 1) occurring in Pile et al. instar categories:</i>							
	<i>CW interval</i>		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>
<i>1</i>	2.2	3.0	97.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>2</i>	3.1	4.2	0.6	98.3	1.1	0.0	0.0	0.0	0.0	0.0
<i>3</i>	4.3	5.9	0.0	2.1	95.7	2.1	0.0	0.0	0.0	0.0
<i>4</i>	6.0	7.4	0.0	0.0	6.7	89.4	3.9	0.0	0.0	0.0
<i>5</i>	7.5	9.1	0.0	0.0	0.0	4.1	75.7	20.1	0.1	0.0
<i>6</i>	9.2	10.6	0.0	0.0	0.0	0.1	11.0	59.5	29.2	0.2
<i>7</i>	10.7	12.6	0.0	0.0	0.0	0.0	1.1	32.1	64.6	2.1
<i>8</i>	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

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 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 J-2. This same basic method is used in Table J-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 J-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 J-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 K
Life stage terminology

General terminologies applied to stages of development of blue crab, with representative citations, are collected below.

Larva	<ul style="list-style-type: none"> (1) All forms preceding the first crab instar, e.g., Robertson (1938), Truitt (1939, “two larval stages, zoea and megalops” (Van Engel, 1958), “zoea and megalopa larvae” (Kalber, 1970), “megalopal larval stage” (Tankersley et al., 1995), “megalopa larvae” (Epifanio, 2007), Dudley and Judy (1971), Adkins (1972), Smyth (1980), Perry and Stuck (1982) (2) Zoeae, including prezoaeae, Kennedy (2007)
Postlarva	<ul style="list-style-type: none"> (1) Any stage after the zoeal, from megalop up to (but not including) mature, e.g., Tagatz (1968a), Jivoff et al. (2007). (2) The megalop stage only, e.g. King (1971), Warner (1977), Welch et al. (1999), “postlarvae = megalopae” (Lipcius et al., 2007), Reyns et al. (2008)
Juvenile	<ul style="list-style-type: none"> (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)
Young crab	Juvenile (1), Perry and Stuck (1982)
Early juvenile	<ul style="list-style-type: none"> (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
Benthic juvenile	The first 5-7 instars (< 20-30mm), 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
Young juvenile	<ul style="list-style-type: none"> (1) The first eight or nine instars (2) Small juvenile
Small juvenile	<ul style="list-style-type: none"> (1) Carapace width less than 60 mm, e.g., Cadman and Weinstein (1985), 12-64 in Wilson et al. (1990), 20-65 mm in Rome et al. (2005) (2) 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
Subjuvenile	Carapace width less than 20 mm, McClintock et al. (1993)
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	Carapace width 120-140 mm, Osborn et al. (1992)

APPENDIX L

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

$$p V = n R T \quad (1)$$

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 cm³ atm/mol K)

At standard temperature (273 K) and pressure (1 atm = 1013 mb = 101.3 kPa = 760 mm Hg),

$$RT/p = V/n = 22.42 \text{ L/mol} \quad (2)$$

which is constant for oxygen, from which

$$1 \text{ mg O}_2/\text{L H}_2\text{O} (= 1 \text{ mg/L}) = 1.428 \text{ mL O}_2/\text{L H}_2\text{O} (= 1.428 \text{ mL/L}) \quad (3)$$

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):

$$\log\{C_s\} = A_1 + A_2 100/T + A_3 \log\{T/100\} + A_4 T/100 + S[B_1 + B_2 T/100 + B_3 (T/100)^2] \quad (4)$$

at standard atmospheric pressure, for C_s in mL/L, S in ppt and T in K, where:

$$\begin{array}{ll} A_1 = -173.4292 & A_3 = 143.3483 \\ A_2 = 249.6339 & A_4 = -21.8492 \\ B_1 = -0.033096 & B_3 = -0.0017000 \\ B_2 = 0.014259 & \end{array}$$

and $\log\{\}$ denotes the Napierian logarithm. C_s is converted to mg/L using (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., $c/C_s \times 100$ (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_{2s} is:

$$pO_{2s} = (n/n_{atm}) p = 0.2095 p \quad (5)$$

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:

$$pO_2 = 0.2095 p \frac{c}{C_s} \quad (6)$$

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 (5) and (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:

$$e_s = 6.11 \exp \left\{ \frac{m_v L}{R^*} \left(\frac{1}{273.15} - \frac{1}{T} \right) \right\} \quad (7)$$

