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. McConaugha, 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/m^2 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 ($\Delta T = 10^{\circ}C$) 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 1.6×10^{-4} W/m^2. Light-adapted larvae remain positive at intensities down at 2×10^{-2} 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 lavae. (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 1.6×10^{-4} 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.

Reference Documents

1. McConaugha, J., A.J. Provenzano, D.F. Johnson and R. Maris. 1982. Horizontal and vertical distribution of larvae of *C. sapidus* in offshore waters adjacent to the mouth of Chesapeake Bay, VA., USA; manuscript submitted.
2. McConaugha, J., D.F. Johnson, A.J. Provenzano and R.C. Maris. (1982) The seasonal distribution of larvae of *C. sapidus* in the waters adjacent to Chesapeake Bay; manscript submitted.
3. Epifanio, C.E., 1982. Project Report.
4. Dittel, A.J. and C.E. Epifanio. 1982. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. Estuaries (in press).

5. Provenzano, A.J., J.R. McConaugha, K.B. Phillips, D.F. Johnson and J. Clark. 1982. Diurnal vertical distribution of first stage larvae of the blue crab Callinectes sapidus at the mouth of Chesapeake Bay. Estuarine Coastal and Shelf Science (in press).

6. Sulkin, S.D., W. VanHeukelem, P. Kelly and L. Van Heukelem. 1980. The behavioral basis of larval recruitment in the crab Callinectes sapidus Rathbun: A laboratory investigation of ontogenetic changes in geotaxis and barokinesis. Biol. Bull., 159:402-417.

7. Sulkin, S.D. 1980. The behavioral basis for blue crab recruitment in mid-Atlantic estuaries. Final Technical Report Project R/F-8, CEES Ref. No. 80-150 HPEL; Maryland Sea Grant UM-SG-TS-81-07.

8. Sulkin, S.D. and W. Van Heukelem. 1982. Larval recruitment in the crab Callinectes sapidus Rathbun: an amendment to the concept of larval retention in estuaries. In: Estuarine Comparisons, ed. V. Kennedy, Academic Press (in press).

9. McConnaughay, R. 1982. The role of thermoclines in the vertical migration of Stage I blue crab larvae. University of Maryland MEES Program. Masters Thesis (in preparation).

10. Sulkin, S.D., I. Phillips and W. Van Heukelem. 1979. On the locomotory rhythm of brachyuran crab larvae and its significance in vertical migration. Marine Ecology-Progress Series, 1:331-335.

11. Pape, H.E., 1981. A drifter study of the Lagrangian mean circulation of Delaware Bay and adjacent shelf waters. Masters Thesis, University of Delaware, Newark, DE. 150 pp.

12. Pape, H.E. and R.W. Garvine. 1982. A drifter study of the subtidal circulation of the Delaware Bay and adjacent shelf waters. Journal of Geophysical Research (in review).

13. Epifanio, C.E. and A. Dittel. 1982. Comparison of dispersal of crab larvae in Delaware Bay and the Gulf of Nicoya, Central America. In: Estuarine Comparisons, ed. V. Kennedy, Academic Press, (in press).

