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THE BEHAVIORAL BASIS OF LARVAL RECRUITMENT IN THE CRAB *CALLINECTES SAPIDUS* RATHBUN: A LABORATORY INVESTIGATION OF ONTOGENETIC CHANGES IN GEOTAXIS AND BAROKINESIS[1]

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Estuarine invertebrates that have planktonic larvae must maintain their populations in the face of net seaward flow of water. One mechanism for this is active retention within the estuary of sufficient offspring to at least replace the population (Sandifer, 1975; Scheltema, 1975).

Retention mechanisms that combine behavioral adaptations with characteristic estuarine circulation have been described for larvae of several estuarine invertebrates, including barnacles and mud crabs (Bousfield, 1955), oysters (Carriker, 1951; Wood and Hargis, 1971) and decapods (Sandifer, 1975). However, it is unlikely that all planktonic larvae will be retained in the face of net downstream flow of water. Indeed, larvae of many estuarine crabs are present in the waters of the continental shelf off the east coast of North America (Nichols and Keney, 1963; Sandifer, 1973; Dudley and Judy, 1971). Among the most common are species of the genus *Callinectes,* including the blue crab *Callinectes sapidus* Rathbun (Sandifer, 1975; Goy, 1976).

C. sapidus inhabits entire estuaries as an adult, but spawns only in high salinity regions near estuary mouths (Hopkins, 1943; Van Engel, 1958). These circumstances increase the probability of loss of larvae from the estuary. It is critical to an understanding of the recruitment process, and hence population dynamics, to determine whether larvae exported from estuarine spawning grounds to ocean waters represent a significant loss from the adult habitat and, if so, whether they may be recruited back to it in significant numbers.

Mechanisms for larval retention within an estuary or exchange between an estuary and its adjacent coastal region depend upon characteristic circulation (Pritchard, 1952; Bousfield, 1955; Scheltema, 1975). Because currents vary in direction and rate with depth, vertical distribution of larvae is significant in determining their ultimate destinations. For some crab species, there is evidence that vertical distribution of larvae varies predictably with age (Bousfield, 1955; Sandifer, 1975; Goy, 1976). There is further evidence that these vertical distribution patterns result from oriented movement controlled by behavioral responses to exogenous stimuli (Sulkin, 1973, 1975; Forward and Costlow, 1974; Ott and Forward, 1976; Latz and Forward, 1977).

Any *C. sapidus* adaptation for retention or exchange would be likely to be manifest in behavioral patterns that regulate vertical distribution through ontogeny. We have examined the behavioral responses of *C. sapidus* at various larval stages to stimuli likely to influence vertical movement. We report here the results of experi-

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ments on orientation and swimming rate in response to gravity, hydrostatic pressure, temperature, and salinity. The results are evaluated in terms of their effects on vertical distribution of *C. sapidus* larvae throughout their ontogeny and consequent patterns of dispersal of this species in the estuarine and coastal marine environments.

Materials and Methods

Larval culture

Ovigerous blue crabs were obtained from lower Delaware Bay and were taken to the laboratory with egg masses intact. Eggs were stripped from the females when they reached the black eyespot stage, or immediately if they were collected at that stage. Approximately 500 eggs from a single female were then placed in each of several 125 ml Erlenmeyer flasks containing 50 ml of filtered seawater at 30‰ salinity (S) and 20°–30°C. Culture water contained either penicillin (60 mg/l) and streptomycin (50 mg/l) or chloramphenicol at 5 mg/l. Unpublished data show that use of antibiotics improves egg and larval survival without altering larval behavior. Eggs were transferred to fresh medium every second day.

Upon hatching, larvae from a given female were placed in several glass culture dishes containing 100 ml of 30‰ S seawater. The standard culture temperature was 25°C, although experiments occasionally dictated acclimation of larvae to 15°C. Each dish initially contained approximately 200 zoeae.

Zoeae were transferred to fresh medium daily and fed either the rotifer *Brachionus plicatilis* Muller (during the first 14 days of development) or freshly-hatched nauplii of the brine shrimp *Artemia salina* L. (after day 15; Sulkin, 1978). Records of mortality and molting were kept.

Samples of larvae were removed for testing as experiments dictated. In order to avoid complicating effects of rhythmicity in locomotory activity (Sulkin *et al.*, 1979), all behavior experiments were run during afternoon hours. Experiments were conducted on zoeal stages I, IV, and VII.

Sinking rates

Larvae of various stages were narcotized using 3% ethyl carbamate. Individuals were timed as they sank vertically through a 10-cm-long space marked off midway along a vertical cylinder filled with seawater (30‰ S; 25°C). At least 50 individuals from three different broods were tested. Data are presented as mean sinking rates (cm/sec.). Differences among stages were tested by analysis of variance.

Geotaxis

Typically the presence and sign of geotaxis in crab larvae has been determined by noting changes over time in net distribution of organisms placed in a vertically oriented test chamber in total darkness (Sulkin, 1973; Ott and Forward, 1976; Latz and Forward, 1977). Oriented movement upward has been termed negative geotaxis; downward, positive geotaxis.