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 M

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 M-1
Literature synthesis of life cycle of blue crab: hatching through megalop

<i>Stage</i>	<i>Hatching</i>		<i>Development of zoeae</i>		<i>Megalop stage</i>		<i>Citation</i>
	<i>Calendar</i>	<i>Peak mos</i>	<i>Duration</i>	<i>Calendar</i>	<i>Duration</i>	<i>Calendar</i>	
<i>Region:</i>							
<i>Mid-Atlantic</i>			3-6 weeks 4-7 weeks		1-2 weeks 5-8 weeks 3-6 weeks		Natunewicz & Epifanio (2001) Costlow and Bookhout (1959) Sulkin & Van Heukelem (1986)
<i>Delaware Bay</i>	Aug--Sep Jun-Sep	Jul-Aug	5 weeks 4-5 weeks			Sep-Oct	Epifanio et al. (1984) Epifanio and Tilburg (2008)
<i>Chesapeake Bay</i>		Jun-Jul			<1 month after hatching		Churchill (1919)
	July			Jul-Aug	1.5-2 mos after hatching	Jul-Sep	Truitt (1939)
	Jun-Aug	late Jul-Aug				Jul-Sep Aug-Dec al. (1989)	McConaugha et al. (1983) Provenzano et al. (1983), Goodrich et al. (1989)
<i>North Carolina</i>		Jun-Aug				Jul-Nov	van Montfrans et al. (1990), Olmi (1995) Dudley & Judy (1971), offshore from Beaufort Inlet Forward et al. (2004a), Newport River
<i>South Atlantic</i>		late Jul-Aug					
<i>South Carolina</i>	late summer summer						Archambault et al. (1990) early sprngMense and Wenner (1989) & fall (main)
<i>Georgia</i>	Mar-Sep	Apr-Jun					Palmer (1974)
<i>Florida</i>	Apr-Sep		2 months	May-Aug			Tagatz (1968a)
<i>Gulf of Mexico</i>							
<i>Mississippi Sound</i>	Mar-Nov					Mar-Nov peaks Jul-Sep	Perry and Stuck (1982)
<i>Louisiana</i>				Feb-Nov		May-Nov Feb-Nov	Stuck and Perry (1981) "abundant" Adkins (1972)
<i>Texas</i>	Mar-Sep May-Jun					Feb-Mar	Gunter (1950), Aransas-Copano 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 M-2
Literature synthesis of life cycle of blue crab: settlement through early development

<i>Stage</i>	<i>Settlement</i>		<i>Development to 20 mm</i>		<i>Development to 60 mm</i>		<i>Citation</i>
	<i>Calendar</i>	<i>Peak</i>	<i>Duration</i>	<i>Calendar</i>	<i>Duration</i>	<i>Calendar</i>	
<i>Region:</i>							
<i>Mid-Atlantic</i>							
<i>New Jersey</i>							
<i>Delaware Bay</i>							
<i>Chesapeake Bay</i>	Aug-Dec	Sep-Oct		Sep - Feb		Jun-Aug	Orth and van Montfrans (1987, 1990)
	Aug-Nov	Aug-Sep					van Montfrans et al. (1990)
<i>North Carolina</i>	Aug-Nov			Aug - Oct			Etherington & Eggleston (2000), APES
	Sep-Nov						Forward et al. (2004a), Newport River
<i>South Atlantic</i>							
<i>South Carolina</i>						Feb-Apr	Archambault et al. (1990)
	Aug-Oct						Boylan and Wenner (1993), intermittent
							Mense and Wenner (1989)
<i>Georgia</i>						Jan-Mar	Palmer (1974)
<i>Florida</i>	Sep-Dec			peak Aug-Dec			Tagatz (1968a)
<i>Gulf of Mexico</i>							
<i>Florida</i>							
<i>Mobile Bay</i>							
<i>Mississippi Sound</i>	Aug-Sep						Perry et al. (1995)
<i>Louisiana</i>					2-3 months	Nov-May	Adkins (1972), Vermilion
						Dec-Apr	Perret (1967), Vermilion
				May-Jun, Sep-Oct		summer	Darnell (1959), Pontchartrain
							Hasek & Rabalais (2001a)
<i>Texas</i>	year-round	Aug-Sep		year-round			More (1969), Galveston Bay
	year-round			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 M-3
Literature synthesis of life cycle of blue crab: grow-out through spawning