14. Hester, B., D.R. Johnson and J. McConaugha. 1982. A physical model of blue crab larval distribution. Abstract, Spring meeting of the Atlantic Estuarine Research Society, Balt., MD., April 23-24, 1982.
15. Cole, T.J. 1982. Gene structure of Atlantic coast blue crab (C. sapidus) populations. Abstract, Spring meeting of the Atlantic Estuarine Research Society, Balt., MD., April 23-24, 1982.
16. McConaugha, J.R. and A.J. Provenzano. 1980. Distribution and migration of blue crab larvae in the lower Chesapeake Bay and adjacent coastal waters. Abstract. Amer. Zool., 20(4):888.
17. McConaugha, J.R., A.J. Provenzano, D.F. Johnson, J. Clark and P. Sadler. 1981. Offshore displacement and reinvasion of Callinectes sapidus larvae in Chesapeake Bay. Estuarine Research Federation Meeting, November 1981, Gleneden Beach, OR. Abstract. Estuaries 4:277.
18. Johnson, D.F. 1981. The use of recruitment mechanisms by the megalopae of selected brachyuran crustaceans of the lower Chesapeake Bay and inner Continental Shelf. Estuarine Research Federation Meeting, November 1981, Gleneden Beach, OR. Abstract. Estuaries 4:277.
19. Johnson, D.F. 1982. A comparison of recruitment strategies among brachyuran crustacean megalopae of the York River, lower Chesapeake Bay, and adjacent shelf waters. Doctoral thesis, Old Dominion University, Norfolk, VA. 100 pp.
20. Boicourt, W.C. 1981. Circulation in the Chesapeake Bay entrance region: estuary-shelf interaction. In: Chesapeake Bay Plume Study Superflux, eds. G.W. Campbell and J.P. Thomas. 1980. NASA Sci. Tech. Information Branch. Dept. of Commerce. NASA Conf. Pub. 2188, NOAA/NEMP III; 81; ABCDFG, 0042. 516 pp.

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 estuarine 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 Callianassa 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.

SELECTED BIBLIOGRAPHY

Anderson, A.M., W.J. Davis, M.P. Lynch and J.R. Schubel (eds.). 1973. Effects of Hurricane Agnes on the environment and organisms of Chesapeake Bay. A report for the U.S. Army Corps of Engineers, Philadelphia District. The Chesapeake Bay Research Council, C.B.I. Contri. No. 187, N.R.I. Contri. No. 529, VIMS Special Report in Marine Science and Ocean Engineering No. 29.

Ayala, F.J. 1976. Molecular genetics and evolution. pp 1-20 In: Molecular Evolution. F.J. Ayala (ed.). Sinauer Associates, Sunderland, Mass. 226 pp.

Ayala, F.F., D. Hedgecock, G.S. Zumwalt and J.W. Valentine. 1973. Genetic variation in Tridcna maxima, an ecological analog of some unsuccessful evolutionary lineages. Evol. 27(2):177-191.

Beardsley, R.C., W.C. Boicourt and D.V. Hansen. 1976. Physical oceanography of the Middle Atlantic Bight. Limnol. Oceanogr. Spec. Symp. 2:20-34.

Beaver, G.F. 1932. A Study of the biology and economic importance of the blue crab. Chesapeake Biological Laboratory Study supported by State of Maryland and Virginia. Unpublished M.S. 27pp.

Bentley, E. and S.D. Sulkin. 1977. The ontogeny of barokinesis during the zoeal development of the xanthid crab, Rhithropanopeus harrisii (Gould). Mar. Beh. & Physiol. 4:275-282.

Bigford, T.E. 1977. Effects of oil on behavioral responses to light, pressure and gravity in larvae of the rock crab Cancer irroratus. Mar. Biol. 43:137-148.

Boicourt, C.C. and P.W. Hacker. 1976. Circulation on the Atlantic continental shelf of the United States, Cape May to Cape Hatteras. Mem de la Soc. Roy. Scie. Liege 6:187-200.

Bousfield, E.L. 1955. Ecological control of the occurrence of barnacles in the Miramichi Estuary. Nat. Mus Canada, Bull. 137, Biol. Sere. 46:1-69.

Brooks, W.K. 1882. The metamorphosis of a crab. In: Handbook of Invertebrate Zoology. S.E. Cassino. Boston. pp. 207-223.

Bumpus, D.F. 1965. Residual drift along the bottom on the continental shelf in the Middle Atlantic Bight area. Limnol. Oceanogr. Suppl. 10:R50-R53.

Bumpus, D.F. 1973. A description of the circulation on the continental shelf of the east coast of the U.S. Progr. Oceanogr., 6:111-157.

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

Carriker, M. 1951. Distribution of oyster larvae in the New Jersey estuaries. Ecol. Monogr. 21(1):17-38.

