

**THE BLUE CRAB
IN MID-ATLANTIC BIGHT ESTUARIES:
A PROPOSED RECRUITMENT MODEL**

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PREFACE

Typical of commercially exploited species, the blue crab has been the subject of numerous studies resulting in a sizeable literature. In spite of this considerable historical effort, few rigorous attempts have been made to understand the basic mechanisms controlling population dynamics in large systems, such as Chesapeake and Delaware bays. In a species such as the blue crab, characterized by high fecundity and a free-living larval stage, such information is essential to focus management effort in an effective and efficient way. In an attempt to address this issue, a program of research on recruitment strategy in the blue crab was initiated in 1978. The program has consisted of individual projects conducted by investigators at universities in Maryland, Delaware and Virginia and supported by respective Sea Grant programs in these states.

It is the purpose of this document to provide a narrative summary of the program as a whole through synthesis of results obtained in the various projects and integration of these results in a proposed conceptual model describing the mechanism of recruitment for the blue crab in estuaries of the Mid-Atlantic Bight. This synthesis effort has been facilitated by a continuing effort at communication among investigators and specifically by a workshop held on March 22-23, 1982, at the Horn Point Environmental Laboratories, University of Maryland, to develop the conceptual model. Participants in the conference included Drs. Stephen Sulkin, William Van Heukelem, Tim Cole and Robert Ulanowicz from the University of Maryland; Drs. Charles Epifanio and Rich Garvine from the University of Delaware; Drs. Anthony Provenzano, Donald Johnson, John McConaugha, Dave Johnson and Ms. Beth Hester from Old Dominion University; and Dr. William Boicourt from the Chesapeake Bay Institute, the Johns Hopkins University. Also present were Mr. Merrill Leffler and Dr. Dave Carley from the Maryland Sea Grant Program which has provided financial support for the workshop and the report arising from it.

The model and recommendations contained herein represent the best efforts of these individuals to interpret the data

generated by the program in the context of the substantial body of information available from other sources. While we assert that our conclusions are well-documented, there clearly remain topics which require further confirmation. Indeed, one measure of value of any conceptual model is the new questions it raises and the new hypotheses it suggests. We invite constructive criticism and look forward to pursuing the general topic of estuary-coastal water exchange in a second phase of the synthesis effort, namely, an invited conference on the topic, tentatively scheduled for Spring, 1983, to be held at the University of Delaware.

Stephen D. Sulkin

INTRODUCTION

Success in understanding and managing the large and commercially significant blue crab populations inhabiting estuaries of the Mid-Atlantic Bight has been limited because of a lack of rigorous information on fundamental questions relating to population dynamics. In a species which has high fecundity and a free-living planktonic larva, success in recruiting the juvenile stage to the adult habitat (estuary) is fundamental to regulation of population dynamics. There are two general categories of factors which influence recruitment success, namely, larval mortality (predation, starvation, environmental stress, etc.) and larval dispersal.

The dispersal question is a significant one in any estuarine species which produces planktonic larvae. As is the case with other estuarine species, the blue crab is faced with the requirement to maintain populations in the face of the net seaward flow of water characteristic of estuaries. In such circumstances, two recruitment mechanisms have been suggested: active retention of propagules within the estuary and/or immigration into the estuary from offshore.

Until recently, most theoretical considerations of population dynamics of blue crabs (and resulting management approaches) implicitly have invoked active retention as the primary method of recruitment of new individuals to the population. According to this model, for example, the large spawning populations present within Chesapeake or Delaware bays produce larvae which remain in the respective estuary and form the reservoir of individuals from which the new year-class will be derived. In order to evaluate critically the phenomenon of larval recruitment, and in response to direct and circumstantial evidence, program participants implemented in 1978 a coordinated research effort to test the hypothesis that the waters of the continental shelf serve as a significant source of new recruits. The hypothesized model involved transport of larvae from the estuary to the open sea and subsequent recruitment back to the estuary from offshore.

The program involved extensive and intensive field sampling to determine the vertical and geographic distribution of

various larval stages with respect to Chesapeake and Delaware bays, experimental studies on relevant larval behavioral adaptations characteristic of the species, genetic consequences of the hypotheses, and description of the physical system in which the larvae are being dispersed.