To account more effectively for non-oriented or random movement that occurs simultaneously with oriented movement or geotaxis, the following experimental design was used. Thirty to fifty larvae were drawn at random from the cultures and divided between two test chambers, one positioned vertically; the other hori-

zontally. Each chamber was constructed of 3-mm-thick transparent lucite, measured 25 × 5 × 5 cm, and was marked off into four sections of equal length. Larvae were placed at the bottom of the vertical experimental chamber and at one end of the horizontal control chamber. At 10-min intervals, the larvae in each quadrant were counted. A dim deep-red light was used to silhouette the larvae when counts were made. This procedure did not appear to disrupt the positions of larvae. Change in distribution over time in both horizontal and vertical chambers was analyzed by construction of a "kite" diagram, which shows the proportion of total sample in each quadrant.

Movement of larvae away from the end of the horizontal chamber was considered random or non-oriented and thus served as a control against which to compare the distributional change which occurred in the vertical chamber. Admittedly, the control was imperfect in that it did not account for sinking, which occurred intermittently in the vertical chamber. Nevertheless, movement along the axis from the initial point source in the vertical chamber exceeding that for the horizontal chamber can be attributed to oriented response—in this case, negative geotaxis. On the other hand, movement in the horizontal control exceeding that in the vertical tank can be attributed to positive geotaxis. If there is no difference between the two, the presumption is that no oriented response can be attributed to geotaxis.

Distributions after 30 min were analyzed. This period proved long enough to separate oriented from random movement while providing for stable distribution in the vertical chamber and random dispersal in the horizontal chamber.

Larvae used in these experiments were acclimated to darkness for at least 2 hr prior to testing and not fed during the experiment. For each larval stage, experiments were conducted at 25, 30, and 35‰ S in the following fashion. A group of larvae was first tested at 30‰ S. Then they were placed in test chambers which contained either 25‰ S seawater or 35‰ S seawater, and distribution shift experiment was repeated. A minimum of three replicates with offspring from three different crabs was conducted for each salinity.

The experimental design permitted statistical analysis as well as the qualitative analysis typically used in behavioral experiments. For each experimental and control replicate, an average distribution at 30 min ("mean position value") was calculated by assigning weights from 0–3 to the quadrants (the end to which the larvae were initially added = 0), multiplying the weights by the number of larvae in the quadrants, and dividing the product by the total number of larvae. The mean position value is a quantitative descriptor of the distribution and provides a commonly derived set of data for all experimental and control replicates. For each salinity, the mean position values for all experimental replicates were compared against those for all control replicates using the non-parametric Mann-Whitney U test.

Swimming rate

Figure 1 shows the apparatus used to measure larval swimming rates. A sample of larvae from a particular brood at a specified stage of development was placed in the behavior chamber. Larvae were attracted to one end of the chamber by means of a broad-spectrum light (75 W/m^2). The larvae were then induced to swim along the axis of the tank by reversing the direction of the light. Approximately 20 individuals were timed during each experiment as they swam through a 5-cm-long section of the chamber.

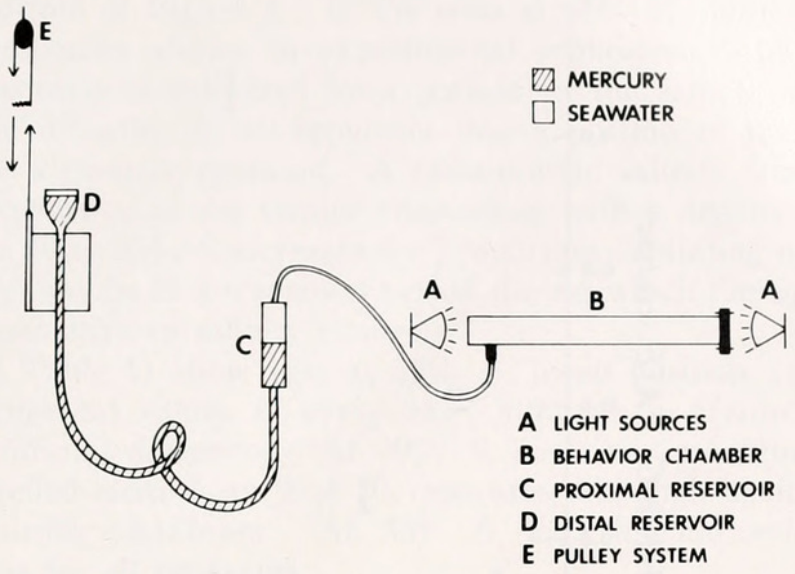

FIGURE 1. Diagrammatic representation of apparatus used to measure swimming rate as a function of hydrostatic pressure.

The effect of pressure on swimming rate was measured by repeating the procedure described above at various pressure increments. Pressure was increased by raising the distal end of the mercury manometer shown in Figure 1 (Sulkin, 1973). In nature, pressure increases with depth at a rate of 1 atm per 10 m of water. In one set of experiments the pressure increments used were 0, 20, 40, and 60 cm Hg (0, 0.26, 0.52, 0.78 atm, respectively). In a second set of experiments, the increments were 0, 1, 2, and 3 atm. The pressures were tested sequentially. Experiments were repeated with larvae from several broods, with total sample sizes ranging from 70 to 140 individuals.