<i>Stage</i>	<i>Grow-out to maturity</i>		<i>Mating</i>		<i>Female migration down-estuary</i>		<i>Citation</i>
	<i>Duration</i>	<i>Calendar</i>	<i>Duration</i>	<i>Calendar</i>	<i>Duration</i>	<i>Calendar</i>	
<i>Region:</i>							
<i>Mid-Atlantic</i>							
<i>New Jersey</i>	14-24 mos	Jun-Jul		Jun-Sep peak Aug-Sep			Truitt (1939)
<i>Delaware Bay</i>	6-20 mos		1-3 days	May-Oct peak Jul-Sep	1 mo	Oct-Nov	Van Engel (1958), Hines (2007) Aguilar et al. (2008)
<i>Chesapeake</i>	14 mos			Jun-Jul			Williams (1984) Blackmon & Eggleston (2001)
<i>North Carolina</i>					1-2 mos	Sep-Nov Oct-Dec	Hines et al. (2008) Medici et al. (2006) Wolcott et al. (2005)
<i>South Atlantic</i>							
<i>South Carolina</i>	11-12 mos	May-Aug		Apr-Jun, Sep-Oct			Archambault et al. (1990)
<i>Georgia</i>		Apr-Nov					Palmer (1974)
<i>Florida</i>	10-12 months			Mar-Jul, Oct-Dec for temp > 22°C		Spring/Fall	Tagatz (1968a) Steele (1982)
<i>Gulf of Mexico</i>							
<i>Florida</i>	12 mos			Mar-Nov		Late fall	Perry and Stuck (1982)
<i>Mobile Bay</i>							Adkins (1972)
<i>Mississippi Sound</i>	10-12 mos	Sep-Oct		May, Sep		Jan-Mar Mar-Jul	Darnell (1959), Pontchartrain Daugherty (1952), Cedar Bayou
<i>Louisiana</i>							More (1969), Galveston Bay
<i>Texas</i>	12-15 mos	Mar-Oct					

Table M-4
Literature synthesis of life cycle of blue crab: spawning through egg development

<i>Stage</i>	<i>Spawning</i>		<i>Development of eggs</i>		<i>Next spawn-hatch</i>		<i>Citation</i>
	<i>Calendar</i>	<i>Peak months</i>	<i>Duration</i>	<i>Calendar</i>	<i>Duration</i>	<i>Calendar</i>	
<i>Region:</i>							
<i>Mid-Atlantic</i>			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)
<i>Delaware Bay</i>	Apr-Oct	Jul-Aug					Dittel & Epifanio (1982), Epifanio et al. (1984)
<i>Chesapeake Bay</i>	Apr-Oct	Jun-Aug					Truitt (1939)
<i>North Carolina</i>	Apr-Nov	Jun-Aug Mar-Oct	7-10 days		1.5-3.5 weeks		Harris (1982) Dickinson et al. (2006) Wolcott et al. (2005)
<i>South Atlantic</i>							
<i>South Carolina</i>	Apr-Aug						Archambault et al. (1990)
<i>Georgia</i>	Mar-Sep						Palmer (1974)
<i>Florida</i>	Mar-Sep			Jun-Oct			Tagatz (1968a)
	Water temps > 15						
<i>Gulf of Mexico</i>							
<i>Mississippi Sound</i>	Mar-Nov				Summer		Perry and Stuck (1982)
	Jun-Aug						Perry et al. (1995)
<i>Louisiana</i>	Mar-Jul			Mar-Jul			Adkins (1972)
	Mar, Aug-Sep						Darnell (1959), Pontchartrain
	Jun-Aug						Hasek & Rabalais (2001a), Terrebonne
<i>Texas</i>	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 N
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.