The following projects which address these issues have been supported by respective Sea Grant programs since 1978.

Maryland

- Significance of Chesapeake Bay spawning stock to recruitment of blue crabs to the Bay (R/F-8). 1978. S.D. Sulkin, Project Director; W. Van Heukelem, Associate Investigator.

Objectives

1. To quantify potential and realized fecundity of the blue crab.
 2. To determine behavioral responses of larvae to stimuli which may affect their vertical distribution and consequent horizontal movement.
 3. To improve methods of inducing out-of-season spawning of blue crabs.
- The source of blue crab recruitment in mid-Atlantic estuaries: larval behavior and genetic variations as indicators of larval exchange among estuarine systems (R/F-8). 1979. S.D. Sulkin, Project Director; W. Van Heukelem, Associate Investigator.

Objectives

1. To determine whether discontinuity layers caused by haloclines or thermoclines will disrupt vertical migration patterns in various larval stages of the blue crab.
2. To determine the effects of salinity and temperature on taxis and kinesis responses in blue crab larvae.
3. To determine whether genetic variability exists between populations inhabiting Delaware and Chesapeake bays and more distant estuaries.

- The source of blue crab recruitment in mid-Atlantic estuaries. The role of the megalopa stage and larval behavior at thermal and salinity discontinuities (R/F-19). 1981. S.D. Sulkin, W. Van Huekelem, Project Directors.

Objectives

1. To determine behavioral responses of the blue crab megalopa stage to gravity and pressure, and to determine the influence of temperature and salinity on these responses.
 2. To determine the presence of diel locomotory rhythm in the megalopa stage.
 3. To describe the behavior of blue crab zoeae to temperature and salinity discontinuities of the magnitude found in nature.
- Investigation of the genetic relationship among populations of the blue crab Callinectes sapidus in Chesapeake Bay (R/F-21). 1981. T. Cole, Project Director.

Objectives

To elucidate and compare the genetic structure of several isolated, commercially exploited populations of C. sapidus.

- Forecasting commercial finfish landings and crab catch from estuarine waters (R/F-22). 1981. R.E. Ulanowicz, Project Director.

Objectives

To identify key environmental factors affecting the size of blue crab stocks.

Delaware

- Dispersal and recruitment of blue crab larvae (R/M-4). 1979-81. C.E. Epifanio, Project Director; R. Garvine, Associate Investigator.

Objectives

1. To determine whether significant numbers of C. sapidus larvae are present in the shelf waters of the Mid-Atlantic Bight.

2. To determine whether exchange of larvae is occurring at the mouth of Delaware Bay.
 - (a) To document vertical distribution of larvae at the mouth of the Bay as a function of stage of development.
 - (b) To determine the relationships, if any, among transport of larvae and season, lunar cycle, and meteorological phenomena on the shelf.
 - (c) To determine changes in abundance of C. sapidus larvae throughout the spawning season.
 - (d) To document in detail the residual motion of surface and bottom water at the mouth of the Delaware Bay and on the adjacent shelf.

Virginia

- Distribution and migrations of blue crab larvae in the lower Chesapeake Bay and adjacent coastal waters (R/CF-2). 1979-1981. A.J. Provenzano, Project Director; J.R. McConaughy, Associate Investigator.

Objectives

1. To determine the role and fate of blue crab larvae hatched near the Bay mouth with respect to recruitment to the Chesapeake Bay.
2. To establish patterns of vertical distribution of blue crab larvae and megalopal stages at and near the Bay mouth with respect to time, tide, lunar cycle and water movements.
3. To use first year information to develop a sampling program for stations in the mouth of the Bay and offshore which will be sampled over the reproductive season to determine the distribution, both vertical and horizontal, of the major populations of blue crab larvae and particularly movements into and out of the area of the Bay mouth.
4. To extend field studies to offshore coastal waters in an attempt to determine more fully the fate of larvae hatched at the mouth of the Bay and the possible contribution of offshore larvae to Bay recruitment.

Although some of these projects are not totally completed, most of the data have been collected and analyzed. It is the purpose of this report to synthesize these results and to integrate them into a conceptual recruitment model.