Carriker, M.R. 1967. Ecology of estuarine benthic invertebrates, pp. 442-487. In: G.H.Lauff (ed.), Estuaries. AAS, Washington, D.C.

Chamberlain, N.A. 1961. Studies on the larval development of Neopanope texana sayi (Smith) and other crabs of the family Xanthidae (Brachyuran). Ches. Bay Inst. Tech. Rept. 22:1-35.

Chapman, J.A. and R.P. Morgan II. 1973. Systematic status of the cottontail complex in Western Maryland and nearby West Virginia. Wildlife Monographs No. 36, 54 pp. The Wildlife Society, Washington, DC.

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

Churchill, E.P., Jr. 1942. The zoeal stages of the blue crab, Callinectes sapidus Rathbun. Chesapeake Biol. Lab. Publ. 49:1-26.

Cole, M.A. and R.P. Morgan II. 1978. Genetic variation in two populations of blue crab, Callinectes sapidus. Estuaries 1(3), (In press).

Costlow, J.D., Jr. 1967. The effect of salinity and temperature on survival and metamorphosis of megalopa of the blue crab Callinectes sapidus. Helgolander wiss. Meeresunters., 15:84-97.

Costlow, J.D., Jr. and C.G. Bookout. 1959. The larval development of Callinectes sapidus R. reared in the laboratory. Biol. Bull. Marine Biological Laboratory, Woods Hole, Mass. 116:373-396.

Costlow, J.D., Jr. and C.G. Bookout. 1961. The larval stages Panopeus herbstii Milne-Edwards in the laboratory. J. Elisha Mitchell Sci. Soc. 77:33-42.

Costlow, J.D., Jr. and C.G. Bookout. 1962. The larval development of Sesarma reticulatum Say reared in the laboratory. Curstaceana 4:281-294.

Costlow, J.D., Jr. and C.G. Bookout. 2966a. The larval development of the crab Hexapanopeus angustifrons. Ches. Sic. 7:148-156.

Costlow, J.D., Jr. and C.G. Bookout. 1966b. The larval development of Ovalipes ocellatus (Herbst) under laboratory conditions. J. Elisha Mitchell Sci. Soc. 82:160-171.

Costlow, J.D., Jr., G.H. Rees and C.G. Bookout. 1959. Preliminary note on the complete larval development of Callinectes sapidus Rathbun under laboratory conditions. Limnol. Oceanog. 4:222-223.

Cox, J. and P.H. Wiebe, 1980. Origin of oceanic plankton in the Middle Atlantic Bight. Est. Coast. Mar. Sci. 9:509-528.

Cronin, T.W. 1979. Factors contributing to the retention of larvae of the crab Rhithropanopeus harrisii in the Newport River estuary, North Carolina. Ph.D. Dissertation, Duke University, Durham, North Carolina. 206 pp.

Cronin, L.E., F.C. Daiber and E.M. Hulbert. 1962. Quantitative seasonal aspects of zooplankton on the Delaware River estuary. Ches. Sci. 3:63-93.

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

DeCoursey, P.J. 1980. A lunar-month scan of egg-hatching in the fiddler crab, Uca pugillator and its internal clock control. Am. Zool., 20:728.

Deevey, G. 1960. The zooplankton of the surface waters of the Delaware Bay region. Bull. Bingham Oceanogr. Coll. 17(2):5-53.

Dittel, A.I. and C.E. Epifanio. 1982. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. Estuaries 5:(in press).

Dudley, D.L. and M.H. Judy. 1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. U.S. Dept. Commerce. NOAA Tech. Rep. NMFS SSRF-637. 10 pp.

Dudley, D.L. and M.H. Judy. 1973. Seasonal abundance and distribution of juvenile blue crabs in Cove Sound, N.C., 1965-68. Ches. Sci., 14(1):51-54.