N-1. Otter trawls

The basic geometry of the otter trawl is sketched in Fig. N-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 N-2, is therefore dependent upon the trawling time **T**. The organism density per sampled volume is therefore:

$$n = R N / (C T A) \tag{1}$$

where

- n = organism density, count per unit volume
- N** = reported count of organisms
- C** = towing speed *relative to the water*

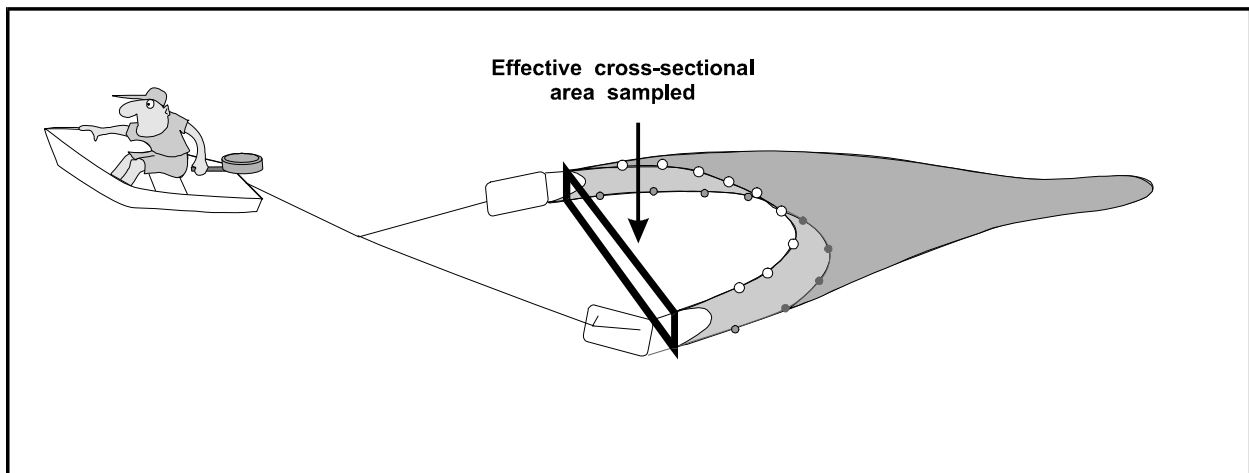


Figure N-1 - Geometry of otter trawl

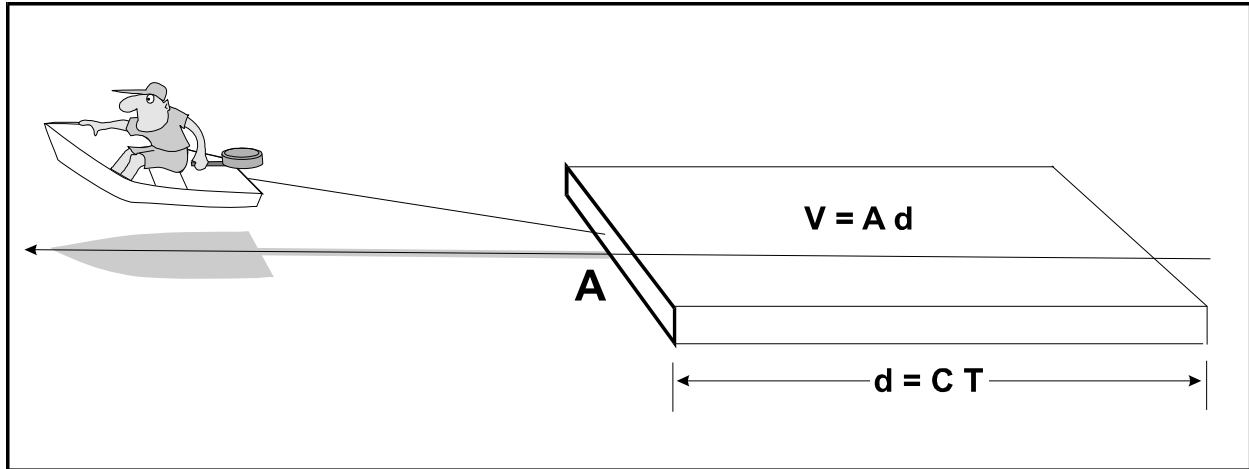


Figure N-2 - Sample volume intercepted by moving trawl

T = towing time duration
A = area of trawl opening
R = units conversion factor

For **A** in m^2 , **T** in *hours*, **C** in *mph*, and the organism density in *number/ac-ft*, $R = 0.7665$. (The choice of units of number/ac-ft is not an exercise in masochism, but turns out to render the density in values that are numerically on the same order as the raw counts, and therefore did not require scaling for several of the graphical displays employed in the data-base processing.)