In the following section, program results from each of the projects are summarized and the documents (proposals, reports, theses, publications) produced by the projects listed and cross-referenced to the program results. The Proposed Recruitment Model section describes the conceptual model which is supported by the evidence collected in this program as well as by the scientific literature. The process of synthesis and integration has revealed new areas of productive research which are itemized in the section entitled Research Needs. The model also suggests management implications which are described under Resource Management. All literature references contained within program documents are listed to provide a selected bibliography containing references which have proved useful to participants in the program.

PROGRAM RESULTS

This section summarizes results obtained during the course of this program. While the order of listing may appear to be somewhat arbitrary, it attempts to follow a logical progression from hatching to eventual recruitment. Many of the results can be attributed to more than one project. Projects credited for each result are indicated as the first item in parenthesis: Alphanumeric designations are identified in the project list presented in the Introduction and summarized at the end of this section (Page 11). The data sources for each result are listed as reference document numbers and are also included at the end of this section. Because the projects are still in various stages of development, the reference list contains papers, reports, theses and abstracts. Although more of this information eventually will make its way to the scientific literature, the present list is designed to provide ready access to the data base.

Summary of Project Results

1. All larval stages are found commonly in waters of the Mid-Atlantic Bight shelf off both Chesapeake and Delaware bays to a distance of at least 60 km, whereas only early larval stages and megalopae are present in significant numbers in the mouths of Delaware and Chesapeake bays. (R/CF-2, R/M-4; Ref. #1,2,3,5,19)
2. Peak abundance of Stage I larvae occurred from late July through mid-August in Delaware Bay in 1979 and from mid-July to mid-August in Chesapeake Bay in 1980, with the earliest appearance in late May in 1980. Earliest occurrence of megalopae was in mid-July offshore from Chesapeake Bay, with a peak in abundance in September in both estuaries. (R/M-4, R/CF-2; Ref. #2,4,19)
3. Greatest abundance of Stage I larvae captured in the spawning areas near the mouth of Chesapeake Bay occurred after nighttime high slack tide. Hatching thus appears to be synchronized with the ebb tide. (R/CF-2; Ref. 5)

4. In the laboratory, Stage I larvae exhibit negative geotaxis; positive phototaxis at intensities greater than 1.6×10^{-4} W/m² when dark-adapted; and high barokinesis at thresholds exceeding 1 atm increment, all of which suggest adaptation to upward migration. (R/F-8; Ref. #6,7)
5. Laboratory studies indicate that neither a sharp thermocline ($\Delta T = 10^{\circ}\text{C}$) nor a sharp halocline ($\Delta S = 10$ ppt) will disrupt upward vertical migration of Stage I larvae. (R/F-19; Ref. #8,9).
6. In field studies, no correlation could be established between vertical position of larvae and environmental parameters. (R/CF-2; Ref. #5) However, a locomotory rhythm keyed to light/dark cycles was observed in laboratory-reared Stage I larvae. (R/F-8; Ref. #10)
7. Stage I zoeae were captured predominantly in surface waters at the mouths of Delaware and Chesapeake bays. The neuston layer was found to be a zone of maximum concentration of first stage larvae in the bay mouths. (R/CF-2, R/M-4; Ref. #1,2,4,5,16)
8. Surface water residual flow is seaward from the Delaware and Chesapeake bays. (R/M-4; Ref. #11,12,20) Stage I larvae therefore will be transported from the estuary in surface waters onto the shelf. (R/F-8, R/F-19, R/M-4, R/CF-2; Ref. #1,2,5,7,8,13,16,17)
9. Low salinity surface waters moving seaward from the estuary mouth will tend to move southward in a plume. The plume decreases in intensity as it diffuses southward and seaward. Its characteristics are also subject to modification by wind stress. (R/M-4, R/CF-2; Ref. #11,12,20)
10. Stage I larvae are found predominantly in surface waters (neuston) offshore. (R/CF-2, R/M-4; Ref. #1,2,3,5,14,16,17) However, substantial densities have been reported near the bottom south of Delaware Bay, both nearshore and in the shelfwater cold pool as far as 20 km offshore. (R/M-4; Ref. #3)

11. Laboratory studies reveal that as zoeal development proceeds, passive sinking rates increase; larvae exhibit increasing tendency toward positive geotaxis, and exhibit reduced swimming rate in response to increased pressure, increased salinity and reduced temperature, all of which could result in increasing depth of distribution. (R/F-8; Ref. #6) See, however, Result #14.

