The Behavioral Basis For Blue Crab Recruitment In Mid-Atlantic Estuaries

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In addition I wish to make special mention of Dr. William Van Heukelem, Associate Investigator on Maryland Sea Grant Project R/F-8, who provided direct support and organized and implemented most of the experiments. I also want to acknowledge Dan Levine, Laurie Van Huekelem, Patti Kelly, Robert McConnaughey, Fred Cassels and Wayne Wargo, all of whom made significant contributions.

Any credit due for the development of new hypotheses and recruitment models should be shared among the participants. However, responsibility for errors in interpretation of the proposed conceptual model is mine alone.

EDITOR'S PREFACE

Crab harvests in Chesapeake Bay over the last 25 years have fluctuated unpredictably--between a high of 97 million pounds and a low of 45 million. Understanding the reasons for these wide fluctuations has been one goal of the Maryland Sea Grant Program since 1978 when Stephen Sulkin began a series of research projects to investigate a new theory of the blue crab's life cycle in the Chesapeake Bay estuary. The rapid growth that this research has produced in fundamental knowledge about blue crab population dynamics should lead to more accurate predictions of abundance and harvests and, thus, will have important implications for management practices.

Until recently, the prevailing hypothesis of blue crab recruitment in Chesapeake Bay has been that large spawning populations remain within the estuary and form the major source of juveniles from which new year-class crabs are derived. According to Dr. Sulkin's theory, however, the significant source of recruitment is the result of a more complex process of larvae loss and recovery: early stage larvae, or zoeae, are flushed from the estuary in surface waters at the mouth of the Bay; in late stages, larvae descend to deeper saline waters and ride the denser tidal waters back into the estuary.

To test this hypothesis, Dr. Sulkin has conducted extensive laboratory experiments on the behavioral responses of crab larvae to light, pressure, salinity, salinity gradients (haloclines) and temperature gradients (thermoclines). Working with the first, fourth and seventh larval stages, he has determined the vertical migration behavior of each stage in response to these environmental stimuli.

These experiments on the three zoeael stages appear to show verifiable differences in adaptive behavior that would lead to: (1) losses of early stage larvae as they swim and rise vertically in the water column and, thus, are flushed out to sea, and (2) the return of many later stage larvae as they descend down into the water column. Further verification of the hypothesis comes from researchers at the University of Delaware and Old Dominion University. Working cooperatively with Dr. Sulkin, they have found evidence of large numbers of early stage larvae in surface waters. Field sampling at the mouths of the Chesapeake and Delaware bays gives strong indications that under wind and hydrographic conditions prevailing during most years, early stage larvae are swept out to their precarious "nursery" at sea.

The implications of this theory of blue crab recruitment for current management could mean that efforts to protect the blue crab fishery must be reconsidered; for example, that regional--rather than state or local management procedures--must be undertaken and that management practices may be better directed at crabs that are recruited to the estuary rather than at blue crab larvae which are subject to unpredictable meteorological events offshore. Such questions are considered in a proposed Sea Grant project that will more formally synthesize the results of Dr. Sulkin's laboratory experiments and the field data from the Chesapeake and Delaware bays.

This report is an interim summary of the new model of blue crab recruitment: it makes an argument for the theory based on the literature, field data and laboratory experiments, which are also explained and summarized.

Merrill Leffler

INTRODUCTION

Success in understanding and managing the large and commercially significant blue crab population in Chesapeake Bay has been limited because of a lack of rigorous information on fundamental questions relating to population dynamics. In a species such as the blue crab, which has a high potential fecundity and an independent, freeliving larval stage, success in recruiting the juvenile stage to the estuarine habitat is paramount to regulation of population dynamics. There are two general types 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 a pelagic larva. As with other such estuarine species, the blue crab is faced with the necessity of maintaining a population in the face of net seaward flow of water characteristic of estuaries. In such circumstances, two mechanisms have been suggested (Sandifer 1975): 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 in Chesapeake Bay, and resulting management approaches, have been based upon the assumption that retention is the operative method of recruitment of new individuals to the population. This implies that the entire life cycle of the blue crab is spent within the parent estuary.

However, in 1978 a broad program of research was initiated to test the hypothesis that a mechanism existed to promote recruitment from offshore and that this source was significant. This program has been conducted by investigators at the Universi-

ty of Delaware, Old Dominion University and the University of Maryland under sponsorship of their respective Sea Grant programs. The program has included field studies (University of Delaware, Old Dominion University) to document distributional patterns of blue crab larvae in Chesapeake and Delaware bays, as well as the coastal waters of the mid-Atlantic bight, and laboratory studies (University of Maryland) to determine the presence of an adaptive behavioral basis for a mechanism of exchange of larvae between the parent estuary and the open sea.

The behavioral studies were conducted during 1978 and 1979. The results of these studies are presented in this report. The objectives of the project may be stated as follows:

To determine behavioral response of larvae to stimuli which may affect their vertical distribution and consequent horizontal dispersal.

To determine the effect of salinity and temperature on taxis and kinesis responses.

To determine whether discontinuity layers caused by haloclines and/or thermoclines will disrupt vertical migration patterns.

To determine whether genetic variability exists between populations inhabiting Delaware and Chesapeake Bays and more distant estuaries.

To develop from this information a model of vertical distribution

through ontogeny and to develop
a recruitment hypothesis

The results are provided in this report in two sections: a comprehensive discussion which consolidates the results of laboratory experiments, places the experimental results in the context of field studies and proposes a recruitment hypothesis. The second section summarizes the laboratory experiments on geotaxis and barokinesis, phototaxis and haloclines and thermoclines and concludes with a treatment of genetics studies.

Offshore Recruitment: A Discussion

CIRCUMSTANTIAL EVIDENCE FOR OFFSHORE RECRUITMENT

A number of estuarine species with pelagic larvae possess active mechanisms for retention of offspring within the estuary. Classic cases were presented by Bousfield (1955) for barnacles and mud crabs and by Carriker (1951) and Wood and Hargis (1971) for bivalves. Although mechanisms differ in detail, they invariably involve the larvae's exploitation of estuarine circulation patterns by selective vertical distribution. More specifically, the mechanisms rely on the larvae making use of tidal currents to move up into the water column at the appropriate time (Carriker 1951) or net non-tidal flow, typical of stratified systems, by changing vertical distribtion patterns during ontogeny (Bousfield 1955).

In the latter case, for example, Bousfield (1955) found that early larval stages were attracted to surface waters where net seaward flow caused downstream displacement; late stages, however, were found in deeper water where net up-stream flow returned larvae to the parental site. Bousfield implied that vertical distribution through ontogeny is regulated by behavioral adaptations.

The same behavioral and physical parameters which contribute to mechanisms for retention of larvae also could contribute to larval exchange between the estuary and open sea. Blue crab larvae attracted to surface waters near the mouth of Chesapeake Bay likely would be flushed from the estuary. Both Sandifer (1975) and Goy (1976) reported that the majority of stage I *C. sapidus* larvae they collected at the mouth of the Bay were in surface samples.

There seems little doubt that *Callinectes* larvae are found in shelf waters. Sandifer (1973) reported that *Callinectes* larvae were more abundant outside of the Bay than within it. Nichols and Keney (1963) reported a high frequency of *Callinectes* sp. larvae in

near-shore samples along the southeastern United States coastline. Late stage larvae were found as far as 40 miles offshore. During the summer of 1977, Epifanio (unpublished) collected unidentified zoeae and megalopa in shelf waters off Delaware Bay. The larvae were returned to the laboratory and cultured until metamorphosis; a number of juveniles were identified as *C. sapidus*. Smyth (1980) reported an abundance of *Callinectes* larvae in shelf waters of the mid-Atlantic bight--late stages and megalopa were prevalent.

Thus, significant numbers of *C. sapidus* larvae are lost from estuarine spawning grounds to shelf waters. The significant question is whether these larvae truly are lost from adult estuarine habitats or whether an offshore population of larvae serves as a source of recruitment for the Bay.

Efford (1970) suggested four mechanisms for retention of pelagic larvae: (1) counter currents, or (2) gyral currents, (3) nursery areas not subject to net flow and (4) migration of juveniles back to parental areas. He explained maintenance of shore populations of the sand crab *Emerita analoga* in the face of consistent dispersal of larvae away from the parental system as a result of counter currents. Lough (1976) argued that larvae of the Dungeness crab, *Cancer magister*, were retained inshore by longshore and onshore currents and by behavioral mechanisms. In a study of decapod larvae, Makarov (1969) concluded "larval belts" occur along the continental shelf, originating from various sources including estuaries and offshore areas and are retained by longshore and onshore hydrographic phenomena.

Scheltema (1975) reviewed data on distribution of crab larvae and estuarine and coastal current patterns along the east coast of North America; he concluded that larvae entrained in bottom waters on the shelf would be carried onshore and swept toward the mouths of major estuaries. Bottom drifter studies by Norcross and Stanley (1967) seem to con-

firm Scheltema's findings (Fig.1). In sampling near the mouth of Chesapeake Bay, both Sandifer (1975) and Goy (1976) reported late larval stages (including *Callinectes* sp.) to be in bottom samples.

Offshore recruitment has been reported for estuarine systems other than Chesapeake and Delaware bays. Tagatz (1968) reported that spawning and hatching of *Callinectes* occur near the mouth of St. John's River, Florida. Recruitment to the river occurs as successive waves of migration of juvenile crabs; this implies considerable prior offshore development.

In a study of blue crabs in Galveston Bay, Texas, More (1969) reports that the presence of spawners within the Bay depends upon salinity: if salinity falls below 20 ppt, most females move out into the Gulf of Mexico to spawn; conversely, the abundance of juvenile crabs in the Bay is higher when salinities during the summer are lower. King (1971) indicates that all zoeal development of *Callinectes* is probably completed offshore in the Gulf of Mexico before immigration to the Texas coastal estuaries begins. In 1970, the year-class entered Cedar Bayou Inlet as a wave of megalopa migration.

There is circumstantial evidence for offshore recruitment in Chesapeake Bay as well. Sulkin (1977) reported that recruitment of juvenile blue crabs in Tangier Sound on the eastern shore of the Bay consistently preceded evidence of recruitment at the mouth of the Potomac River at the same latitude on the western shore. These results could be explained by the effect of Coriolis force moving the dense, high salinity waters up the eastern shore first. Post-larvae and juveniles entrained in these waters, perhaps originating offshore, would thus be carried to Tangier Sound first.

In late June 1972, rains from Tropical Storm Agnes caused sharp reductions in salinity Bay-wide

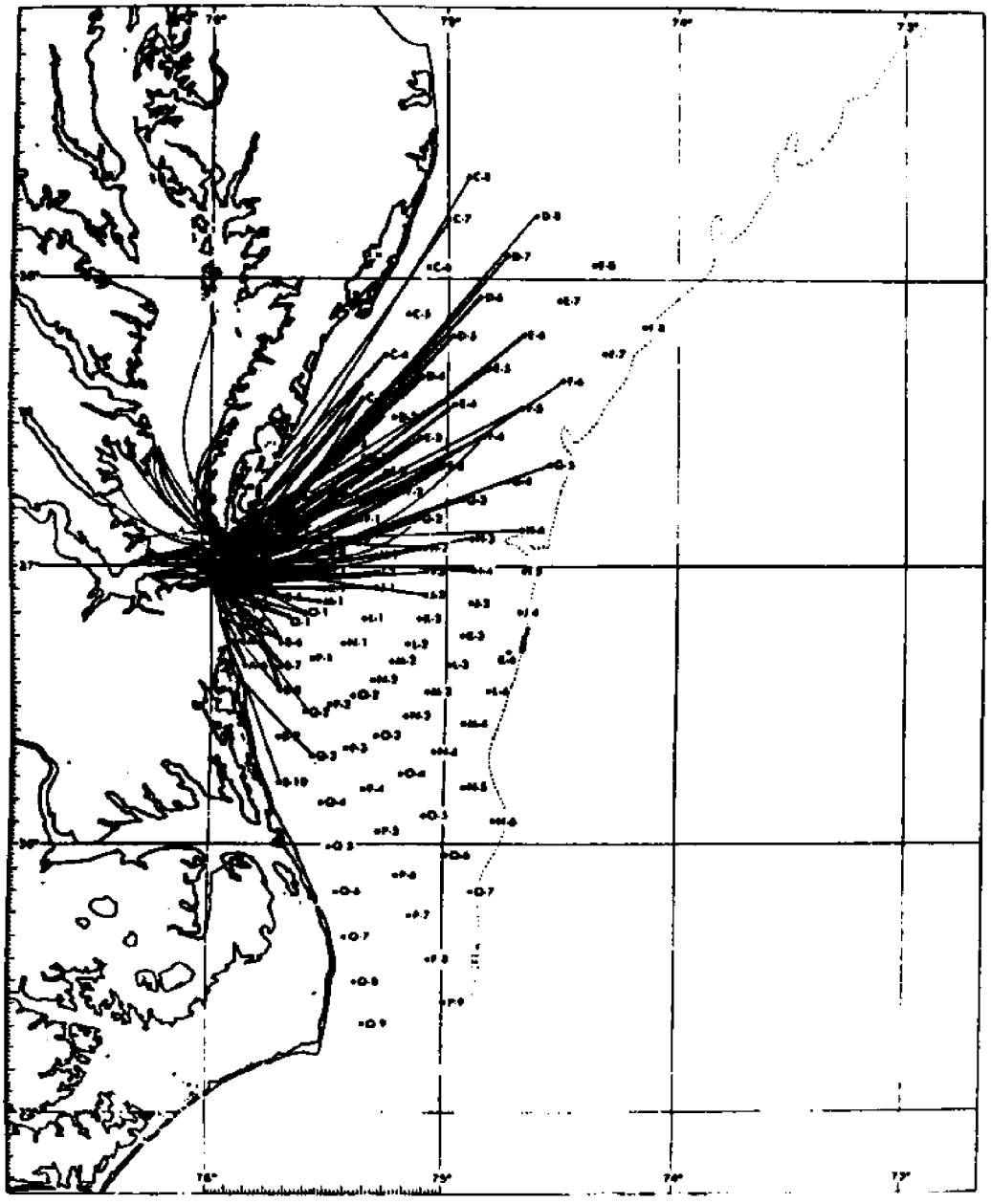

Figure 1. Plots of trajectories of seabed drifters which drifted or penetrated Chesapeake Bay. (From Norcross and Stanley 1967.)