Efford, I.E. 1970. Recruitment to sedentary marine populations as exemplified by the sand crab, Emerita analoga (Decapoda, Hippidae). Crustaceana 18:293-308.

Ewald, E.F. 1912. On artificial modification of light reactions and the influence of electrolytes on phototaxis. J. Exp. Biol. 13:591-612.

Forward, R.B., Jr. 1974. Negative phototaxis in crustacean larvae: possible functional significance. J. Exp. Mar. Biol. Ecol., 16:11-17.

Forward, R.B., Jr. 1976. A shadow response in a larval crustacean. Biol. Bull., 151:126-140.

Forward, R.B., Jr. 1977. Occurrence of a shadow response among brachyuran larvae. Mar. Biol. 39:339-341.

Forward, R.B., Jr. and J.D. Costlow, Jr. 1974. The ontogeny of phototaxis by larvae of the crab, Rhithropanopeus harrisii. Mar. Biol. 26:27-33.

Forward, R.B., Jr. and T.W. Cronin. 1979. Spectral sensitivity of larvae from intertidal crustaceans. J. Comp. Physiol. 133:311-315.

Fraenkel, G. 1931. Die Mechanik der Orientierung der Tiere im Raum. Biol. Rev. 6, 36-87.

Goellner, K.E. 1941. Report on the blue crab investigations, lower Chesapeake Bay, summer 1941. Unpublished M.S. Chesapeake Biological Laboratory.

Gooch, J.L. 1977. Allozyme genetics of life cycle stages of brachyurans. Chesapeake Sci. 18:284-289.

Gore, R.H. 1968. The larval development of the commensal crab Polyonyx gibbesi Haig 1956 (Crustacea: Decapoda). Biol. Bull. Marine Biological Laboratory, Woods Hole, Mass. 135:111-129.

Goy, J.W. 1976. Seasonal distribution and the retention of some decapod crustacean larvae within the Chesapeake Bay, Virginia. M.S. Thesis, Old Dominion University, Norfolk, Virginia. 334 pp.

Graham, J.G. and G.F. Beaven. 1972. Experimental spongecrab plantings and crab larvae distribution in the region of Crisfield, MD. Chesapeake Biological Laboratory, Solomons, MD. Publ. No. 52, 18 pp.

Harder, W. 1968. Reactions of plankton organisms to water stratification. Limnol. Oceanogr., 13:156-160.

Hopkins, S.H. 1943. The external morphology of the first and second zoeal stages of the blue crab, Callinectes sapidus Rathbun. Biol. Bull. 87:145-152.

Hyman, O.W. 1920. Development of Gelasimus after hatching. J. Morphol. 33:485-525.

Jackson, G.A. and R.R. Strathmann. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. Am. Nat. 118:16-26.

Javaid, M.Y. and J.M. Anderson. 1967. Thermal acclimation and temperature selection in Atlantic salmon, Salmon salar, and rainbow trout, S. gairdneri. J. Fish. Res. Bd. Canada, 24:507-1513.

Johns, D.M. and W.H. Lang. 1977. Larval development of the spider crab, Libinia emarginata (Majidae). Fish. Bull. 75(4):831-841.

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

King, III, B.D. 1971. Study of migratory patterns of fish and shellfish through a natural pass. Texas Parks & Wildlife Dept. Technical Series, 9:29-37.

Kramarsky, E., R.P. Morgan II and S.D. Sulkin. 1978. Biochemical changes during larval development of the xanthid, Rhithropanopeus harrisii, III. Isozyme changes during ontogeny. Mar. Biol. (In press).

Lance, J. 1962. Effects of water of reduced salinity on the vertical migration of zooplankton. J. Mar. Biol. Assoc. U.K. 42:131-154.

Latz, M.U. and R.B. Forward, Jr. 1977. The effect of salinity upon phototaxis and geotaxis in a larval crustacean. Biol. Bull 153:163-179.

Lewotin, R.C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York and Long 346 pp.