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 A-3 is assumed to apply. We further assume that the headrope length L is controlling and under tow describes a semicircular arc, Fig. N-4. The resultant effective opening width w is therefore:

$$w = 2 L/\pi$$

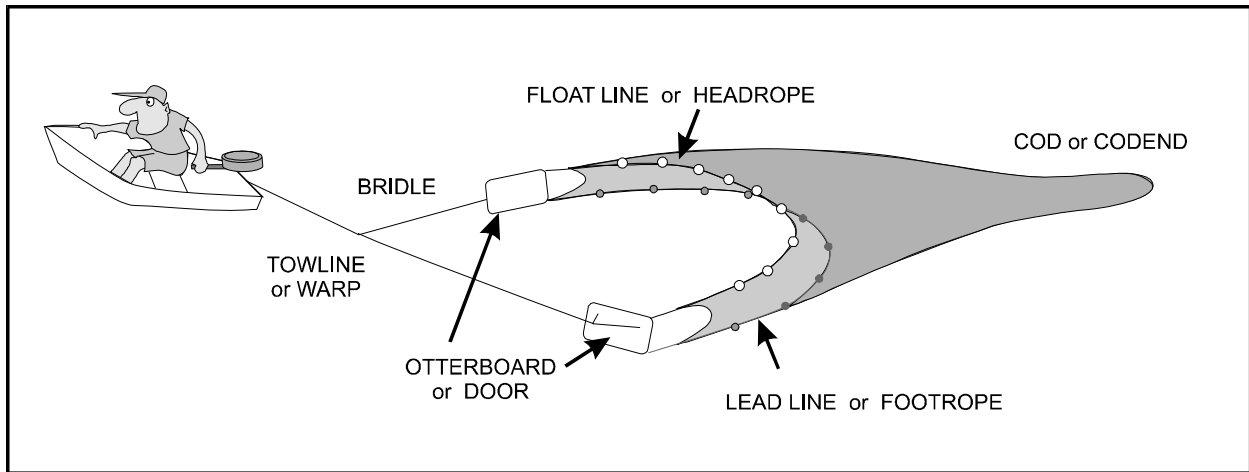