and a significant increase in runoff (Anderson 1973). This occurred at what is generally considered to be the height of the blue crab spawning season (Van Engel 1958). It is reasonable to assume that large numbers of blue crab larvae were either killed by the reduced salinities or washed out of the Bay. However, data from Tangier Sound and the Patuxent River, Maryland, showed little delay or reduction in juvenile recruitment of the 1972 year-class (Sulkin 1977). Among the numerous explanations, one that is consistent with the observed phenomenon suggests that normal offshore development may have occurred, that is, many larvae typically were flushed from the system, while recruitment to the Bay in the deep waters was not affected.

BEHAVIORAL BASIS OF VERTICAL DISTRIBUTION IN BLUE CRAB ZOEAE

Experiments (See Laboratory Studies) indicate that during the course of blue crab zoeal development changes occur in critical behavioral responses which, through ontogeny, produce a characteristic pattern of differential vertical distribution.

Zoeal Stage I

The first larval stage possesses a pervasive negative geotaxis which so orients larvae that their active swimming results in upward movement. Furthermore, larvae respond to increased pressure by an increase in swim rate, a response which in combination with negative geotaxis serves as a depth regulatory function. The larval response to pressure, however, has a relatively high threshold when compared to blue crab megalopa (Naylor and Isaac 1973) and to other species (Sulkin 1973; Bentley and Sulkin 1977; Wheeler and Epifanio 1979). This high threshold suggests that a negative feedback depth regulatory system is not activated in shallow water. However, the increase in swim rate in response to increased salinity may either substitute for or complement the

larval response to pressure. In addition, swim rate is maintained even with a 10°C temperature decrease. These responses suggest that if stage I larvae sink from surface waters, they possess behavioral adaptations to enhance their return. Thus, the hatching stage responds to conservative stimuli in ways likely to produce upward movement and/or maintenance of vertical position high in the water column.

The first zoeal stage shows positive phototaxis--or movement towards light--over a wide range of intensities and wavelenghts. However, in light-adapted animals, indifference to light is evident at low intensities and negative phototaxis is observed at long wavelength. In dark-adapted animals, a lower intensity threshold for positive phototaxis as compared with light-adapted larvae, suggests a mechanism for some degree of diurnal vertical migration. This conclusion is supported by evidence of diel rhythm in locomotor activity in the first zoeal stage (Sulkin) et al. 1979).

Sign of phototaxis is independent of temperature (15°C to 25°C); however, a 5 ppt reduction in salinity will render the majority of a sample inactive or indifferent to light. If early stage larvae hatch in deep, high salinity water, this response to reduction in salinity could effectively trap the larvae below the pycnocline. Further evidence of this possibility is indicated by the inhibitory effects of sharp thermoclines and haloclines upon vertical migration.

Zoeal Stage IV

By the fourth zoeal instar, important changes in behavior have occurred with implications for vertical distribution. This intermediate zoeal instar appears to be in a transitional stage between negative and positive geotaxis. Furthermore, in lower salinity (25 ppt), positive response dominates; at 30 ppt S, response is variable within a sample; at 35 ppt S, negative response dominates. As larvae in surface

waters develop through several instars, increasing numbers of individuals will reverse the sign of geotaxis and will begin to migrate downward, particularly at night. However, with downward migration, they are likely to encounter increased salinities which may again reverse the geotaxis sign. The result will be a deeper net distribution than is the case for the first instar, but maintenance of position off the bottom.

As larvae migrate downward, they will likely encounter increased salinity, increased hydrostatic pressure and reduced temperature. Our results indicate that in contrast to the first zoeal stage, the fourth zoeal stage does not respond to increasing salinity with increased swim rate. Indeed, as fourth stage larvae become acclimated to higher salinities, their swim rate drops. Reduced swim rate is also noted as pressure increases and temperature drops. This combination of responses to conservative stimuli reduces the probability that these intermediate stages will return to surface waters. Although positive phototaxis was noted at intensities above 2×10^{-3} W/m^2, light response is difficult to evaluate due to a lack of quantitative data for light penetration in the coastal marine environment. Furthermore, the consistent response to wavelength through ontogeny tends to support the hypothesis of Forward and Cronin (1979) that spectral sensitivity in crab larvae may reflect adult adaptation rather than requirements for larval biology.

Zoeal Stage VII

By the seventh (terminal) instar, positive geotaxis is pervasive. Furthermore, there is a decrease in swim rate as larvae acclimate to increased salinity, increased hydrostatic pressure and reduced temperature. Again light response is difficult to analyze. However, in zoeal Stage VII, negative phototaxis occurs at a higher intensity threshold than is the case with Stage IV. These results suggest strong-

ly that late stage larvae frequent deep waters.

Thus, there exists an adaptive behavioral basis for differential vertical distribution through zoeal development. Early stages which enter surface waters are likely to be retained there, whereas changes in behavior as development proceeds are likely to produce movement to deeper waters.

REVIEW OF FIELD EVIDENCE

Extensive field studies of larvae distribution are being conducted by Dr. Charles Epifanio (University of Delaware) and Dr. Anthony Provenzano (Old Dominion University). Their preliminary results tend to confirm the models of vertical distribution through zoeal development suggested by the behavior studies. The vast majority of zoeae captured are early stages and are found in surface waters. Indeed the neuston appears to be a favored site, especially in early morning hours. Recent field evidence also indicates high densities of the megalopa stage in surface waters, with apparent tidal influence.

Literature reports on field surveys also support the vertical distribution model. Both Sandifer (1973) and Goy (1976) reported early stages to prevail in surface waters and late zoeal stages to be in deep water. The distribution of the megalopa remain a matter of controversy and requires further investigation.

Smyth (1980) has reported a high density of *Callinectes* larvae in the neuston of the mid-Atlantic bight shelf waters. Larvae were predominately late zoeae and megalopa and were most prevalent more than 10 km offshore in the neuston at night. His conclusion that there exists an affinity for surface waters by these late larval instars is a tenuous one, however. A comparison between surface (neuston) and sub-surface samples is inappropriate because sub-surface samples were integrated over the entire

water column. Thus high density patches of larvae at depth were diluted by the method of calculation. Nevertheless, Smyth's work confirms the presence of a large pool of *Callinectes* larvae in shelf waters.

DISPERSAL CONSEQUENCES OF THE VERTICAL DISTRIBUTION MODEL

The pattern of vertical distribution described here has predictable consequences to larval dispersal in the estuarine and nearshore marine environment and leads to a dispersal-based recruitment model. Our results suggest mechanisms for both retention and offshore recruitment. If early larvae are retained at depth below the pycnocline, they are likely to be retained within the parent estuary. Early stage larvae introduced to deep waters of the estuary and acclimated to the higher salinity at depth likely will be retained at depth. This conclusion is supported by our results on the influence of reduced salinity on locomotory behavior and our preliminary results from thermocline and halocline experiments. Larvae retained at depth will be transported landward. In addition, in some estuaries, such as Chesapeake Bay (William Boicourt, pers. comm.), surface current along the eastern shore will have a net landward flow. This flow is a consequence of Coriolis force which cause the pycnocline to break the surface before reaching the eastern shore. As a consequence, landward movement of high salinity waters originating offshore will occur from the surface to the bottom, along the eastern shore. Larvae entrained in these surface waters likely will be retained within the estuary. Significant retention is most likely to occur, therefore, in stratified estuaries, which are wide with respect to their depth near the mouth. Prevailing evidence suggests that the vast majority of larvae are introduced to surface waters upon hatching. The proximity of spawning grounds to the estuarine mouth, the complementary adaptations which insure the presence of the early stages in surface

waters, and the net seaward flow which predominates should result in export of larvae from the estuary to coastal marine waters. An impressive and growing array of field evidence confirms this phenomenon.

Our laboratory results, partially confirmed by field evidence, suggest that later zoeal stages will move to deeper waters. Deep currents on the shelf have a pronounced landward drift, with convergence at the mouths of estuaries (Bumpus 1965; Norcross and Stanley 1967; Scheltema 1975). Figure 1 gives a dramatic representation of this hydrographic phenomenon, showing the tracks of those bottom drifters released on the shelf and recovered within Chesapeake Bay. While this may be an over-dramatization of the phenomenon, the potential mechanisms for offshore recruitment is readily apparent. Larvae entrained in nearshore bottom waters will be transported back toward the coast, with a tendency for concentration near the mouth of the estuary. Although details are the subject of continuing research, the evidence suggests a mechanism for offshore recruitment.

Factors which control the probability of offshore recruitment become central to regulating population dynamics. In contrast to the conservative processes which could regulate retention within estuaries, control of offshore recruitment is problemmatic and subject to a number of environmental vagaries which are not well understood nor perhaps in some cases, even described. Indeed conceptual models of offshore dispersal based on characteristic current patterns raise significant questions.

The diagrams in Fig. 2 illustrate the characteristic surface current patterns of mid-Atlantic bight shelf waters (Bumpus 1965; Norcross and Stanley 1967). Larvae exported from the estuarine spawning grounds in surface waters typically will be transported to the south. This suggests a southerly progression of larvae. For example, larvae exported