Longhurst, A.R. and D.L.R. Seibert. 1967. Skill in the use of Folsom's plankton sample splitter. Limnol. and Oceanogr. 12:334-335.

Lough, R.G. 1975. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oregon State University, Corvallis, Oregon. 298 pp.

Lough, R.G. 1976. Larval dynamics of the Dungeness crab, Cancer magister, off the central Oregon coast, 1970-71. Fish. Bull., 74(2): 353-376.

Makarov, R.R. 1969. Transport and distribution of Decapoda larvae in the plankton of the Kamchatka shelf. Oceanology 9:251-261.

Maurer, D.L. Watling, R. Lambert and A. Pembroke. 1978. Seasonal fluctuation of zooplankton populations in lower Delaware Bay. Hydrobiologia 61(2):149-160.

Mayr, E. 1966. Animal Species and Evolution, Belknap Press, Cambridge, Mass.

McConaugha, J.R., A.J. Provenzano, D.F. Johnson, J. Clark and P. Sadler. 1981. Offshore displacement and reinvasion of Callinectes sapidus larvae in Chesapeake Bay. Estuaries 4:277.

McEwen, G.F., M.W. Johnson and T.R. Folsom. 1954. A statistical analysis of the performance of the Folsom plankton splitter based upon test observations. Archiv. fur Meteorologie, Geophysik and Bioklimatologie, Series A: Meteorologie und Geophysik, Vol. 7.

Moore, W.R. 1969. A contribution to the biology of the blue crab (Callinectes sapidus Rathbun) in Texas, with a description of the fishery. Tex. Parks Wildl. Dept. Tech. Ser. 1, 31 pp.

Morgan, II, R.P., S.B. Block, S.D. Sulkin, D.W. Meritt and M.A. Cole. 1976. Biochemical identification of the mallard and black duck. Chesapeake Biological Lab. Center for Environmental and Estuarine Studies, Ref. No. 76-79CBL.

Morgan, II, R.P., T.S.Y. Koo and G.E. Krantz. 1973. Electrophoretic determination of populations of the striped bass, Morone saxatilis, in the upper Chesapeake Bay. Trans Am. Fish. Soc. 102:31-32.

Naylor, E. 1963. Temperature relationships of the locomotor rhythms of Carcinus. J. Exp. Biol. 40:669-679.

Naylor, E. and M.J. Isaac. 1973. Behavioral significance of pressure responses in megalopa larvae of Callinectes sapidus and Macrorpipus sp. Mar. Behav. Physiol. 1:341-350.

Nei, M. 1971. Genetic distance between populations. Am. Natu. 106:283-293.

Nelson, K. and D. Hedgecock. 1980. Enzyme polymorphism and adaptive strategy in the decapod Crustaces. Am. Natu. 116(2):238-280.

Nichols, P. and P.M. Keney. 1963. Crab Larvae (Callinectes) in plankton collections from cruises of M/V Theodor N. Gill, South Atlantic Coast of the United States 1953-54. U.S. Fish. & Wildl. Serv. Spec. Sci. Rpt. Fisheries 448:1-14.

Norcross, J.J. and E.M. Stanley. 1967. Part II. Inferred surface and bottom drift. In: W. Harrison, J.J. Norcross, N.A. Pore and E.M. Stanley. Circulation of shelf waters off the Chesapeake Bight. ESSA Professional Paper 3. U.S. Dept. of Commerce, Environmental Sciences Services Adm.

Norse, E.A. and M. Estevez. 1977. Studies on portunid crabs from the eastern Pacific. I. Zonation along environmental stress gradients from the coast of Colombia. Mar. Biol. 40:365-373.

Oesterling, M.J. 1976. Reproduction, growth and migration of blue crabs along Florida's Gulf Coast. Mar. Advisory Bull., Univ. Florida, Gainesville, FL. 19 pp.