12. Controlled laboratory studies indicate that the sign of phototaxis in Stage IV larvae (dark-adapted) varies according to intensity, with positive response shown at intensities greater than $1.6 \times 10^{-4} \text{ W/m}^2$. Light-adapted larvae remain positive at intensities down at $2 \times 10^{-2} \text{ W/m}^2$, become neutral and finally negative as intensity continues to drop. Stage VII zoeae show similar patterns, although intensity thresholds are generally higher than those for Stage IV zoeae in light-adapted larvae. (R/F-8; Ref. #7)

13. In the laboratory, progressively smaller haloclines are capable of disrupting vertical migration as zoeal development proceeds, although even in late zoeae, laboratory haloclines which are effective in inhibiting vertical movement will exceed those found in nature. (R/F-19; Ref. #8)

14. Numbers of larvae collected in the field decreased progressively through zoeal development. However, the greatest proportion were collected at the surface (neuston) at considerable distance from shore. (R/CF-2, R/M-4; Ref. #1,2,3)

15. In field studies off Chesapeake Bay, 83% of megalopae collected were found offshore in the neuston, whereas 17% were within the Capes of Chesapeake Bay. Only 2.2% of the total number collected were within the Chesapeake Bay proper. (R/CF-2; Ref. #1,17,18,19)

16. Laboratory studies reveal that megalopae exhibit negative geotaxis and high barokinesis to low pressure thresholds, indicating adaptation for precise depth regulation. Dark-adapted megalopae are positively phototactic at intensities in excess of $1.6 \times 10^{-4} \text{ W/m}^2$ and neutral at lower intensities. Light-adapted post-larvae show similar

patterns of response, although the intensity threshold is higher. (R/F-19; Ref. #8)

17. Field studies documenting vertical distribution of megalopae reveal several patterns of interest. Although megalopae were most abundant in the neuston when the water column was stratified, there was a downward shift in vertical distribution when the water column was vertically homogeneous. (R/CF-2; Ref. #19) There is also some indication of shifts in vertical distribution related to tide stage, with more megalopae high in the water column during flood tides than during ebb tides. (R/M-4; Ref. #3) Laboratory studies support the possibility of locomotory rhythms in megalopae. (R/F-19; Ref. #8)

18. In the southern Mid-Atlantic Bight, wind stress during July and August is characteristically poleward. Although the stress is light in intensity, analytical modelling indicates that it is sufficient to create a narrow corridor of poleward flowing water between the shoreline and the pressure-induced equatorward flow farther offshore. Windstress during September is such that it can cause shoreward and equatorward return of water. (RC/F-2; Ref. #14) Bottom water flows into Delaware Bay at a velocity 0.1 that of outflowing surface waters from all points within an arc extending from the Bay mouth to a distance of 40 km onto the shelf. (R/M-4; Ref. #11,12)

19. A comparison of commercial catch values with a wind index which governs the poleward drift currents shows significant relationship for both a one year and two year offset. (RC/F-2; Ref. #14)

20. Statistical analysis of frequencies of polymorphic loci indentified indicates that blue crab populations south of Cape Hatteras are more similar genetically to each other than to those north of this region. (R/F-21; Ref. #15)

Sea Grant Project Titles

- R/F-8: Significance of Chesapeake Bay spawning stock to recruitment of blue crabs to the Bay. S.D. Sulkin and W. Van Heukelem.
- R/F-8: The source of blue crab recruitment in Mid-Atlantic estuaries: larval behavior and genetic variations as indicators of larval exchange among estuarine systems. 1979. S.D. Sulkin and W. Van Heukelem.
- R/F-19: The source of blue crab recruitment in Mid-Atlantic estuaries. The role of the megalopa stage and larval behavior at thermal and salinity discontinuities. 1981. S.D. Sulkin and W. Van Heukelem.
- R/F-21: Investigation of the genetic relationship among populations of the blue crab Callinectes sapidus in Chesapeake Bay. 1981. T. Cole.
- R/F-22: Forecasting commercial finfish landings and crab catch from estuarine waters. 1981. R.E. Ulanowicz.
- R/M-4: Dispersal and recruitment of blue crab larvae. 1979-1981. C.E. Epifanio and R. Garvine.
- R/CF-2: Distribution and migrations of blue crab larvae in the lower Chesapeake Bay and adjacent coastal waters. 1979-1981. A.J. Provenzano and J.R. McConaugha.