Figure N-3 - Trawl rigging nomenclature

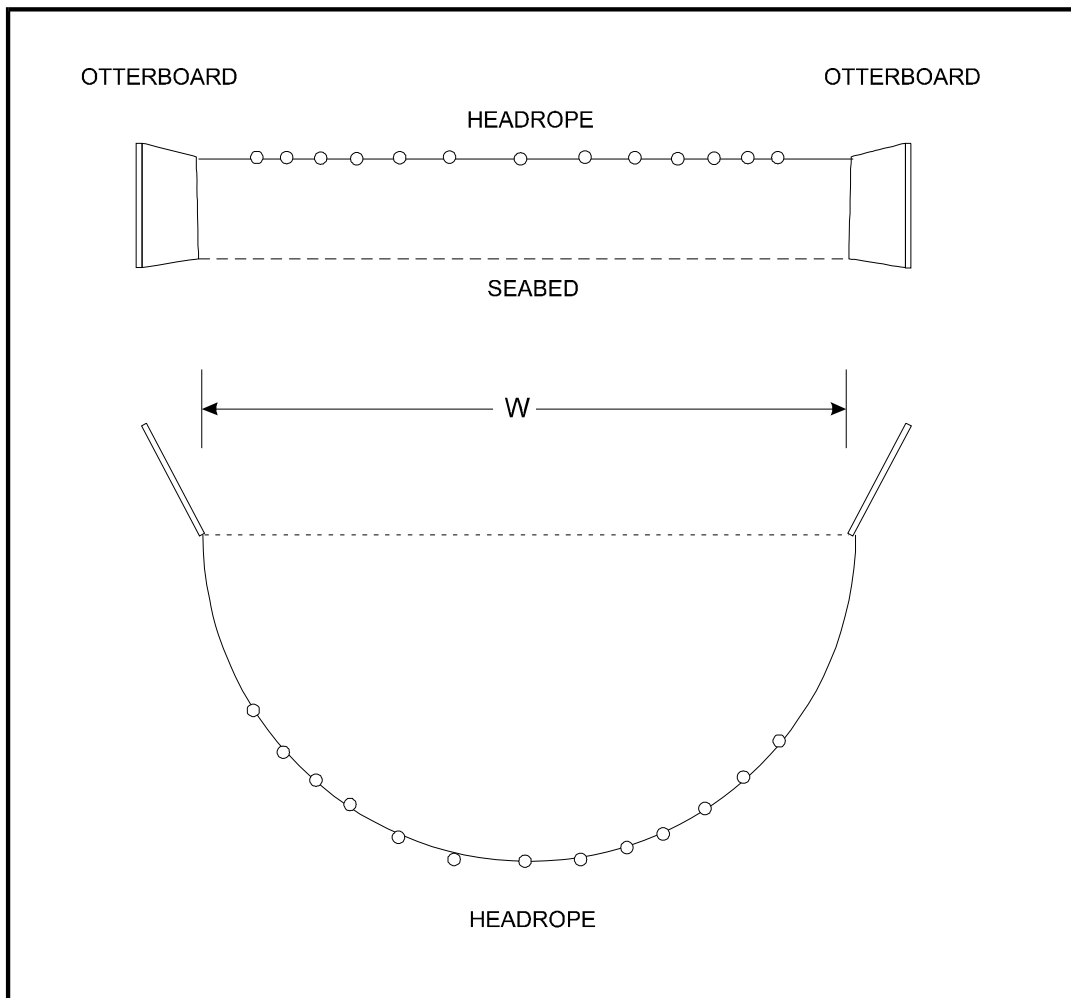


Figure N-4 - Trawl opening geometry in plane perpendicular to tow (above) and horizontal (below)

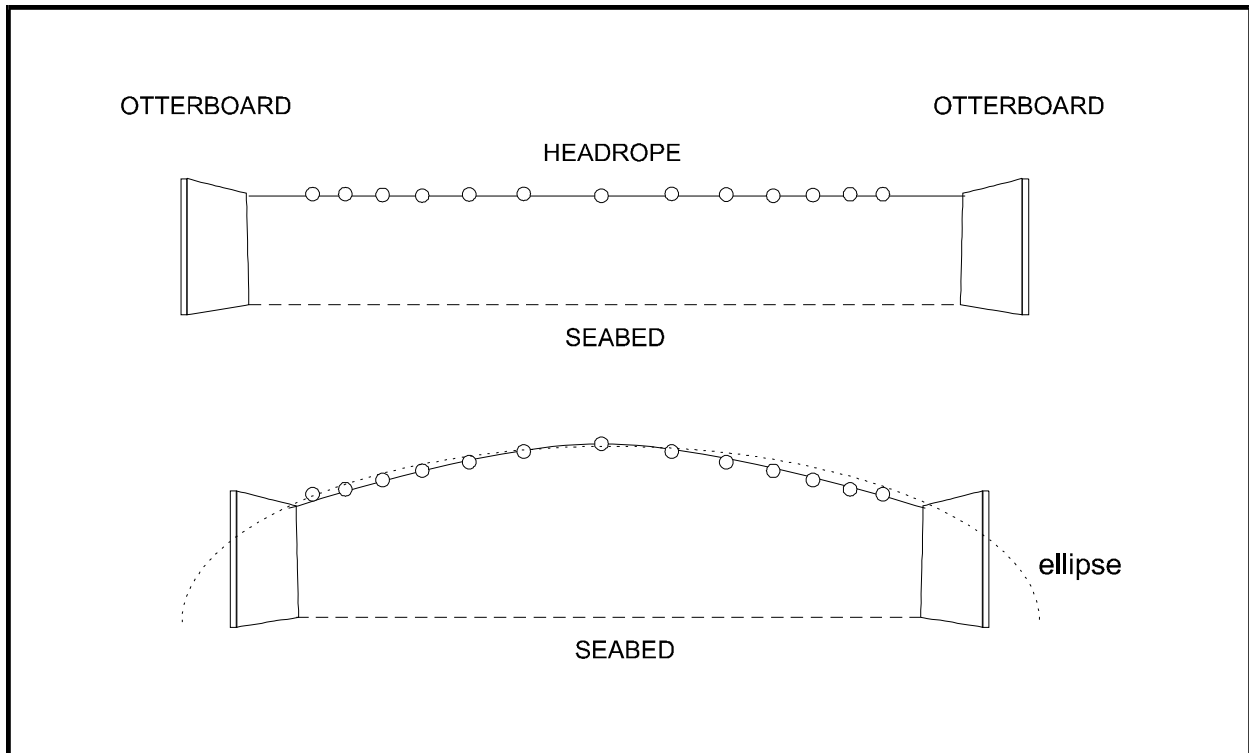


Figure N-5 - Hypothesized trawl opening geometry as in Fig. N-2 (above) and with buoyancy of headrope (below)