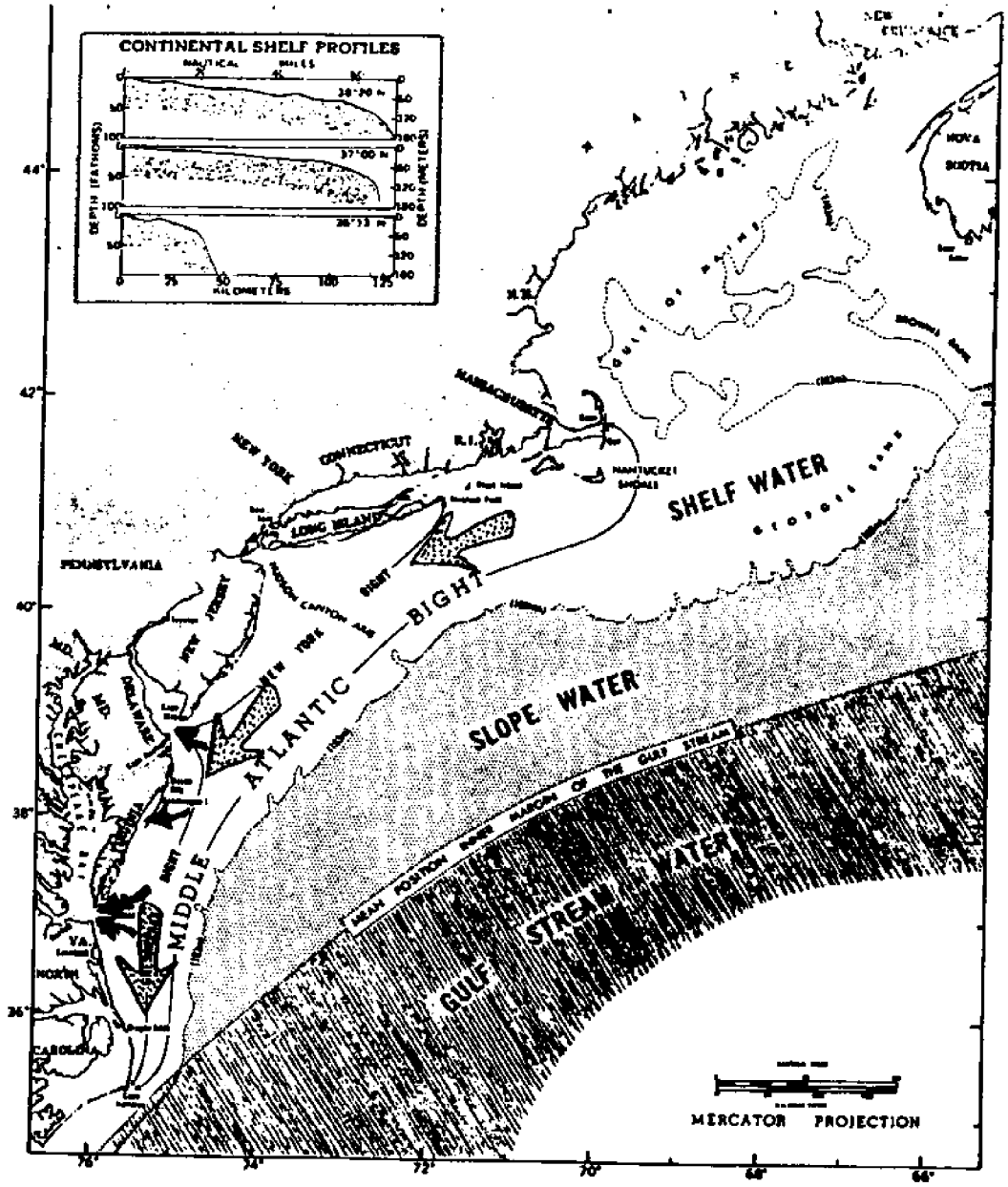

Figure 2. Characteristic surface currents (stippled arrows) and bottom currents (solid arrows) in the mid-Atlantic Bight. (Adapted from Norcross and Stanley 1967.)

from New Jersey estuaries and marshes would be transported towards the south, move to deeper waters, and, perhaps, be transported into Delaware Bay; larvae originating in Delaware Bay would be transported to the south and recruited into the Chesapeake Bay, and so forth. Current speeds and the length of planktonic existence make this model feasible. Under these circumstances, however, how does recruitment occur in the northern-most populations and what is the fate of the tremendous production of larvae from Chesapeake Bay? Characteristic circulation patterns will carry these larvae southward to be entrained in the northeastward flowing Gulf Stream, or, perhaps, to populate regions of the South Atlantic bight.

We propose the following, admittedly speculative, hypothesis to address these questions. The probability and incidence of offshore recruitment will be enhanced when characteristic southerly surface currents in shelf waters of the mid-Atlantic bight are reversed for "significant" periods of time. Flow reversal would "capture" the large production of larvae from Chesapeake Bay within the mid-Atlantic bight and position them advantageously for recruitment to mid-Atlantic estuaries all along the coast. Although the effect is a passive one, its impact could be substantial.

Unfortunately the spotty hydrographic record of the region and a lack of recruitment data make this hypothesis difficult to test. Bumpus (1965) described the conditions which promote flow reversal. These include a dry spring causing reduced runoff resulting in a shallow surface-water zone in the shelf by mid-summer, accompanied by strong southwesterly winds. Norcross and Stanley (1967) reported just such circumstances in 1963-4. They further reported a flow reversal which appeared especially persistent in August 1964. Larvae present in shelf waters in 1964 and recruited to the estuary would reach maturity by late 1965 and form the basis of the fishery in 1966. Fig. 3 shows catch records for a twenty-year period between 1953 and 1973. The highest catch of the period occurred in 1966.

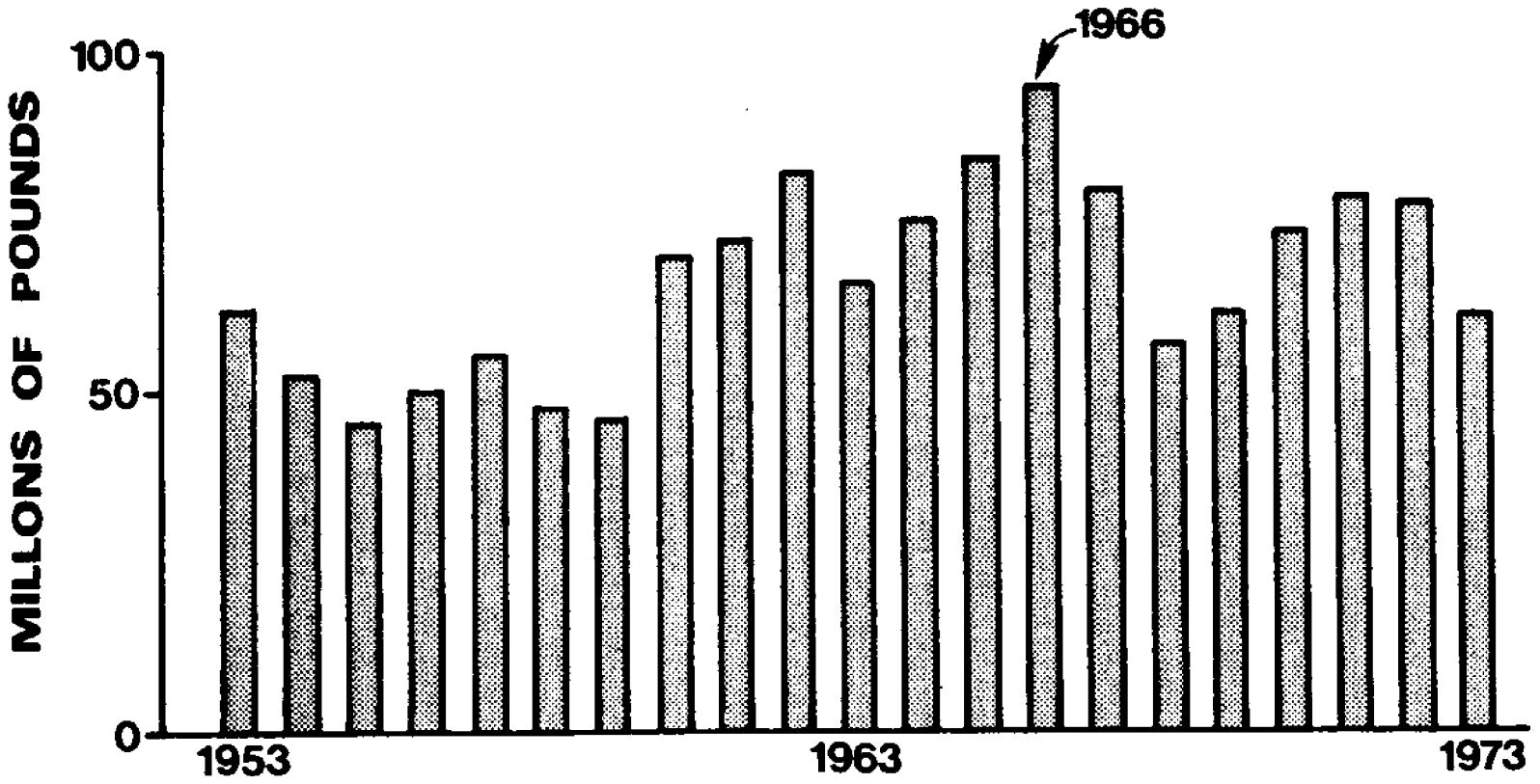

Figure 3. Catch records for Chesapeake Bay, 1953-1973. (Source: National Marine Fisheries Service, Fisheries Statistics Series.)

Though one data point is not enough to prove the hypothesis, this data is supporitve. However we are unable to find field data which demonstrate the probability for flow reversal at other times. Futhermore, it is unclear just how significant persistence of reversal is, how critical the timing of reversal, and how the extraordinary meterological events offshore influence reversal. An investigation of these questions is currently underway with Sea Grant support.

Reports in the popular literature that are relevant to the hypothesis (Warner 1976, for example) suggest that exceptionally good catches north of Cape Hatteras are inversely related to good catches south of Cape Hatteras. If true, this would be consistent with our hypothesis. The presence of flow reversal may remove a significant source of larvae to the area south of Cape Hatteras.

PROPOSED RECRUITMENT MODEL

Based on data, literature reports and hypotheses reported here, we propose the following model for recruitment of blue crabs to mid-Atlantic bight estuaries.

In stratified estuaries, a residual level of larval retention occurs which, because it is governed by conservative processes, is fairly stable from year to year and thus provides a conservative, base level of annual recruitment. However, most larvae are exported from the estuary in surface waters soon after hatching and develop in coastal waters where they are subject to passive transport. As larvae proceed through zoeal development, they move deeper in the water column where they are subject to transport back toward the coast. This mechanism may concentrate large numbers of late stage larvae and post-larvae near the mouth of estuaries and thus position them advantageously for transport back into the estuary. Based on field results and literature reports, it appears that the major re-

cruitment from offshore occurs at the megalopa stage, although the precise mechanism remains to be clarified. If "average" conditions pertain, early stage larvae normally will be transported to the south of the estuary of origin. Under these circumstances, a considerable proportion of larval production from Chesapeake Bay and, to a lesser extent, Delaware Bay will be lost from the mid-Atlantic bight system. However, episodic events, such as flow reversal in surface waters of the shelf, will retain larvae within the mid-Atlantic bight and disperse the large Chesapeake Bay larval production up along the coast. This phenomenon will enhance the probability of substantial recruitment from offshore.

Thus the model suggests, for stratified estuaries, a low, but stable, base-level of annual recruitment via retention, augmented by a highly variable degree of recruitment from offshore. The presence, absence or degree of offshore recruitment which occurs will be responsible for annual variation in recruitment success and therefore fluctuation in population abundance. The model predicts that in smaller estuaries, in which stratification is less stable and where landward transport of surface waters along the eastern or northern shore is less likely, blue crab populations will be more sensitive to the vagaries of offshore recruitment and therefore more highly variable than will be the case for larger, more physically stable estuaries.

CONSEQUENCES OF RECRUITMENT MODEL

If accurate, the recruitment model proposed here has the following consequences and management implications:

1. The success of the Chesapeake Bay as a habitat for blue crab populations may be attributed not only to favorable adult habitat, but to conditions that enhance retention, particularly a strong stratification

and landward flow at the surface along the eastern shore. Conversely, the large spawning stock of Chesapeake Bay may be significant in providing recruits to estuaries of both the mid and south Atlantic bights. As a consequence, factors that exert density-independent mortality on juveniles and larvae should be carefully controlled, particularly if they occur in the lower Bay spawning and recruitment sites.

2. Predictions of adult population abundance can be made as much as two years in advance when the factors controlling offshore recruitment are confirmed. The predictions should be fine-tuned periodically based on evaluations of post-recruitment mortality particularly due to density-independent phenomena and after each winter.

3. Management activities must be on a regional basis and must take into account the considerable time the animals spend in the waters of the continental shelf.

4. Given density-dependent mortality factors during larval development and the significance of recruitment from offshore, a direct relationship between fishing pressure and subsequent recruitment level is difficult to defend on theoretical grounds.

5. Environment impact of offshore development of resources on larval survivorship and water circulation should be investigated.

6. Because effective management procedures that will enhance recruitment do

not seem feasible, husbandry of the year-class that is recruited becomes of added significance. Understanding of factors that control post-recruitment dispersal and mortality is paramount.

NEED FOR FURTHER RESEARCH

Field data essential to full development of the recruitment model is currently in progress in Sea Grant-supported projects at University of Delaware (Dr. Charles Epifanio) and Old Dominion University (Dr. Anthony Provenzano). These studies are scheduled to proceed through 1981.

Field studies already have raised questions regarding distribution of the post-larval megalopa and hence its role in recruitment. Large numbers of megalopa have been reported in neuston samples (Provenzano per. comm.). Williams (1971) noted that in shallow estuaries of North Carolina, *C. sapidus* megalopa were common in surface waters at night. On the other hand, Tagatz (1968) and Sandifer (1975) found megalopa in bottom samples. It is important to determine whether megalopa are concentrated at the surface, whether neuston samples provide unbiased estimates of vertical distribution and whether megalopa undertake substantial vertical excursions on a regular (predictable) basis. These questions will be addressed in the 1981 field studies and in a new project in the Maryland Sea Grant program for 1981, entitled "The source of blue crab recruitment in mid-Atlantic estuaries: the role of the megalopa stage and larval behavior at thermal and salinity discontinuities." The 1981 Maryland Sea Grant program contains projects on expanding the genetics studies only just begun in the present project and on using correlative models to test the relationship between flow reversal and commercial catch.