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PROPOSED CONCEPTUAL MODEL

Based on results of the three Sea Grant programs and on the considerable literature background which exists on the blue crab, the workshop participants propose a generalized conceptual model of blue crab recruitment in the estuaries of the Mid-Atlantic Bight. The model, while consistent with the available data base, nevertheless leaves room for considerable refinement. Furthermore, it is based necessarily on an assumed hydrographic model for the near-shore to mid-shelf region. A narrative description of the assumed hydrographic model is presented, followed by a description of the recruitment model and summary.

Hydrographic Model

The hydrographic model is based on research of program participants, Drs. Richard Garvine and Donald Johnson as well as the work of Dr. William Boicourt who participated in the synthesis workshop and has collaborated with the program participants.

The two major estuaries of the Mid-Atlantic Bight, the Chesapeake and Delaware bays, exhibit classical circulation patterns characteristic of stratified estuaries. Residual flow of surface waters is seaward, with greatest net flow along the western (southern) shore. Low salinity water exported from the estuary forms a characteristic plume, which tends to be deflected towards the south of the estuary along the coast. The strength and extent of this plume depends upon both the magnitude of the estuarine outflow and wind stress. Strong southwesterly winds typical of late summer conditions can increase the seaward diffusion of the plume and conceivably even deflect it northward if wind stress is sufficiently high and outflow is relatively low. Probability of such reversal is relatively low at the Chesapeake Bay due to the magnitude of outflow. Reversals may occur occasionally at Delaware Bay and the Hudson River estuary, and may be apparent frequently at smaller estuaries, given necessary wind stress conditions. It seems likely that under average conditions of outflow and wind stress, the surface plume at Chesapeake and Delaware bays will be towards the south in a narrow band

along the coast. Its influence will gradually dissipate seaward and southward.

The shelf region seaward of the plume influence may be considered as two zones, the outer shelf and the inner shelf. The outer shelf circulation is dominated by longshore pressure gradients and is characterized by equatorward (southerly) drift; circulation in this region is relatively independent of wind stress, although extraordinary wind events could cause flow reversal. The shallow inner shelf region, however, is more responsive to wind stress.

Analytical models predict that because of strong and persistent southwesterly winds in mid to late summer, a corridor of poleward (northerly) flowing water typically will be present between the shoreline and the outer shelf. The extent and dominance of this northward flowing corridor will depend upon the wind stress and to some extent the characteristics of the estuarine plume. In contrast to late summer conditions, wind stress in the fall typically will produce a component of onshore drift in surface currents in the shelf region.

Bottom currents in the shelf region typically are directed onshore. This influence has been measured to a distance of 40 km offshore from the mouth of Delaware Bay and 60 km from the mouth of Chesapeake Bay. Typical of partially stratified estuaries, net residual flow is landward at depth within both Chesapeake and Delaware bays.

Recruitment Model

The hatching stage of blue crabs exhibits a combination of behavioral traits which will promote upward swimming and maintenance of position high in the water column. The vast majority of Stage I larvae are indeed found in the top one meter of the water column. Proximity of the spawning grounds to the estuary mouth and presence of larvae in surface waters will result in export of larvae from the estuary. Apparent synchronization of spawning just prior to or during ebb tide will complement this effect by selectively exploiting tidal as well as residual flow. Although past studies have reported blue crab zoeae within the estuary, the densities are

exceedingly low in comparison with those reported in present studies both at the surface near the estuary mouth and in offshore waters. The characteristic absence of intermediate stages in virtually all estuarine samples supports the significant and strongly documented conclusion that virtually all blue crab larvae produced within the estuary are exported to the waters of the continental shelf.