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 N-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

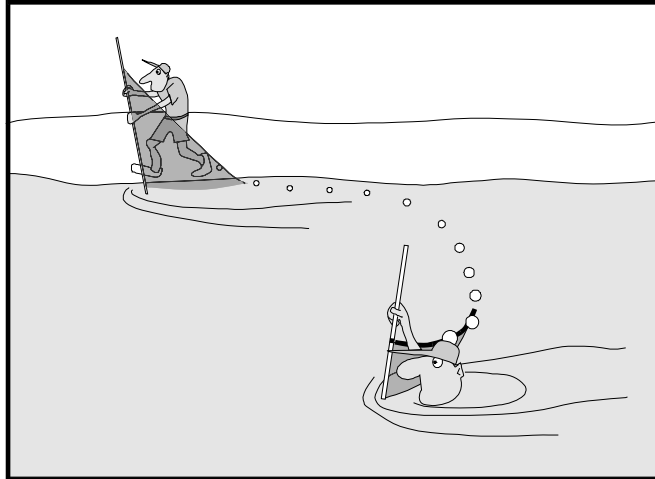


Figure N-6 - Bag seine execution

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.

N-2. Bag seines

The bag seine is a net drawn parallel to the shore (Figure N-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 N-7, the length S along the shore, and the depths at the shoreline terminus of the seine d_s and at the offshore terminus d . In principle, d_s should be zero, but there may be instances, such as sampling along the front of a marsh or a