Proposals to the 1982 Sea Grant program include

investigation of post-recruitment mortality and dispersal of young-of-the-year blue crabs to upper Chesapeake Bay, and a formal synthesis of all Sea Grant supported projects to date which relate to this project.

Laboratory Experiments

GEOTAXIS AND BAROKINESIS

The results of experiments on orientation and swimming rates of the first, fourth and seventh larval instars in response to gravity, hydrostatic pressure, temperature and salinity have been published in Sulkin, S.D. et al. (1980) and as Maryland Reprint UM-SG-RS-80-05. What follows is a summary of these results evaluated in terms of their effects on vertical distribution of *Callinectes sapidus* larvae throughout ontogeny and consequent patterns of dispersal of this species in the estuarine and coastal marine environments.

1. The first zoeal stage of *Callinectes sapidus* shows negative geotaxis unaffected by salinity changes of 5 ppt; high barokinesis at pressure increments above 1 atm; an increase in swimming rate with a salinity increase; and maintenance of swimming rate as temperature drops.

2. Stage IV larvae show both positive and negative geotaxis. As salinity drops, positive geotaxis prevails; as it increases negative geotaxis prevails. Stage IV larvae show a tendency to reduce swimming rate as pressure increases, as temperature drops and as they become acclimated to higher salinities.

3. Stage VII larvae show positive geotaxis and reduced swimming rate in response to increased pressure, reduced temperature, and as they are acclimated to increased salinity.

4. Between hatching and the seventh (terminal) zoeal stage, passive sinking rate increases 3.2-fold, while swimming rate increases 4.4-fold.

5. These responses to environmental stimuli produce a pattern of early stages moving to surface waters and later stages to deeper waters.

6. Because of characteristic circulation in lower estuarine and coastal marine systems, this pattern of vertical distribution could provide a mechanism for exchange of larvae between the estuary and the coastal marine environment.

7. In stratified estuaries, offshore recruitment may significantly influence population dynamics in *C. sapidus*.

Materials and Experimental Methods

Larval Culture. All larvae tested were raised in laboratory culture. Ovigerous females were collected near the mouth of Delaware Bay and held in the laboratory until their eggs reached the black eyespot stage of development. Eggs were then removed from the parent, placed in 50 ml of filtered seawater (30 ppt salinity, 25°C) in 125 ml Erlenmeyer flasks, and agitated on a reciprocating shaker (120 rpm). Antibiotics and a fungicide were added to the seawater (Sulkin et al. 1980).

Upon hatching, larvae were placed in 100 ml of culture water in 200 mm diameter dishes (200 larvae/dish). Larvae were transferred to fresh seawater and fed daily. Diet consisted of the rotifer *Brachionus plicatilis* Muller for the first 14 days of development, followed by nauplii of the brine shrimp *Artemia salina* L. until metamorphosis. These mass cultures were held at 30 ppt salinity (S), 25°C and white light (Fluorescent) at 6 W/m^2. Larvae to be tested in other than standard acclimation conditions were drawn randomly from mass cultures and placed in appropriate conditions of temperature, salinity or light. Dark-adapted larvae were held in darkness for 2 hr prior to testing. Larvae were acclimated to temperatures or salinities other than that of the mass cultures for 24 hr prior to testing. All experiments were conducted between 1300 and 1700 h.

Experimental Apparatus. The sign of phototaxis was measured using the apparatus shown diagrammatically in Fig. 4. The light source was a 300 W quartz-halide lamp (Fig. 4A). The behavior chamber consisted of six parallel raceways, each fitted with a light filter system (Fig. 4C, D). Each raceway measured 5 x 5 x 30 cm and was fitted with a quartz glass window at the proximal end. Intensity in each raceway was regulated by passing the light first

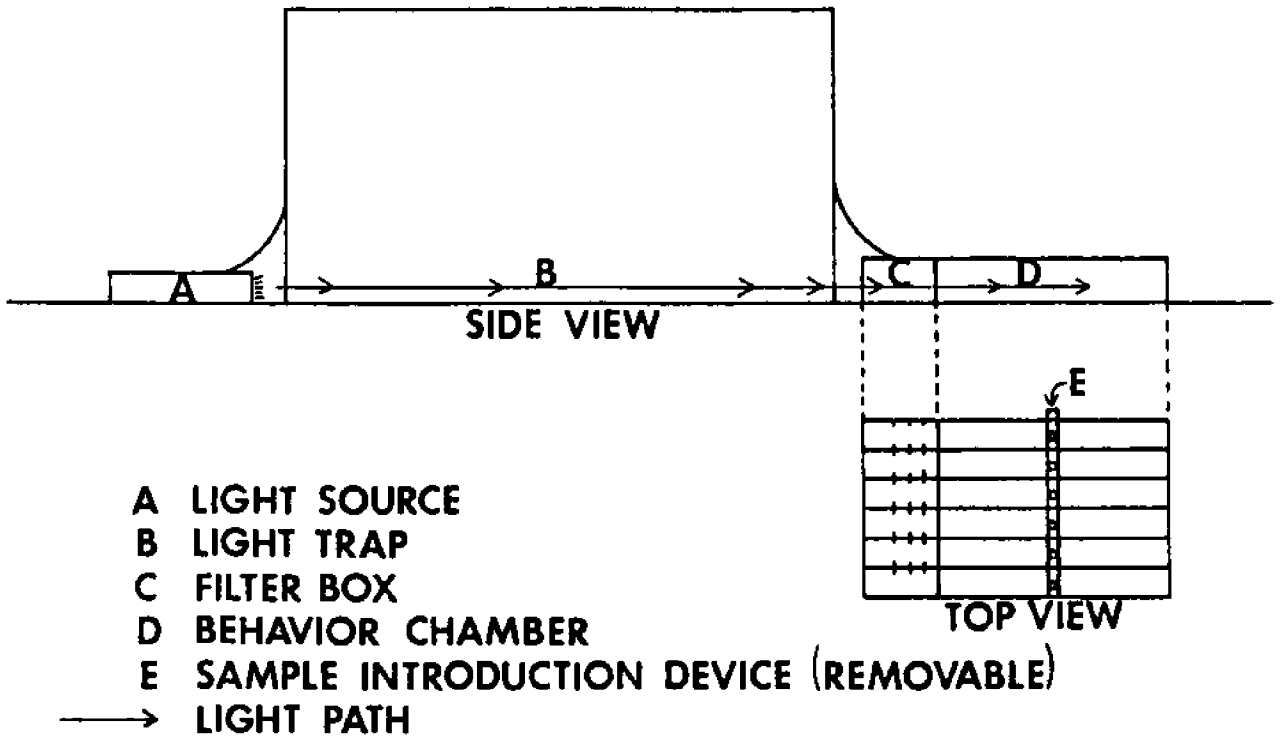

Figure 4. Phototaxis behavior chamber.

through a 500 nm bandpass filter, then through a specified neutral density filter. Light intensity was measured at the proximal end of the chamber with a YSI Model 65A radiometer. Wavelength was controlled by the use of bandpass filters. The bandwidth of these filters ranged from 6.8 to 11.4 nm at 50% of peak transmission. Intensities were adjusted to be approximately equal (0.2 W/m^2 at 420 nm to 0.8 W/m^2 at 650 nm).

Sign of phototaxis was determined by placing a sample of larvae in the middle of each raceway in the tubes held by the release bar (Fig. 5E). Appropriate light conditions were established for each raceway and larvae in all six chambers were released simultaneously by raising the bar and tube assembly. Individual larvae were then free to move toward the light, away from it, or remain in the middle of the chamber. Phototaxis was determined by counting the numbers of larvae in each raceway that were in the third of the chamber nearest the light (+), farthest from the light (-), or in the middle (0).

The design of the apparatus permitted testing up to six different wavelengths, intensities, or acclimation temperatures or salinities simultaneously with sibling larvae.

Intensity and Wavelength. Intensities were selected to provide a range similar to those used by other investigators (Forward and Costlow 1974; Forward 1977). Judicious use of the neutral density filters provided the following six intensities, at 500 nm: 0.25, 9×10^{-2}, 4×10^{-2}, 2×10^{-2}, 2×10^{-3}, and 4×10^{-4} W/m^2. In separate experiments, the following six wavelengths were tested: 420, 480, 540, 580, 600 and 650 nm.

At the beginning of each experiment, 10 larvae were entered into each release tube. Distribution of each sample was determined at 10 min. Percent of sample responding positively, negatively, or in-

differently to each intensity or wavelength was calulated. A total of five replicates for each intensity and wavelength was run (n = 50 larvae per condition). Each replicate was conducted with larvae from a different brood. Results from the five replicates were pooled and presented as "kite" diagrams. All experiments were repeated with light- and dark-adapted larvae of zoeal stages I, IV and VII.

Temperature and Salinity Acclimation. Larvae were acclimated for 24 hr in 25, 30 or 35 ppt S. Sign of phototaxis as a function of salinity and salinity acclimation was determined by testing all possible combinations in the following manner. All six chambers were set up in identical fashion (e.g., 25°C, 500 nm, 0.25 W/m^2, 25 ppt S). For each experiment, larvae acclimated to each of the three salinities were introduced to two of the chambers selected randomly. Thus, when the test salinity was set up at 25 ppt, larvae in two chambers were tested at the salinity of acclimation; in two chambers, at a salinity 5 ppt above that of acclimation; and in two chambers, at a salinity 10 ppt above that of acclimation. The experiment was repeated with larvae from five different broods (n = 100 larvae per condition). The experiments were then repeated at a test salinity of 30 ppt, and finally, at 35 ppt. In all experiments, distributions were determined at 5 min after release of larvae. Data analysis was as described for intensity experiments.

Temperature acclimation experiments were conducted in a similar fashion. Samples of larvae were acclimated to 15°, 20° and 25°C and tested at these three temperatures in sequential manner. Replicates from five different broods were tested. Standard test conditions were 30 ppt S, 0.25 W/m^2, 500 nm. All experiments were conducted on light-adapted larvae of zoeal stages I, IV and VII.

Experimental Results

Figure 5 shows sign of phototaxis as a function

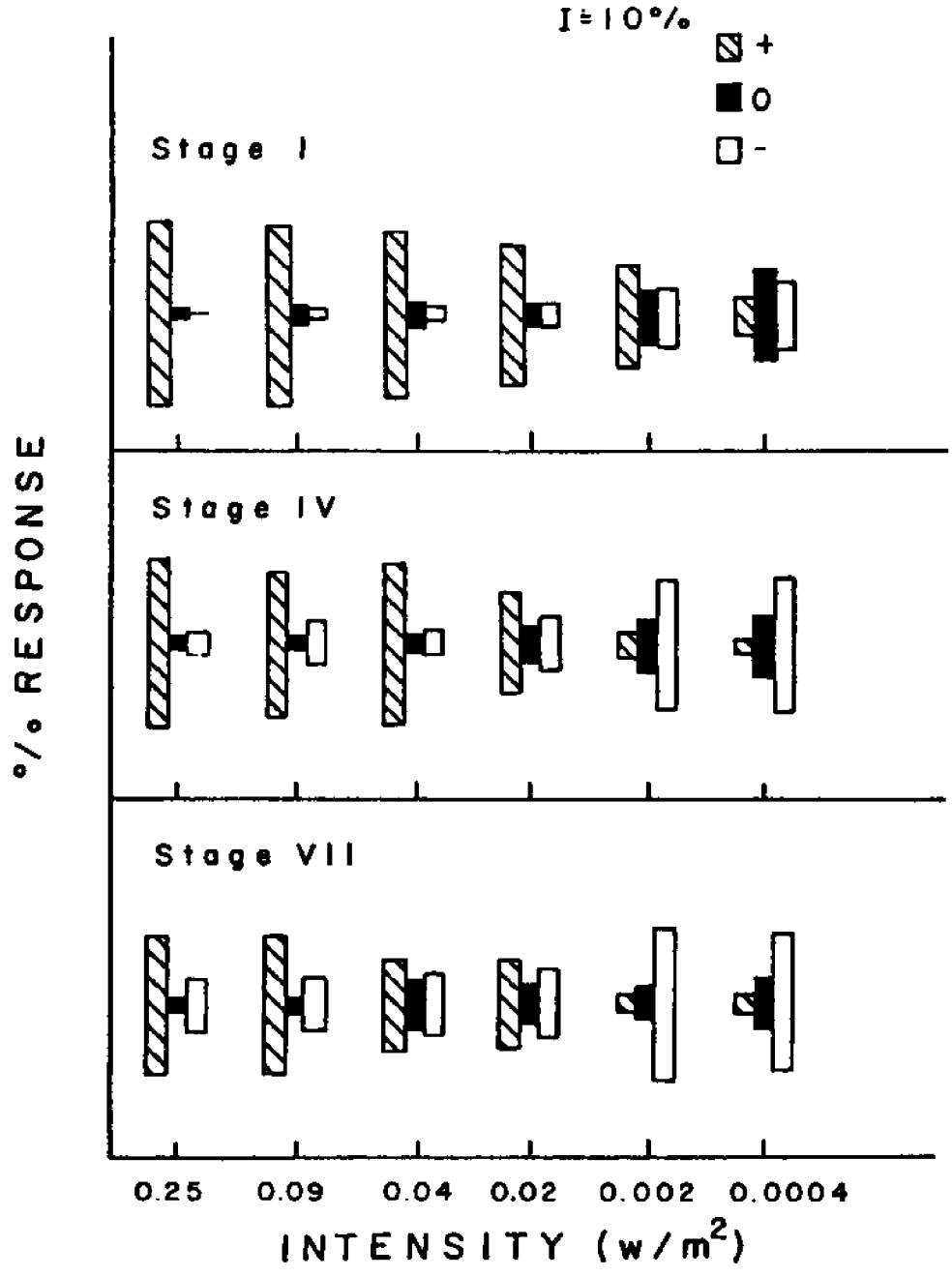

Figure 5. Sign of phototaxis as a function of light intensity for light-adapted larvae of zoeal Stages I, IV and VII. (Each kite diagram represents a mean of five replicates: n=50.)