Ott, F.S. and R.B. Forward, Jr. 1976. The effect of temperature on phototaxis and geotaxis by larvae of the crab, Rhithropanopeus harrisii (Gould) J. Exp. Mar. Biol. Ecol. 23:97-107.

Pape, E.H. 1981. A drifter study of the Lagrangian mean circulation of Delaware Bay and adjacent shelf waters. M.S. Thesis. University of Delaware, Newark, DE. 148 pp.

Perry, H.M. 1975. The blue crab fishery in Mississippi. Gulf Res. Rpt., 5(1):39-57.

Peterson, C.L. 1958. The physical oceanography of the Gulf of Nicoya, Costa Rica, a tropical estuary. Bull Inter-Am. Trop. Tuna Comm. 3:139-216.

Pinschmidt, W.C. 1963. Distribution of crab larvae in relation to some environmental conditions in the Newport River Estuary, North Carolina. Ph.D. Disertation, Duke University, Durham, 111 pp.

Polis, D.F. and S.L. Kupferman. 1973. Physical oceanography. Delaware Bay Report Series Vol. 4. University of Delaware, Newark, DE 143 pp.

Porter, H.H. 1956. Delaware blue crab. Est. Bull., Univ. of Del. Mar. Lab. 2:3-5.

Porter, H.H. 1956. Starch gel electrophoresis in a discontinuous system of buffers. Nature, 180:1477-1479.

Pritchard, D.W. 1952. Salinity distribution and circulation in Chesapeake Bay estuarine system. J. Mar. Res., 11: 106-123.

Provenzano, Anthony J., Jr. 1979. Distribution and migration of blue crab larvae in the lower Chesapeake Bay and adjacent coastal waters. Final Reprot for Virginia Institute of Marine Science, Contract No. NA79AA-D-00055, Old Dominion University Research Foundation Report no. 79-126, Norfolk, Virginia.

Rees, G.H. 1959. Larval development of the sand crab Emerita talpoida (Say) in the laboratory. Biol. Bull. Marine Biological Laboratory, Woods Hole, Mass. 117:356-370.

Ridgway, J.G., S.W. Shelburne and R.D. Lewis. 1970. Polymorphism in the esterases of Atlantic herring. Trans. AM. Fish. Soc. 99:147-151.

Roberts, M.H. Jr. 1971. Larval development of Pagurus longicarpus Say reared in the laboratory. III. Behavioral responses to salinity discontinuities. Bio. Bull., 140:489-501.

Robertson, R.L. 1938. Observations on the growth stages in the common blue, Callinectes sapidus Rathbun with special reference to post-larval development. Unpublished M.S. thesis, University of Maryland, 30 pp.

Sameoto, D.D. 1975. Tidal and diurnal effects on zooplankton sample variability in a nearshore marine environment. J. Fish. Res. Bd. Can. 32(3):347-366.

Sandifer, P.A. 1972. Morphology and ecology of Chesapeake Bay decapod crustacean larvae. Ph.D. Dissertation. Univ. of Virginia, Charlottesville, Virginia. 523 pp.

Sandifer, P.A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-69. Ches. Sci. 3(4):235-257.

Sandifer, P.A. 1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. Estuarine and Coastal Mar. Sci. 3:269-279.

Sandifer, P.A. and W.A. Van Engel. 1971. Larval development of the spider crab, Libinia dubia H. Milne Edwards (Brachyura, Majidae, Pisnae) reared in laboratory culture. Ches. Sci. 12(1):18-25.

Sandoz, M. and S. Hopkins. 1947. Early life history of the oyster crab, Pinnotheres ostrerum (Say). Biol. Bull. 93:250-258.

Sandoz, M. and R. Rogers. 1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab Callinectes sapidus Rathbun, Ecology 25:216-228.

Sastry, A.N. 1977. The larval development of the rock crab, Cancer irroratus Say, 1817 under laboratory conditions (Decapoda: Brachyura). Crustaceana 32(2):155-168.