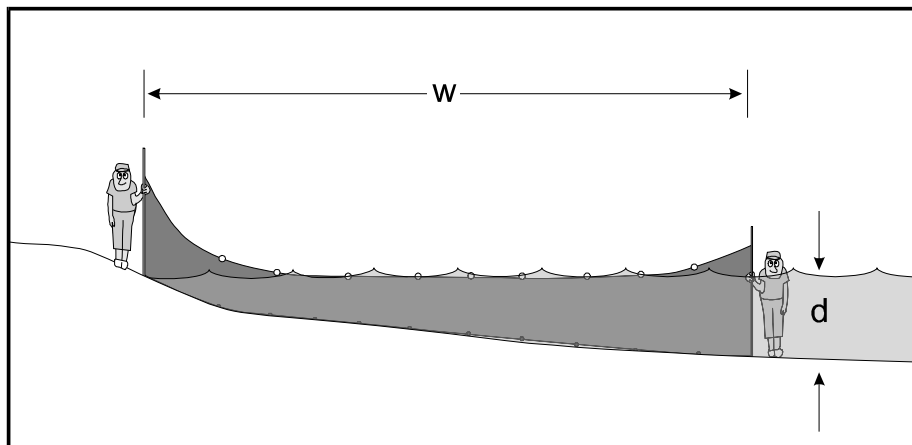


Figure N-7 - Bag seine position

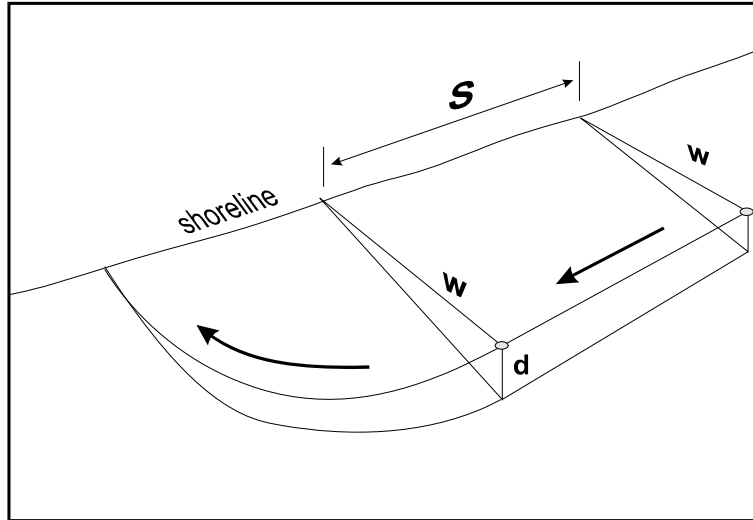


Figure N-8 - Volume sampled by bag seine

bulkhead, in which the shoreline is inaccessible. The execution of the bag seine haul is diagrammed in Figure N-8. The area sampled is a composite of a rectangle of area $w \times S$ 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 $302 \text{ m}^2 \approx 0.030$ 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 d_s , whereupon

$$\text{Volume (m}^3) \approx 10^4 \text{ AREA(ha)} 0.5(d + d_s) \quad (2)$$

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:

$$\text{Volume (m}^3) = 10^4 \text{ AREA(ha)} 0.5(d + d_s) - 0.118 (d - d_s) w^2$$

If $w = 12.2$ m,

$$\text{Volume (m}^3\text{)} = 10^4 \text{ AREA(ha)} 0.5(\mathbf{d} + \mathbf{d}_s) - 17.6 (\mathbf{d} - \mathbf{d}_s) . \quad (3)$$

or $\text{Volume (ha-m)} = \text{AREA(ha)} 0.5(\mathbf{d} + \mathbf{d}_s) - 17.6 (\mathbf{d} - \mathbf{d}_s) 10^{-4} .$

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 (3) gives a better estimate of volume than equation (2).

In summary, the corresponding organism density is then:

$$n = R \mathbf{N} / (\mathbf{A} \bar{d} + \text{corr}(\Delta d)) \quad (4)$$

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

\mathbf{d} = reported depth of water at deep pole

$\text{corr}(\Delta d)$ = correction term, a function of Δd , in units of **A** x units of **d**

$\Delta d = (\mathbf{d} - \mathbf{d}_s)$

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*,

$$\text{corr}(\Delta d) \approx 0.00176 \Delta d \quad \text{ha-m}$$

For organism density n in *number/m*³

$$R = 10^{-4} \quad \text{ha-m/m}^3$$

and for organism density n in *number/ac-ft*,

$$R = 0.1233 \quad \text{ha-m/ac-ft}$$

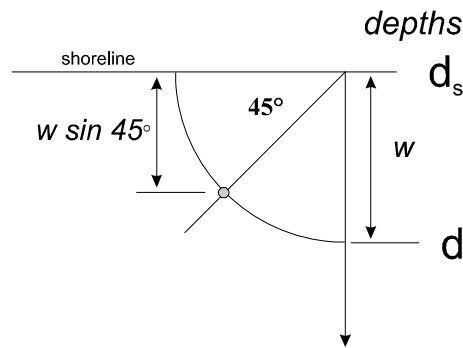
Unlike the otter trawl, the trajectory of the bag seine is referenced to coordinates fixed in space, *viz.* the shoreline and seabed. The volume of fluid intercepted by the seine as it passes from its starting position perpendicular to the shore to its ending position at the shoreface (Fig. N-8) depends 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. 8), a shoreline depth **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 ft³ out of 6000 ft³) will pass through the seine. Here "additional" means in the algebraic sense. The intercepted volume given by (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 8, in the rectangle, $\bar{d} = \frac{1}{2}(d+d_s)$.

In the quarter circle:



depth $D(y) = d_s + [(d-d_s)/w] y$

$$D(w/\sqrt{2}) = d_s + [(d - d_s)/w] w/\sqrt{2}$$

$$\begin{aligned} \text{average } \bar{D} &\approx \frac{1}{2} [d_s + D(w/\sqrt{2})] = \frac{1}{2} [d_s + d_s + (d - d_s)/\sqrt{2}] \\ &= \frac{1}{2} [(d + d_s) - d + d_s + (d - d_s)/\sqrt{2}] \\ &= \frac{1}{2} (d + d_s) - \frac{1}{2} [(1 - 1/\sqrt{2})(d - d_s)] \\ &\approx \frac{1}{2} (d + d_s) - 0.15 (d - d_s) \end{aligned}$$