Once larvae are exported to the shelf, the pattern of dispersal will be governed by the circulation described previously. Several scenarios are suggested by the data and all may occur to some extent.

A small fraction of larvae are found at depth. These larvae will tend to be transported towards shore and may reenter the estuary. However, because of the comparatively small numbers of larvae and the possibility that larvae trapped below the thermocline will be subjected to high mortality, the significance of this source of recruitment from offshore is thought to be low.

Much greater densities of zoeae are found consistently in surface waters throughout the shelf region of the Mid-Atlantic Bight. The proposed model invokes wind driven circulation as a key factor in retaining larvae within the Mid-Atlantic Bight region. This mechanism is particularly important considering the potential size and significance of the larval populations exported from Chesapeake Bay and transported in the plume towards Cape Hatteras, where significant loss to the Gulf Stream and slope waters could occur.

Let us consider two extreme circumstances that the model predicts. If wind stress from the southwest is low, the predicted northward corridor will be reduced in size and speed. Larvae entrained in the estuarine plume will be transported towards the south and substantial numbers may be entrained in the Gulf Stream or transported around Cape Hatteras into the South Atlantic Bight. As a result, there could be a substantial reduction in the pool of larvae available for recruitment to Mid-Atlantic Bight estuaries. Alternatively, strong wind stress from the southwest could result in a broad northward corridor, reducing the southward influence of estu-

arine plumes (reversing some), and could even reverse outer shelf flow for a short time. As a consequence, there would be almost total retention of larvae within the Mid-Atlantic Bight, increasing substantially the pool of larvae available for recruitment back to the estuary.

There are two kinds of intermediate scenarios, one in which wind stress is steady, but moderate. Assuming that the minimum threshold of wind stress required to create some degree of flow reversal is exceeded, the effects upon retention within the Bight will be intermediate, depending upon the degree and extent of reversal which occurs. Alternatively, there could occur major, short-term wind events. The influence upon retention of the latter event will vary depending upon its timing, frequency and persistence.

The model thus invokes wind-driven shelf circulation as a dominant mechanism in creating and regulating the pool of larvae from which recruitment to the estuarine habitat will occur. The relative size of this pool (degree of retention within the Bight) is particularly significant given the apparent absence of a conservative mechanism for re-entry of offspring to the estuary.

In spite of behavioral responses which suggest a mechanism to promote deeper distribution of late zoeal stages which thus could result in a conservative retaining mechanism through onshore bottom drift, extensive field sampling does not indicate the presence of large numbers of larvae at depth. Furthermore, the megalopa stage exhibits a change in behavioral response which should result in surface distribution, a pattern that is confirmed by field sampling. There exist both anecdotal accounts and hard data to suggest that appearance of the new year-class is characterized by a substantial and sudden increase in numbers of megalopae at the estuary mouth and very small juveniles within the estuary. This suggests strongly the presence of mass transport of immigrants from the near-shore pool of potential recruits. The second controlling phase of the recruitment process is therefore the re-entry to the estuary by post-larvae and/or early juveniles due either to fortuitous on-shore drift or via selection of flood tides. The latter mechanism has been invoked for other

crustaceans, including the anomuran crab Callinassa californiensis (Johnson and Gonor 1982). Re-entry to the estuary is dependent upon the presence of large numbers of potential recruits near the estuary mouth. The degree of recruitment from offshore therefore will depend upon the size of the available larval pool and the presence and appropriate timing of factors inducing landward transport in surface waters.

Summary

Larvae produced within estuaries of the Mid-Atlantic Bight are exported to shelf waters. Their initial subsequent dispersal will depend upon plume characteristics and will vary among estuaries. From Chesapeake Bay and usually from Delaware Bay, initial transport likely will be toward the south. The degree of retention within the Mid-Atlantic Bight is dependent upon wind driven circulation in the near-shore region. Prevailing southwesterly winds in late summer will result in some degree of retention annually. However, the degree of retention which occurs annually will establish the size of the pool of potential recruits and is the first major factor regulating recruitment success. Re-entry to the estuary occurs when post-larvae or juveniles are transported landward, although the precise mechanism remains to be described. The co-occurrence between appropriate on-shore driving forces and availability of post-larvae is most likely the second major factor regulating recruitment success. This highly problematic second-phase mechanism could influence ultimate recruitment success, not only directly by determining numbers of new recruits, but indirectly by affecting the timing of initial recruitment and, in so doing, influencing subsequent survival of juveniles in the estuarine habitat.