Schaal, B.A. and W.W. Anderson. 1974. An outline of techniques for starch gel electrophoresis enzymes from the American oyster Crassostrea virginica Gmelin. Tech. Rep. Ser., Georgia Mar. Sci. Center. Unpublished manuscript.

Scheltema, R.S. 1970. The frequency of long-distance larval dispersal and the rate of gene-flow between widely separated populations of sipunculans. Proc. Internat. Sym. on the Biology of the Sipuncula and Echiura I. Kotor, June 18-25, 1970.

Scheltema, R.S. 1971a. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biol. Bull. 140:284-322.

Scheltema, R.S. 1971b. The dispersal of the larvae of shoal water benthic invertebrate species over long distance by ocean currents. In: Fourth European Marine Biology Symposium (ed. D. Crisp), pp. 7-28.

Scheltema, R.S. 1972. Eastward and westward dispersal across the Tropical Atlantic Ocean of larvae belonging to the germs Bursa (Prosobranchia, Mesogastropoda, Bursidae). Int. Revue ges. Hydrbiol. 57:863-873.

Scheltema, R.S. 1974. Relationship of dispersal to geographical distribution and morphological variation in the polychaete family Chaetroperidae. Thalassia Jugoslavica, 10:297-312.

Scheltema, R.S. 1975. Relationship of larval dispersal, geneflow and natural selection to geographic variation of benthic invertebrates in estuaries and along coastal regions. In: Estuarine Research, Vol. 1., L.E. Cronin (ed.) Academic Press, New York, pp 372-391.

Seitz, R.C. 1971. Temperature and salinity distributions in vertical sections along the logitudinal axis and across the entrance of the Chesapeake Bay (April 1968 to March 1969). C.B.I. Graphical Summary No. 5, Ref. No. 71-7.

Selander, R.K. 1976. Genetic variation in antural populations. In: F.J. Ayala, (ed.) Molecular Evolution. Sinauer Associates, Sundeland, Mass. pp 21-45.

Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson and F.B. Gentry. 1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (Peromysus polionolus). Studies in Genetics IV. Univ. Texas Publ. 7103:49-90.

Shaw, C.R. and R. Prasad. 1970. Starch gel electrophoresis of enzymes--a compilation of recipes. Biochem, Genet. 4:297-320.

Shulenbeger, E. 1978. Vertical distributions, diurnal migrations and sampling problems of hyperiid amphipods in the North Pacific central gyre. Deep Sea Res. 25:605-623.

Smyth, P.O. 1980. Callinectes (Decapoda: Portunidae) larvae in the middle Atlantic Bight, 1975-77. Fishery Bulletin 78(2):251-265.

Sulkin, S.D. 1971. Behavioral responses of the developmental stages of two xanthid crabs to light, gravity, and pressure under laboratory conditions. PhD. Thesis, Duke University.

Sulkin, S.D. 1973a. Depth regulation of crab larvae in the absence of light. J. Exp. Mar. Biol. Ecol. 13:73-82.

Sulkin, S.D. 1973b. Completion report blue crab study in Chesapeake Bay—Maryland. UMCEES ref. No. 73-94.

Sulkin, S.D. 1975a. The influence of light in the depth regulation of crab larvae. Biol. Bull. 148:333-343.

Sulkin, S.D. 1975b. The significance of diet in the growth and development of larvae of the blue crab, Callinectes sapidus Rathbun, under laboratory conditions. J. Exp. Mar. Biol. Ecol., 20:119-135.

Sulkin, S.D. 1977. Factors influencing blue crab population size: nutrition of larvae and migration of juveniles. Chesapeake Biol. Lab., Center for Environmental and Estuarine Studies. Ref. No. 77-16 HPEL.

Sulkin, S.D. 1978. Nutritional requirements during larval development of the portunid crab, Callinectes sapidus Rathbun. J. Exp. Mar. Biol. Ecol. 34:29-41.

Sulkin, S.D., E.S. Branscomb and R.E. Miller. 1976. Induced winter spawning and culture of larvae of the blue crab, Callinectes sapidus Rathbun, Aquaculture, 8:103-113.