of light intensity in light-adapted larvae of Stage I, IV and VII. Stage I larvae show a reduction in incidence of positive phototaxis at an intensity of 2×10^{-3} W/m^2. At 4×10^{-4} W/m^2, neutral response dominates, while a significant proportion are actually negatively phototactic. Stage IV larvae show a similar response, although a higher intensity threshold (2×10^{-2} W/m^2) occurs for the shift away from positive phototaxis. Below this threshold, negative phototaxis dominates. In Stage VII, the intensity at which the incidence of positive response diminishes is higher than in earlier instars tested (4×10^{-2} W/m^2) . It thus appears that as larval development proceeds, the intensity threshold above which positive phototaxis dominates in light-adapted larvae gradually increases.

Figure 6 shows sign of phototaxis as a function of light intensity in dark-adapted larvae of Stages I, IV and VII. A majority of Stage I larvae respond positively to light down to intensities as low as 4×10^{-4} W/m^2, although the incidence of positive phototaxis is reduced at 2×10^{-3} W/m^2. Stage IV larvae show an identical pattern of sign of phototaxis. Stage VII larvae show positive phototaxis at intensities as low as 2×10^{-3} W/m^2; however, unlike earlier stages tested, a shift away from positive phototaxis occurs at 4×10^{-4} W/m^2. In dark-adapted larvae, positive phototaxis dominates at lower intensities than is the case with light-adapted larvae.

Figure 7 shows sign of phototaxis as a function of wavelength in light-adapted larvae of Stages I, IV and VII. In all three stages positive phototaxis dominates in wavelengths from 420 nm to 580 nm. At 600 nm there is a reduction in incidence of positive response and at 650 nm a majority of larvae show negative phototaxis.

Figure 8 shows sign of phototaxis as a function

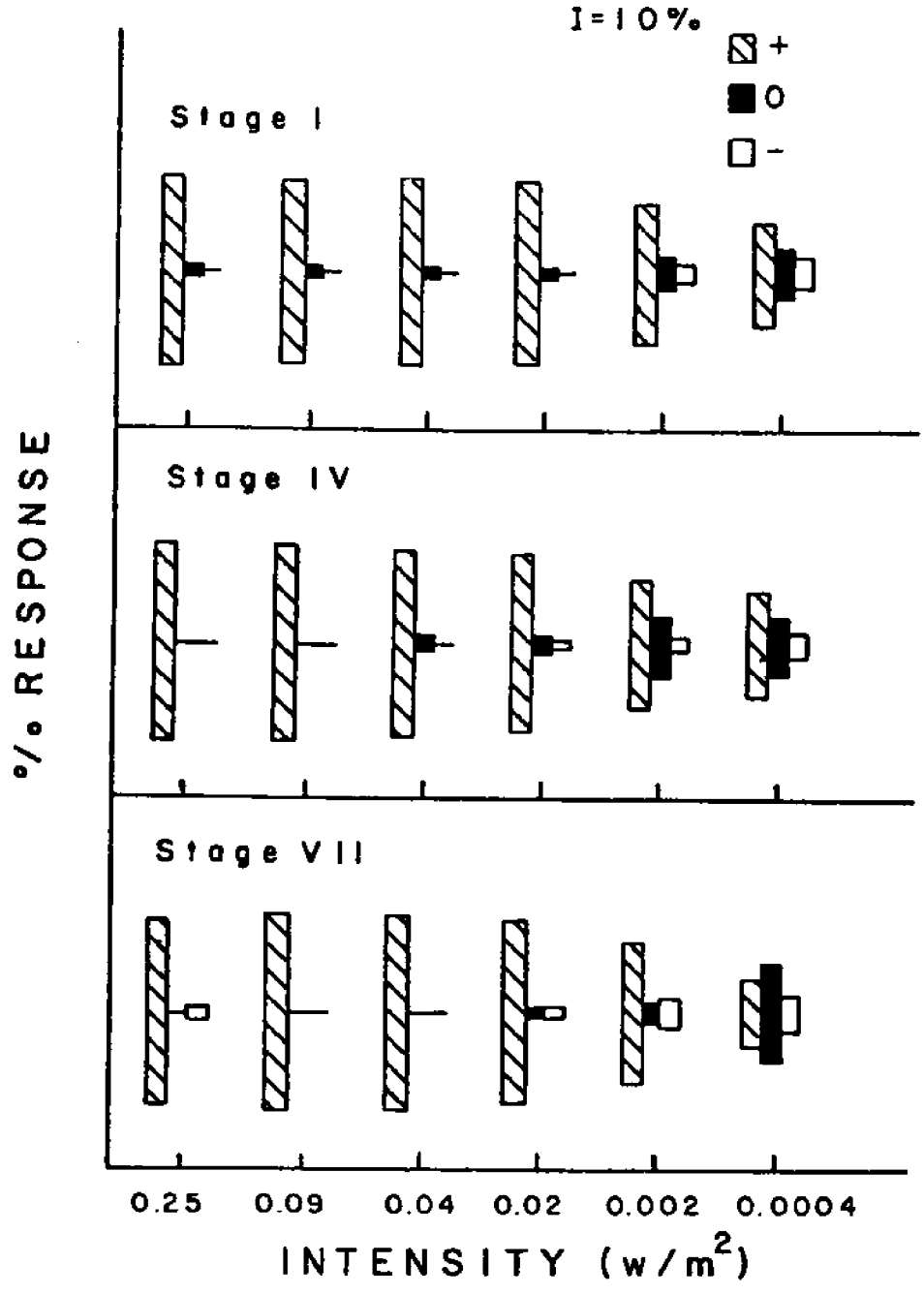

Figure 6. Sign of phototaxis as a function of light intensity for dark-adapted larvae of zoeal Stages I, IV and VII. (Each kite diagram represents a man of five replicates: n=50.)

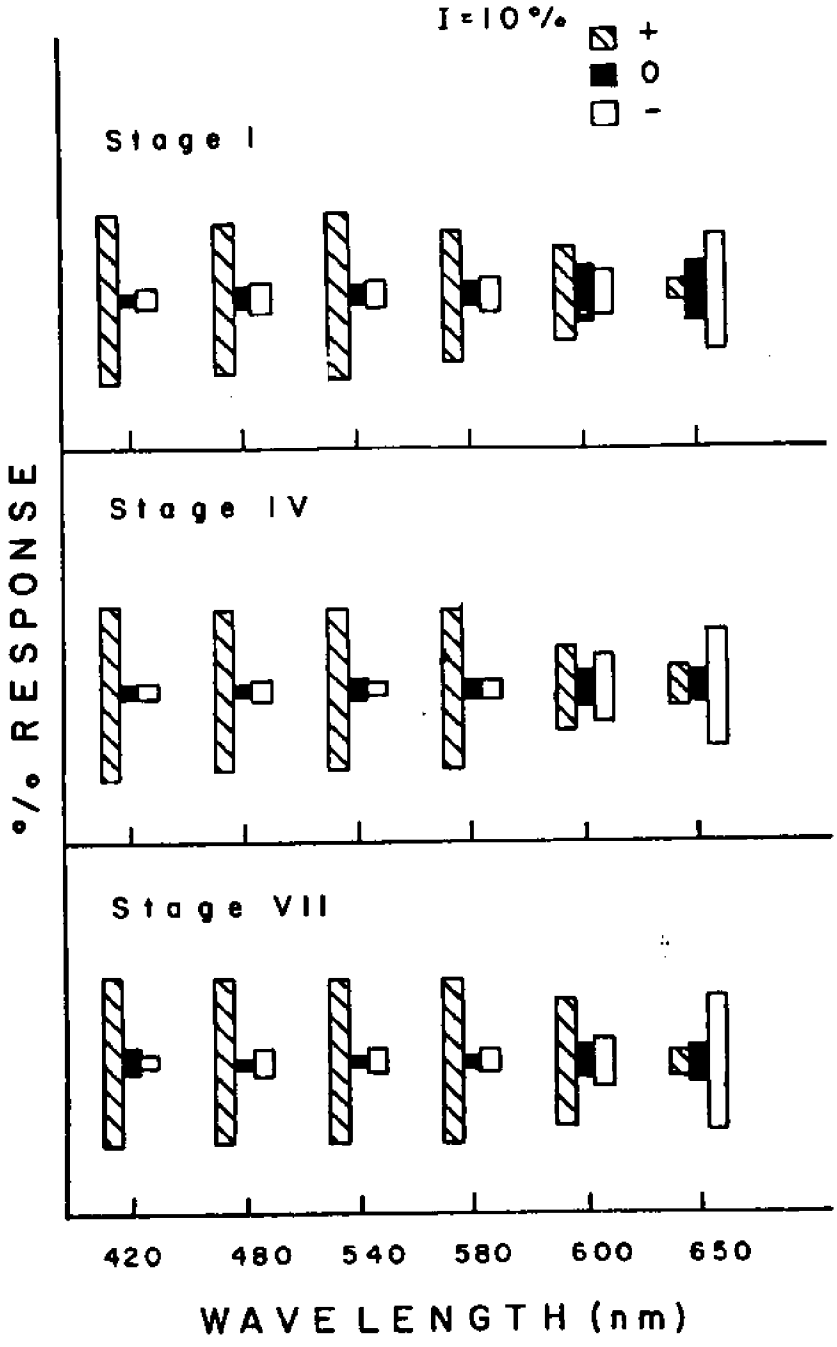

Figure 7. Sign of phototaxis as a function of wavelength for light-adapted larvae of zoeal stages I, IV and VII. (Each kite diagram represents a mean of five replicates: n=50.)