The body of available evidence supports a model which is dominated by abiotic driving forces and is sensitive to episodic events. There are a number of points in the process where more conservative mechanisms eventually may be demonstrated. These include the previously mentioned possibilities that late developmental stages are at depth for a period of time and that megalopae or juveniles preferentially exploit tidal currents to invade the estuary. However, should new evidence support either possibility, the consequences to

the model will represent fine-tuning rather than substantive change.

RESEARCH NEEDS

The attempt to integrate available information into a model for recruitment of the blue crab has revealed several areas where additional research is needed. We identify below topics of research which can refine and test the proposed recruitment model.

1. Additional data are needed on distribution of larval stages offshore and specifically in shallow water regions near the estuary mouth. Of specific significance is the geographic and vertical distribution of intermediate and late zoeal stages and tidal, diurnal and ontogenetic shifts in vertical distribution of megalopae. Near-shore distribution patterns are needed to assist in development of a population dynamics model which relates distance transported to subsequent catch. These topics also can clarify whether more conservative options to the model indeed exist.
2. Confirmation is needed regarding the predicted banding characteristics of inner shelf waters, specifically a calibration of analytical models which predict reversal of inner shelf currents. Models which predict flow and configuration of plumes at the mouths of Delaware and Chesapeake bays are also needed.
3. The dynamic fisheries models which seek to relate environmental driving forces to subsequent catch require further development.
4. Temporal and spatial distributions of juveniles in shelf waters and in lower estuaries are required in order to interpret the influence of driving forces on re-entry to the estuary. Behavior of juveniles with respect to currents and endogenous locomotory rhythm will also be helpful in interpreting population dynamics models.
5. To interpret and test predictive models, a reliable index on juvenile abundance is essential. Available data should be assessed and a reliable, systematic survey should be initiated.

RESOURCE MANAGEMENT IMPLICATIONS

1. The nature of the recruitment process suggests that a regional approach is necessary in evaluating crab populations. The Mid-Atlantic Bight system should be considered to support an integrated population, although recruitment back to the parent estuary will occur frequently, especially in those systems contributing substantially to the offshore pool of larvae.
2. A recruitment process which is dependent upon abiotic driving forces, such as the one described here, should be amenable to development of predictive models for recruitment success.
3. Although there obviously must exist a theoretical threshold of spawning stock size below which inadequate numbers of larvae will be produced, the proposed model of recruitment renders improbable direct relationship between size of the spawning stock and subsequent year-class strength. In marine species which exhibit a broadcast strategy in reproduction, density-dependent mortality of offspring typically reduces the relationship between spawning stock size and year-class strength. In the blue crab, there is the additional domination of abiotic factors which influence the success of recruitment to the adult habitat. For example, although a large spawning stock may yield comparatively large numbers of larvae, unfavorable wind conditions may deplete the pool of potential recruits below that which may occur when a smaller larval production is combined with favorable retention conditions. On the other hand, when complementary biotic and physical factors are present (low production X low retention; high production X high retention) the net size of the pool of potential recruits may be more subject to regulation by density-dependent phenomena.
4. Although there presently exist few data on blue crab catch in northern estuarine systems, collection of such data could provide for a useful test of the model. It is a consequence of the model that because of the southern location of Chesapeake and Delaware bays within the bight and the relative numbers of larvae they contribute to the offshore pool, annu-

al recruitment in these two large estuaries is likely to be less variable than in estuaries which are smaller and located farther to the north. Indeed it is reasonable to speculate that the most northern estuarine systems (Long Island, Cape Cod) are likely to receive substantial recruitment only in the years when the northward flow is pronounced.

5. A theoretical basis exists for a reciprocal level of recruitment north and south of Cape Hatteras depending upon the fate of larvae produced in Chesapeake Bay. When the northward flow is not well-established, some larvae may be transported to the estuarine systems of North Carolina, augmenting the naturally produced pool of recruits in that region.

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