Sulkin, S.D. and C.E. Epifanio. 1975. Comparison of rotifers and other diets for rearing early larvae of the blue crab, Callinectes sapidus Rathbun. Est. Coastal Mar. Sci., 3:109-113.

Sulkin, S.D., I Phillips and W. Van Heukelem. 1979. On the locomotory rhythm of brachyuran crab larvae and its significance in vertical migration. Mar. Ecol. Prog. Ser. 1:331-335.

Sulkin, S.D. and W. Van Heukelem. 1982. Larval recruitment in crab Callinectes sapidus Rathbun: An amendment to the concept of larval retention in estuaries. Estuarine Comparisons (in press).

Sulkin, S.D., W. Van Heukelem, P. Kelly and L. Van Heukelem. 1980. The behavioral basis of larval recruitment in the crab Callinectes sapidus Rathbun: A laboratory investigation of ontogenetic changes in geotaxis and barokinesis. Biol. Bull. 159:402-417.

Tagatz, M.E. 1968. Biology of the blue crab Callinectes sapidus NOAA Tech. Rept. NMFS SSRF 640:1-94.

Tagatz, M.E. 1968. Biology of the blue crab, Callinectes sapidus Rathbun in the St. Johns River, Florida. Fish. Bull. U.S. Fish. Wildl. Sev., 67:17-33.

Taylor, W. and W.B. Cronin. 1974. Plankton ecology project station data, Aesop Cruises April 1969 to April 1971. C.B.I. Special Report 38, Ref. No. 74-6.

Thompson, B.G. 1981. Fisheries of the United States, 1980. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, D.C. 132 pp.

Thorson, G. 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophlia, 1:167-208.

Tracey, M.L., K. Nelson, D. Hedgecock, R.A. Shleser and M.L. Pressick. 1975. Biochemical genetics of lobsters: genetic variation and the structure of American lobster (Homarus americanus) populations. J. Fish. Res. Board Can. 32:2091-2101.

Tranter, D.J. and P.E. Smith. 1968. Filtration performance, In: Zooplankton Sampling, D.J. Tranter, Ed. Nesco monographs on oceanographic methodology.

Truitt, R.V. 1934. Preliminary report--blue crab investigation 1932-1933. In: 35th Annual Report, Commission of Fisheries of Virginia, Fiscal year ending June 30, 1933. pp. 14-18. Division of Purchase and Printing, Richmond.

Truitt, R.V. 1939. Our water resources and their conservation. Chesapeake Biol. Lab., Solomons, Md. Contr. No. 27. 103 pp.

Van Engel, W. 1958. The blue crab and its fishery in Chesapeake Bay. Part I. Reproduction, early development, growth, and migration. Comm. Fish. Ref. 20(6):6-17.

Warner, W.W. 1976. Beautiful Swimmers: Watermen, crabs and the Chesapeake Bay. Little, Brown and Co., Boston, MA.

Wells, H.W. and I.E. Gray 1960. Seasonal occurrence of Mytilus edulis on the Carolina coast as a result of transport around Cape Hatteras. Biol. Bull., 119:550-559.

Wheeler, D.E. and C.E. Epifanio. 1978. Behavioral response to hydrostatic pressure in larvae of two species of xanthid crabs. Mar. Biol. 46:167-174.

Williams, A. 1965. Marine decapod crustaceans of the Carolinas. U.S. Fish and Wildlife Service. Fish Bull., 65:1-298.

Williams, A.B. 1971. A ten-year study of meroplankton in North Carolina estuaries: annual occurrence of same brachyuran developmental stages. Ches. Sci., 12(2):53-61.

Wood, L. and W.J. Hargis. 1971. Transport of bivalve larvae in a tidal estuary. Fourth European Marine biology Symp., ed. D.J. Crisp. Cambridge University Press, Cambridge pp. 29-44.