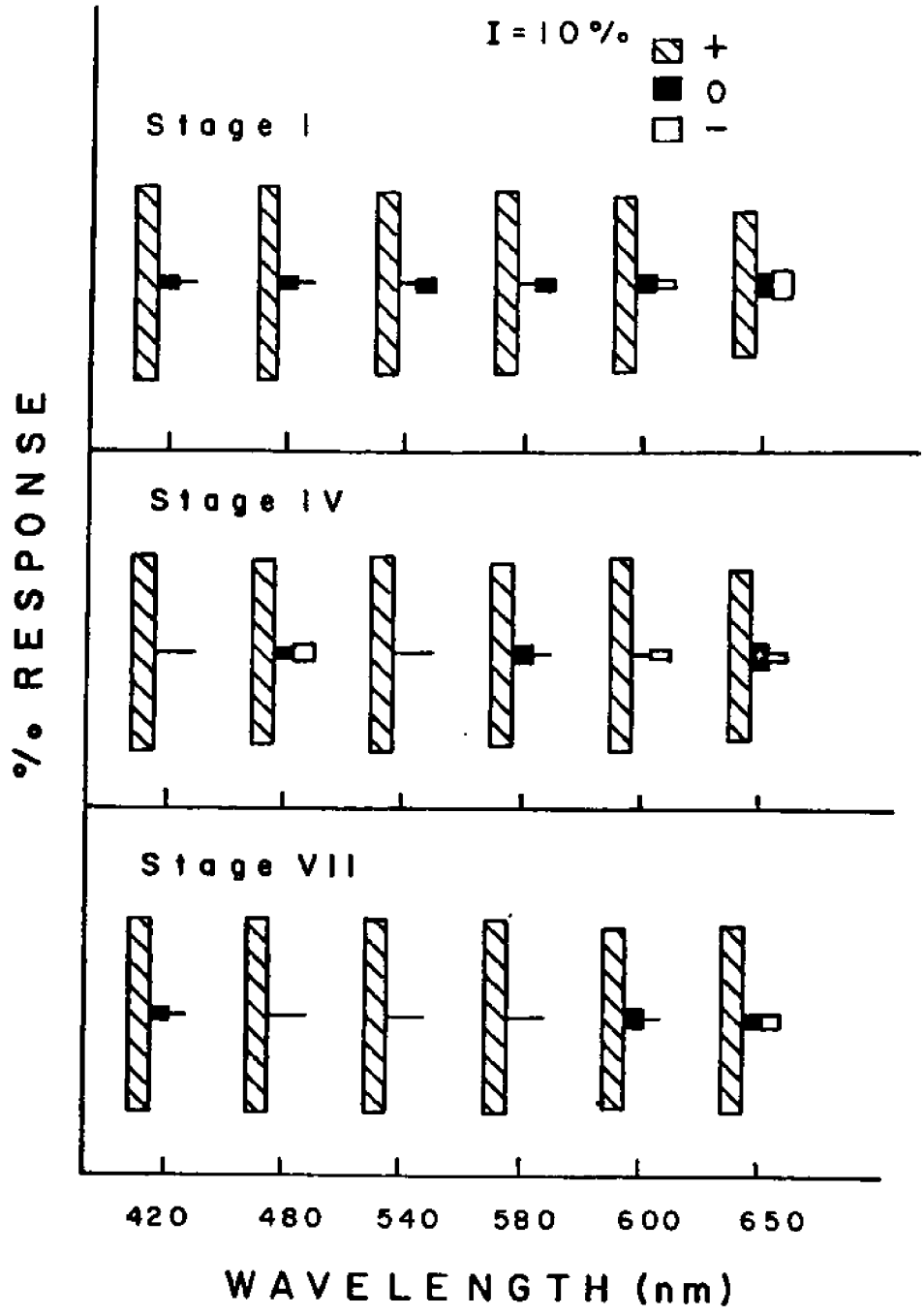

Figure 8. Sign of phototaxis as a function of wavelength for dark-adapted larvae of zoeal stages I, IV and VII. (Each kite diagram represents a mean of five replicates: n=50.)

of wavelength in dark-adapted larvae of Stages I, IV and VII. A majority of larvae in all three stages respond positively to all wavelenghts tested between 420 nm and 650 nm. Although there is a difference in sign of response at long wavelengths between light- and dark-adapted larvae, there is no apparent change in response to wavelength during ontogeny in either condition.

The graphs in Fig. 9 show the effects of temperature acclimation on sign of phototaxis in Stages I, IV and VII. In all three stages, larvae tested at the temperature of acclimation show positive phototaxis in a majority of individuals. Larvae tested at temperatures 5^{o} or 10^{o}C above or below that of acclimation show little change in response.

The graphs in Fig. 10 show the effect of salinity acclimation on sign of phototaxis in Stages I, IV and VII. In all three stages, larvae tested at or above the salinity of acclimation show positive phototaxis in a majority of individuals. In Stages IV and VII, larvae tested at 5 or 10 ppt salinity below that of acclimation show little change in response. However, in Stage I a 5 to 10 ppt reduction in salinity results in an apparent shift to neutral response. Direct observation of the larvae indicated that this response was due to general reduction of locomotory activity on the part of most of the larvae.

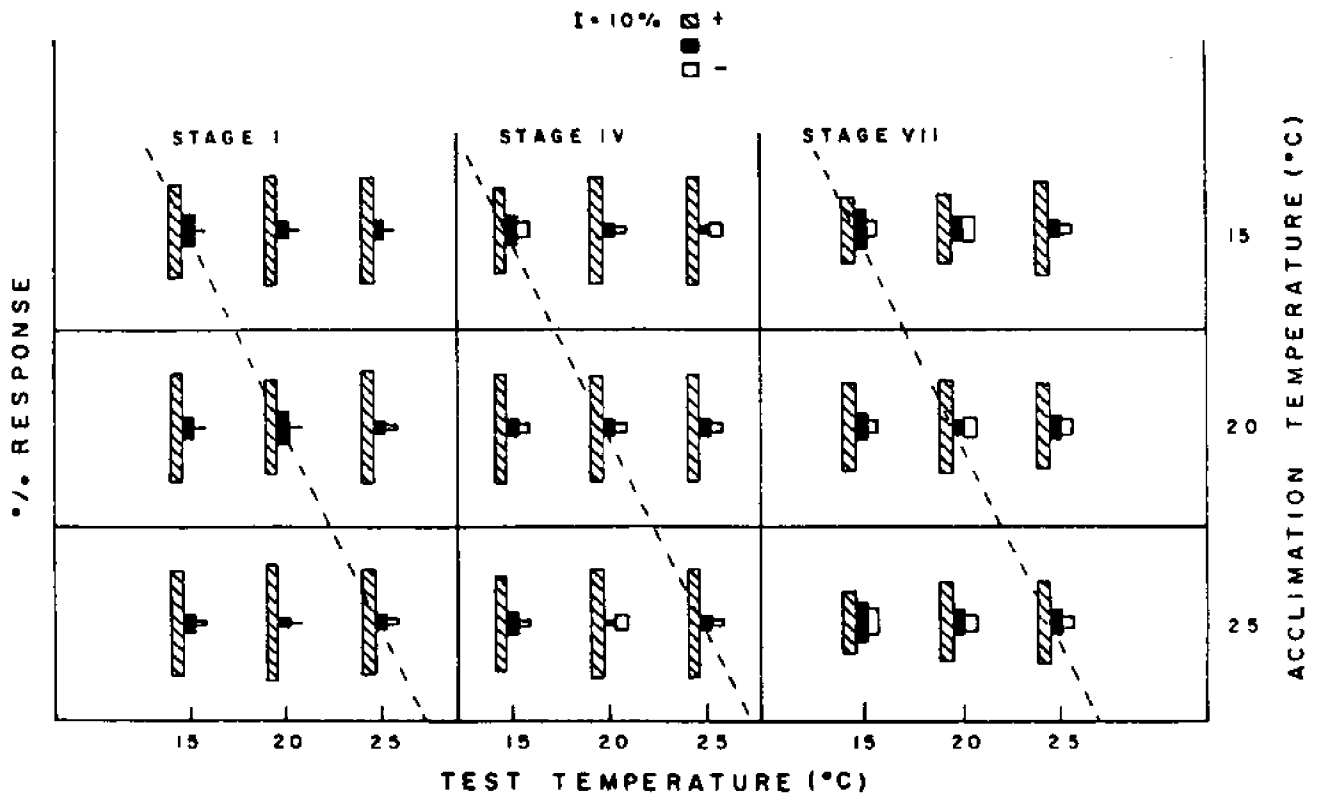

Figure 9: Sign of phototaxis for larvae acclimated to temperatures of 15, 20 or 25°C and tested at 15, 20 or 25°C. (Light conditions described in text. Each kite diagram represents a mean of ten replicates: n=100.)

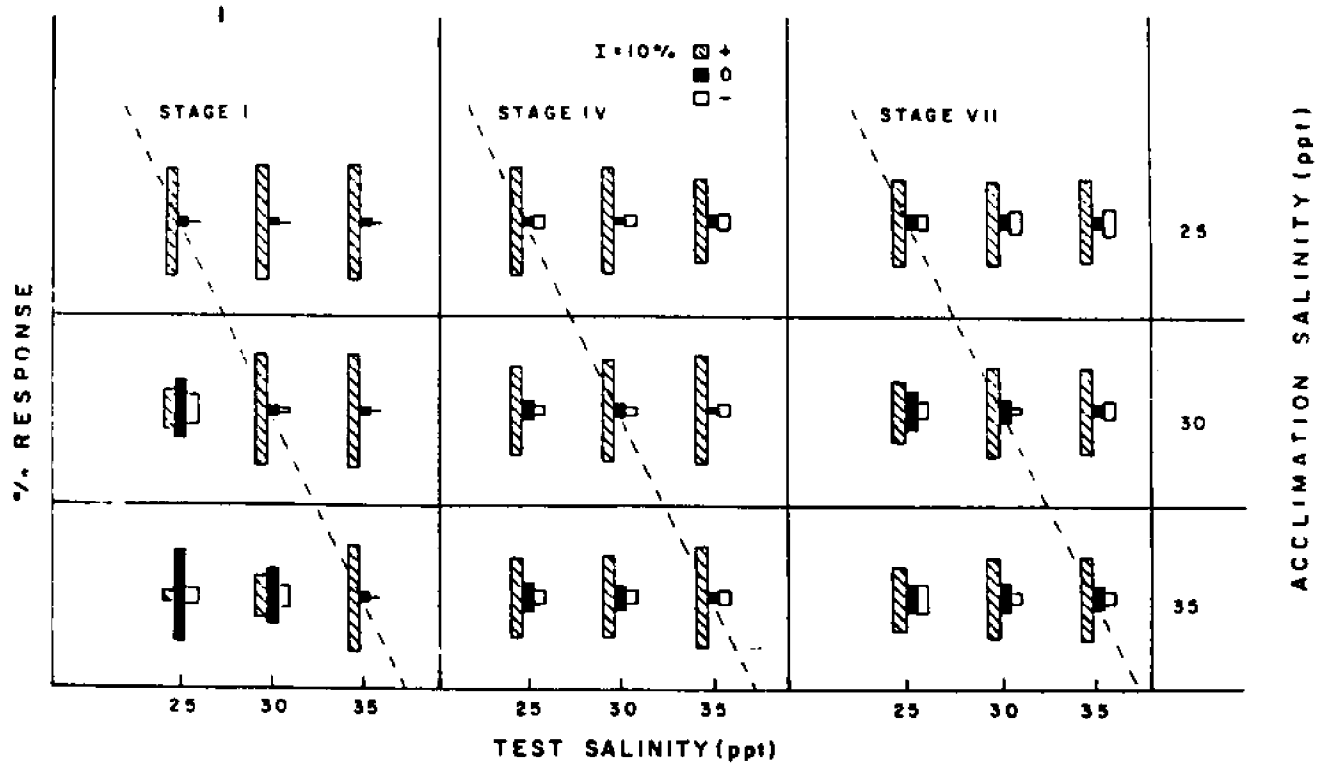

Figure 10. Sign of phototaxis for larvae acclimated to salinities of 25, 30, or 35 ppt S and tested at 25, 30 or 35 ppt S. (Light conditions described in text. Each kite diagram represents a mean of ten replicates: n=100.)

HALOCLINES AND THERMOCLINES

Our experiments in 1978-1979 were designed to provide general conclusions concerning the effect of discontinuities on vertical migration. The studies were initiated because in the natural habitat there is evidence of a sharp and persistent pycnocline (Pritchard 1952; Taylor et al. 1974; Seitz 1971). Furthermore, reports from the literature suggest that such discontinuities affect vertical migration in zooplankton. Response of zooplankton to salinity discontinuities has been the subject of numerous detailed studies, among them, Harder (1968), Lance (1962) and Roberts (1971). Harder's results are representative. He reported that zooplankton generally collect at discontinuity layers, sometimes both above and below. Minimum threshold gradient varied widely with species. Harder asserts that the density gradient is generally the operative stimulus. In the anomuran *Pagurus longicarpus*, Roberts (1971) found that larvae collected at discontinuity layers due to avoidance of the alternate salinity. Larval response varied according to stage of development. Response was induced either by avoidance of absolute salinity or by the encounter of specific increments of salinity change (ΔS) depending upon the upper and lower layer salinity values. The larvae were capable of detecting ΔS of only 2.5 ppt.

Changes in behavioral response to light and gravity as a function of salinity and temperature have been documented for a number of meroplankters. Thorson (1964) reported that larvae of 14 species which are normally positively phototactic become negative with an increase in temperature. Ewald (1912) reported similar behavior in *Balanus* larvae. On the other hand, Fraenkel (1931) showed that normally negatively phototactic *Squilla* larvae become positive when temperature is reduced. Ott and Forward (1976) showed that geotactic and phototactic response in larvae of *Rhithropanopeus harrisii*

varied with temperature. The sign of phototaxis remained the same, although reduced response occurred at the extremes of temperatures tested. The normally negative geotactic sign reversed in both the first and last zoeal stage depending upon temperature. Late stage larvae both sank and swam downward, while early stage larvae sank only. Latz and Forward (1977) reported in *R. harrisii* larvae that a sudden change in salinity of 1-2 ppt can temporarily reverse the signs of both phototaxis and geotaxis. Larvae regained normal phototactic response in as little as 5.5 min.

Materials and Experimental Methods

To evaluate the impact of salinity and temperature discontinuities on vertical movement of the blue crab larvae, sharp gradients were established in an experimental apparatus and larvae were induced to swim through them. Haloclines were set up in a vertical tank by introducing high salinity water beneath lower salinity water. As the denser water was added at the bottom of the tank, the lighter (lower salinity) water was displaced upward. In this way sharp salinity gradients could be established. (Higher salinity was always 30 ppt S.) A control was used, consisting of a vertical tank containing no halocline. Larvae were introduced at either the top or bottom of the tank and induced to swim up or down along the vertical axis. Larvae were acclimated to the salinity of introduction and the control salinity was that of introduction. Larvae of Stages I, IV and VII were tested at ΔS of 10 ppt and larvae of Stage I were tested at all three ΔS.

A similar experimental system was used to test thermoclines. However, in this case, an insulated water bath was used to control temperatures (see Figure 11). A thermocline of 10°C (15°C→25°C) was used on larvae of Stages I, IV and VII. Again, both

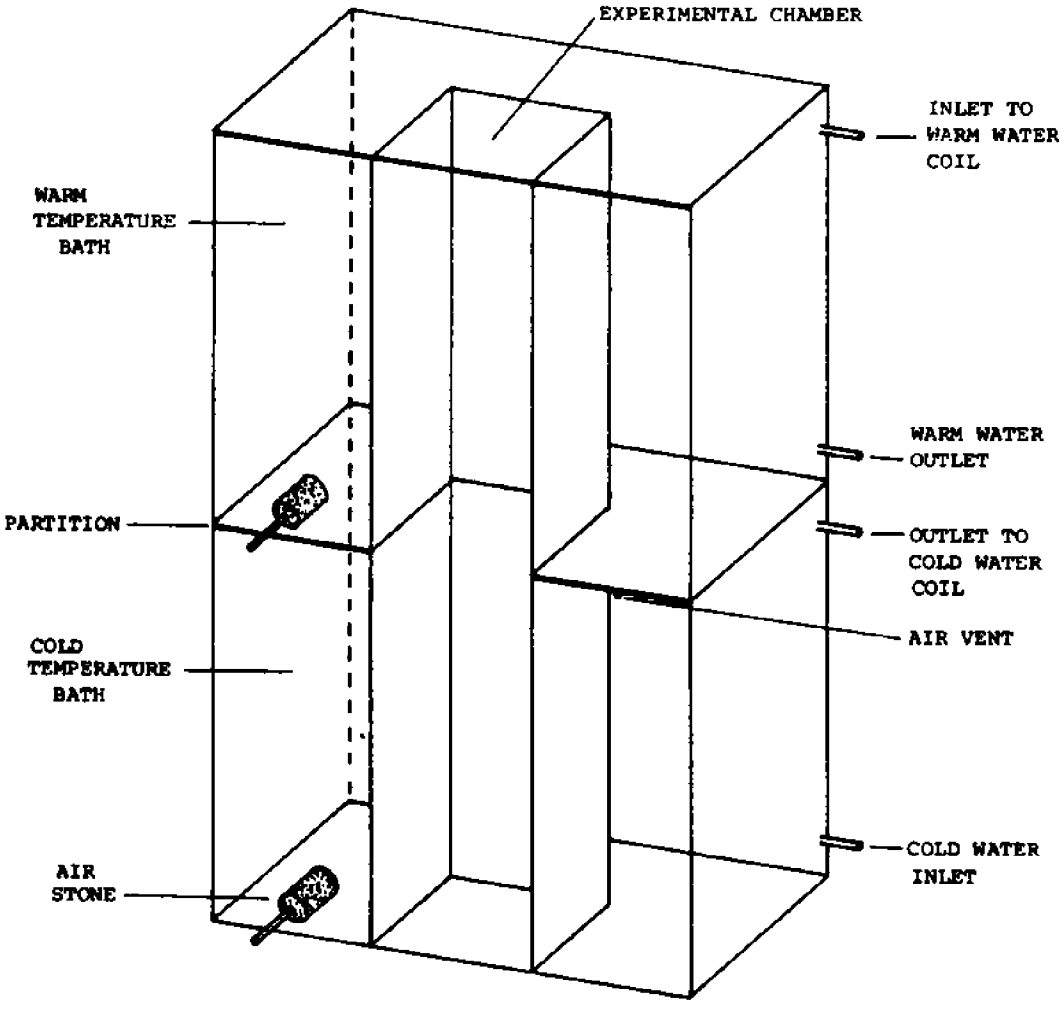

Figure 11. A device for establishing a thermocline in an experimental chamber. Water of different temperatures can be circulated through the separate coils (not shown) of the upper and lower temperature baths.

top and bottom introduction experiments were conducted. Larvae were acclimated to the temperature of introduction and the control was established at that temperature.

Results

The results of these preliminary experiments are summarized in figures 12 to 15. The discontinuity layer was present in the middle region of the tank. The distributions shown were those measured 30 min after introduction of larvae.

Figure 12a shows data for bottom introduction of larvae in a 10 ppt ΔS. The presence of the halocline clearly disrupted upward movement of larvae. Note the increased incidence of larvae in the segment containing the halocline. Figure 12b shows the results of bottom introduction of Stage I zoeae previously acclimated to lower (upper layer or top) salinity conditions. Acclimation history clearly has an effect on behavior at the halocline. In contrast to the results for stage I larvae acclimated to the lower layer salinity (Figure 12a), these larvae moved through the halocline, suggesting that the halocline is not acting as a physical barrier. Figure 13 shows the results of top introduction of larvae. The disruptive influence of the halocline on vertical movement is again clearly shown: in this case, downward movement in all three stages, whether by passive or active forces, is disrupted. Figure 15 shows the effect of different ΔS on Stage I larvae. Although the disruptive effect appears diminished at a 2.5 ppt ΔS, there is evidence that some larvae were congregating near the halocline.

Figure 15 shows the effects of a $10^{\circ}C$ thermocline on upward and downward vertical movement. It is apparent that this sharp temperature gradient disrupted upward and downward movement in all stages. (Because of a lack of upward vertical migration in

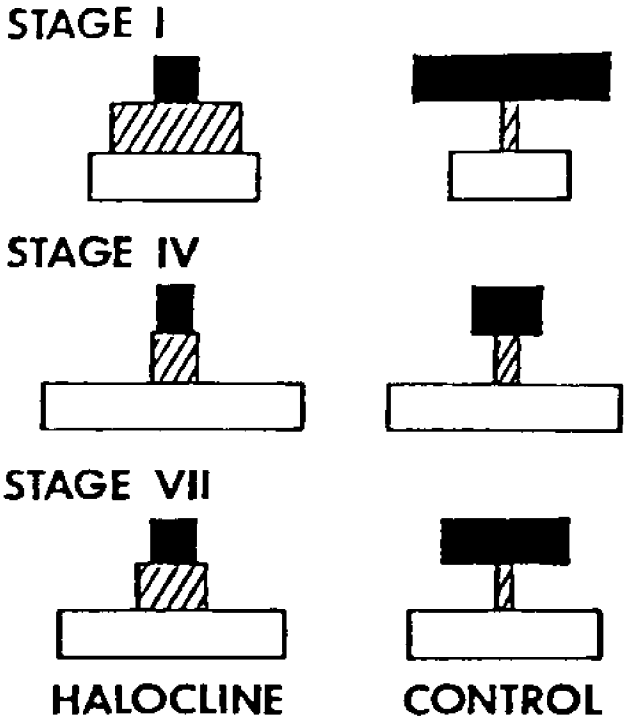

Figure 12a. The vertical distribution of larvae 30 min after introduction to bottom of columns. Salinity was 20 ppt in upper layer and 30 ppt in bottom layer. (Note: pressure of the halocline interfered with upward movement in all three stages.)

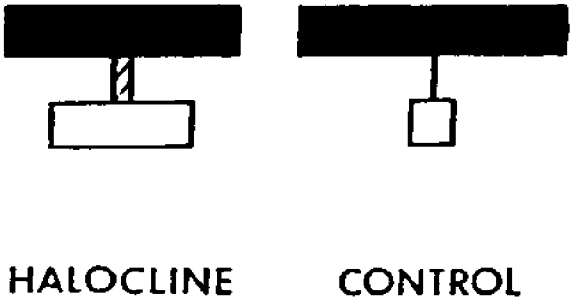

Figure 12b. Vertical distribution of Stage 1 zoeae acclimated to the upper layer salinity but introduced to the bottom layer.

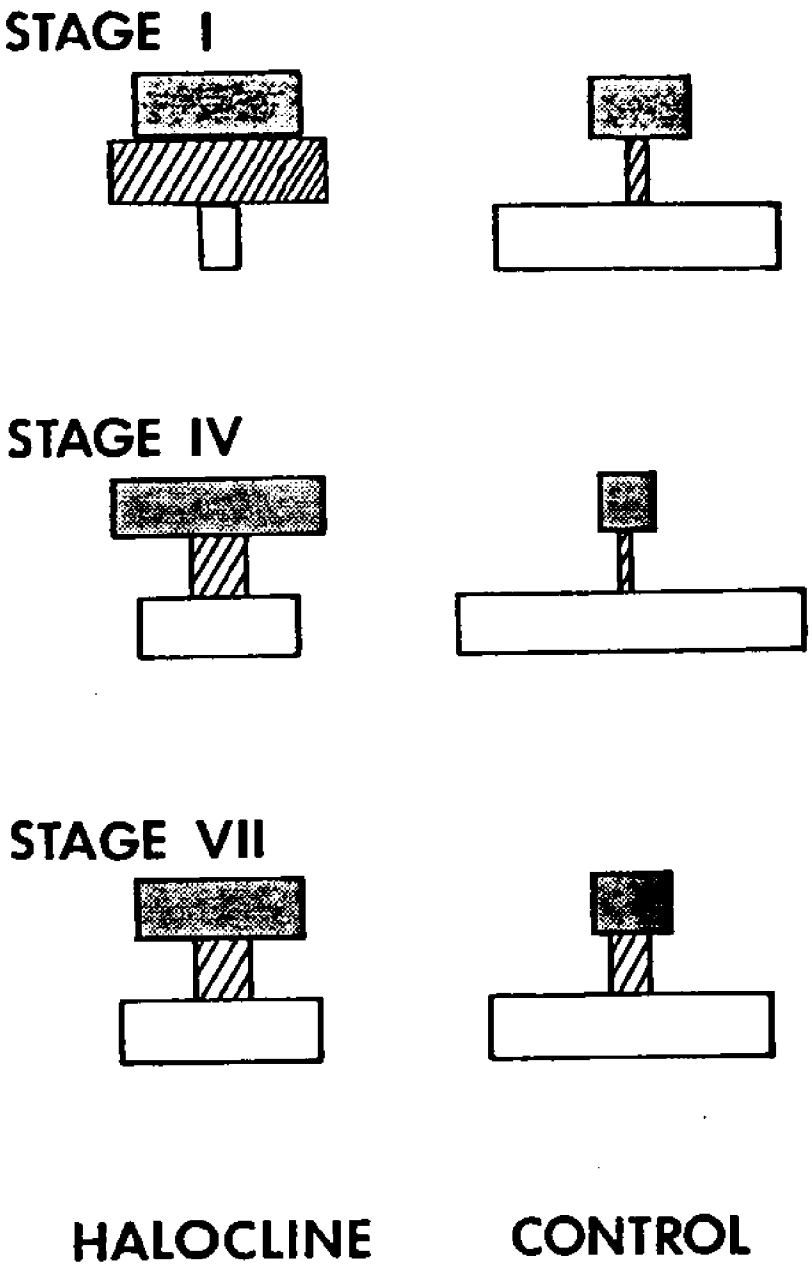

Figure 13. The vertical distribution of larvae 30 min after introduction to the top of columns. Salinities were 20 to 30 ppt in the top and bottom layers, respectively.

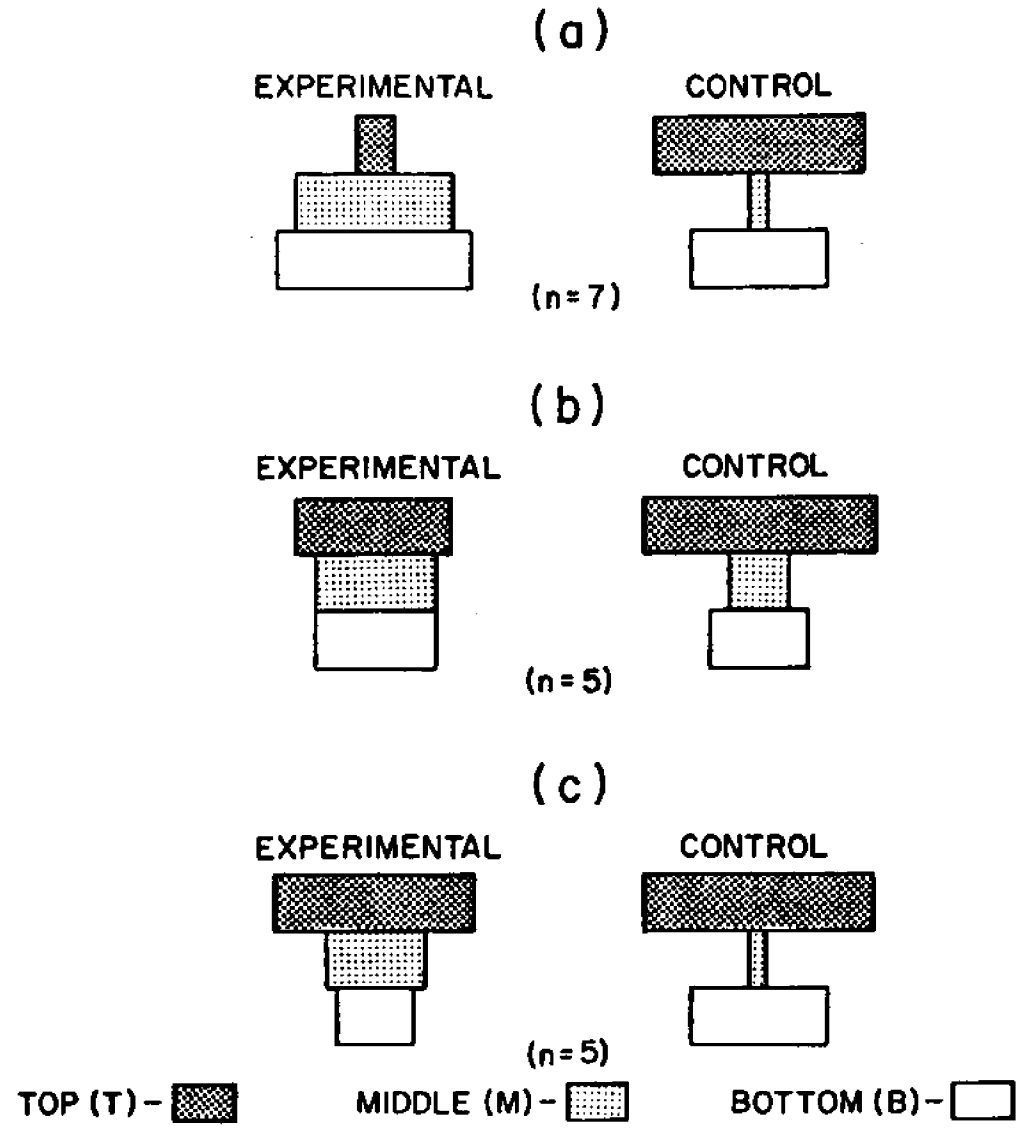

Figure 14. The effects of haloclines of different magnitude on vertical movement of Stage I zoeae. Salinity difference between top and bottom was 10 ppt in (a), 5 ppt in (b), 2.5 ppt in (c). Larvae were introduced in each case to bottom layer. (Paired tests were conducted for percent of larvae in the top segment in each case. Significance between experimental and control was found only at at 10 ppt.)

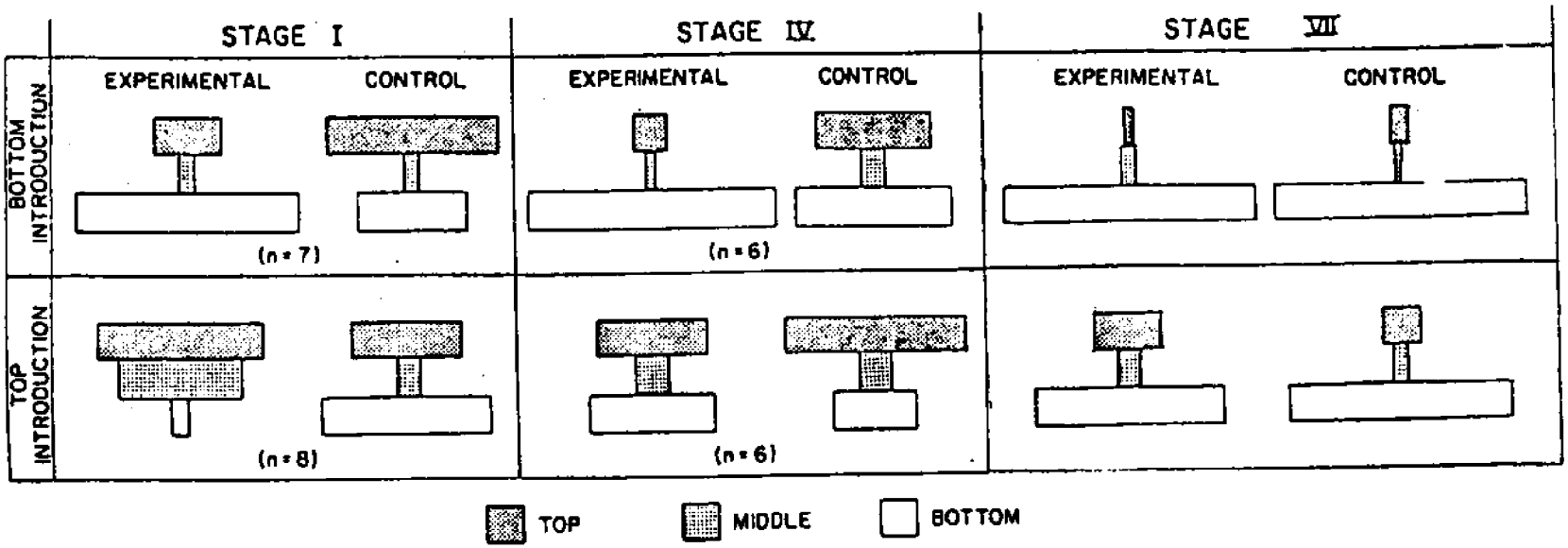

Figure 15. Vertical distribution of zoeae 30 min after introduction to columns. The thermocline interfered with upward movement introduced at the bottom of Stages I and IV. (The thermocline prevented downward movement of larvae introduced at the top of the chamber in all three stages.)

Stage VII control, an evaluation of the thermocline is not possible.) Note that in the bottom introduction experiment, larvae were not gathering at the discontinuity layer.

These results indicate that sharp haloclines and thermoclines can indeed disrupt vertical movement. The apparent influence of acclimation condition on ability of larvae to penetrate the discontinuity suggests a mechanism other than the effects of a physical barrier induced by density differences. Furthermore it would appear that the causes of disruption of vertical movement are different for salinity and temperature discontinuities, as evidenced by the different distribution patterns elicited.

Clearly the experiments as designed do not simulate natural conditions where the rate of change will be much reduced as compared to our laboratory studies. Until the mechanisms of disruption are understood, the effects of natural gradients will be difficult to evaluate. The significance of natural gradients is illustrated by the role discontinuities may play in regulating larval retention by preventing early larvae hatched at depth from entering surface waters and conversely by preventing sinking to retention depths of early larvae introduced to surface waters.

POPULATION GENETICS

The alternate theories of recruitment source for blue crabs in Chesapeake and Delaware bays have implicit genetic consequences. If there is little or no exchange of larvae among estuarine adult populations, genetic divergence may occur. The hypothesis that Chesapeake Bay, Delaware Bay and neighboring estuarine populations exchange larvae via an offshore nursery predict that no genetic divergence will be apparent.

Genetic divergence among populations may be studied by electrophoretic examination of enzyme systems. Parameters such as the number of alleles per locus, the percent polymorphism, and the percent heterozygosity may be compared among samples drawn from various populations. The amount of genetic divergence may be quantified (Nei 1972). This electrophoretic technique has been used widely for establishing divergence and sub-speciation for a variety of organisms, including the striped bass (Morgan et al. 1973), the American lobster (Tracey et al. 1975), mallards and black ducks (Morgan et al. 1976) and cottontail rabbits (Chapman and Morgan 1973).

An attempt was made to compare crabs from Chespeake and Chincoteague Bays and the Gulf of Mexico. As originally proposed, the methods of Tracey et al. (1975) were used to prepare the tissue and separate the loci. Unfortunately the blue crab tissue was not readily amenable to this standard electrophoretic technique. When these experiments were initiated, Dr. Dennis Hedgecock had begun similar experiments. After consulting with Dr. Hedgecock, we modified our technique according to those published in Nelson and Hedgecock (1980). Dr. Hedgecock visited our laboratory and assisted in evaluation of our results and found them to be compatible with his. Considerable time and effort was

expended in working on these techniques. As a consequence, sample sizes were too small to test for similarity according to Nei's (1972) equations.

Nevertheless the results reported here have provided a useful basis for further studies; with Sea Grant support, further studies are in process under the direction of Dr. Tim Cole, a geneticist with considerable experience in working with marine invertebrate systems.

Materials and Methods

Blue crabs were collected from Tilghman Island and Chincoteague Bay, Maryland, and purchased from Gulf Specimen Company, Panacea, Florida. Tissue samples were prepared from green gland, eye, gonad, hepatopancreas, heart, gill and backfin muscle. These tissues were homogenized in an equal volume of 0.05 M TRIS-HCl in a tissue grinder, certifuged at 12,000 rpm for 20 minutes (Tracey et al. 1975) and stored in an ultracold freezer at -70°C. Samples were analyzed by the electrophoretic techniques of Tracey et al (1975), using the procedure for horizontal starge gels described by Ayala et al. (1973). Assays were run for the enzymes listed in Table 4. The gels were stained according to experimental procedures worked out during the course of the study.

Results

The best tissues for analyses proved to be backfin muscle and hepatopancreas. A summary of the enzyme systems, number of loci, number of alleles, and whether they are monomorphic or polymorphic are summarized in Table 1, and generally agree with the results of Hedgecock's group (pers. comm.).

The results of this preliminary study will serve as a basis for further work on this species. Of the 50 species studies by Nelson and Hedgecock

(1980), the blue crab had the highest average heterozygzosity, indicating that for genetic studies it is the most promising crustacean species currently known (Hedgecock, pers. comm.). Compared with other invertebrates, however, the heterozygzosity is low.

Polymorphic loci, which provide potential for further study, were found for the following enzymes: EST (II, IV-VI), FUM, GOT, HK (II), PGI, GA-3-PDH, G-PGDN, Pt (II, III, VI).

TABLE 1: Summary of Electrophoretic Examination of Enzyme Systems

ENZ	ACTIVITY	NO. ZONES PRESUMED LOCI	MONOMORPHIC POLYMORPHIC	NO. ALLELES
Acid Phosphatase (ACPH)	✓	1	MONO	2
Esterase (EST)		5-7		
	Zone	I	MONO	1
	"	II	POLY	2
	"	III	MONO	?
	"	IV	POLY	2
	"	V	POLY	3
	"	VI	POLY	2
		VII	MONO	?
Fumerase (FUM)	✓	1	POLY	2
Glutamate-Oxaloacetic-Transaminase (GOT)	✓	1	POLY	2
Glyceraldehyde-3-Phosphate Dehydrogenase (GA-3-PDH)	✓	1	POLY	2

TABLE 1 (continued)

ENZ	ACTIVITY	NO. ZONES PRESUMED LOCI	MONOMORPHIC POLYMORPHIC	NO. ALLELES
Hexokinase (HK)		2		
	Zone	I	MONO	1
	"	II	POLY	2
Isocitrate Dehydrogenase(IDH)	✓	1	MONO	1
Malate Dehydrogenase (MDH)	✓	2	MONO	
	Zone	I		1
	"	II		1
Malic Enzyme (ME)	✓	1	MONO	1
Peroxidase (PER)	✓	1	MONO	1
6-Phosphogluconic Dehydrogenase (6-PGDH)	✓	1	POLY?	2?
Phosphoglucomutase (PGM)	✓	1	MONO?	1?

TABLE 1 (continued)

ENZ	ACTIVITY	NO. ZONES PRESUMED LOCI	MONOMORPHIC POLYMORPHIC	NO. ALLELES
Phosphoglucose Isomerase (PGI)	✓	1	POLY?	2
Total Protein (Pt)	✓	5-8		
	Zone	I	MONO	1
	"	II	POLY	2
	"	III	POLY (Possibly part of Zone 4)	?
	"	IV	Too close to Zone 3 to score	
	"	V	MONO	1
	"	VI	POLY	2
	"	VII	MONO	1
	"	VIII	MONO	1
Tetrazolium Oxidase (TD)	✓	5?	?	?
Triosephosphate Isomerase (TPI)	✓	1	MONO?	1

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