The effects of temperature and salinity on swimming rate were measured by repeating the procedure described above. Larvae were acclimated to the specified temperature or salinity for 24 hr before testing.

RESULTS

Sinking rates

Mean passive sinking rates are shown for zoeal stages I, IV, and VII in Figure 2. Analysis of variance confirms a significant increase in sinking rate from the hatching stage to zoeal stage VII ($P < 0.001$).

Geotaxis

Figure 3 shows the distributions at 30 min for all replicates conducted on stage I larvae at the three salinities. The mean distribution for each salinity is shown at the bottom of Figure 3. It is apparent that negative geotaxis is strong and pervasive in stage I larvae. It also appears that a 5‰ salinity change between 25 and 35‰ S has little, if any, effect upon the presence or sign of geotaxis in zoeal stage I.

Statistical analysis supports these conclusions. The results in Table I indicate that the experimental mean position values were higher than the control in every case and that the differences were significant in all three salinities.

Figure 4 shows the distributions at 30 min for all replicates conducted on stage IV larvae at three salinities. The mean distribution for each salinity is

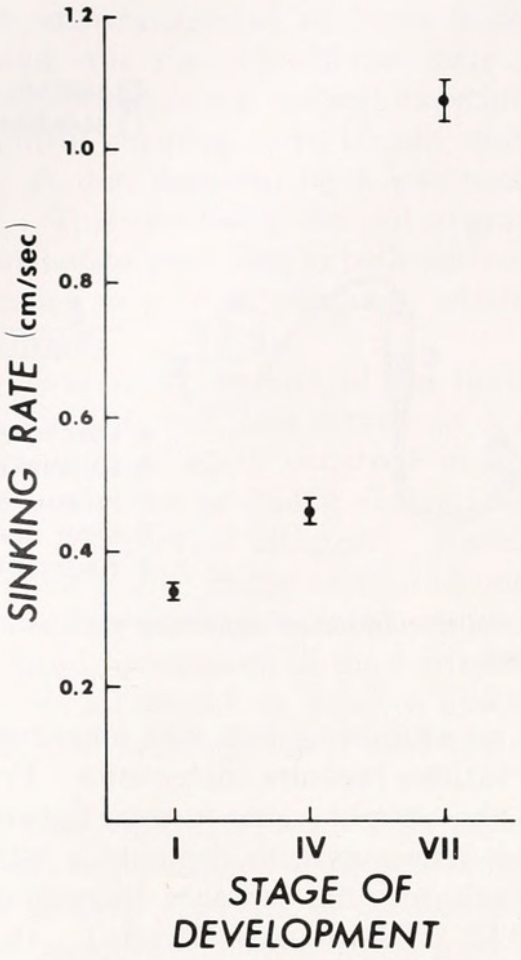

FIGURE 2. Mean passive sinking rates for zoeal stages I, IV, and VII of *Callinectes sapidus*. Vertical bars represent ± 1 standard error.

TABLE I

Analysis of relative distributions between vertical experimental and horizontal control tests for stage I larvae at three salinities. Calculation of mean position value described in text.

Salinity (‰)	Mean position value		Mann-Whitney *U* test probability
	Experimental	Control	
25	2.50	1.17	
	2.50	0	<0.05
	2.95	0.33	
30	2.85	1.31	
	2.11	0.45	
	3.00	0.45	
	2.32	1.28	
	2.40	0.76	<0.001
	2.76	0.76	
	1.61	1.05	
	2.10	0.55	
	2.80	0.80	
35	2.35	0.85	
	2.45	0.85	<0.05
	3.00	0.68	

shown at the bottom of Figure 4. In the tests at 30‰ S, there was considerable variability in responses shown in experimental replicates. Although it appears that negative geotaxis is exhibited by a portion of the sample in each replicate, there is also an indication in all replicates that a portion of the sample may be responding with a positive geotaxis. A reduction in salinity from 30 to 25‰ S decreases the proportion of the sample responding with a negative geotaxis, while an increase from 30 to 35‰ S increases the proportion exhibiting negative geotaxis. The fourth stage may be in a transition period during which the sign of geotaxis is variable and is sensitive to salinity change.

The data in Table II show that at 25‰ S, mean position values of controls exceeded experimental values in every case, although a Mann-Whitney *U* test indicates no significant difference. At 30‰ S, however, experimental mean position values exceeded controls in 9 of 10 replicates, although again the differences were not statistically significant. At 35‰ S, experimental values significantly exceeded controls for all replicates.

Figure 5 shows the distribution at 30 min for all replicates conducted on stage VII larvae at the three salinities. The mean distribution at each salinity is shown at the bottom of Figure 5. Dispersal from a point source (bottom quadrant) in the vertical chamber is clearly lower than that attributable to random movement alone. We interpret these results as indicating positive geotaxis in the vast majority of individuals. A 5‰ S increase or decrease from 30‰ S appears to have little effect.

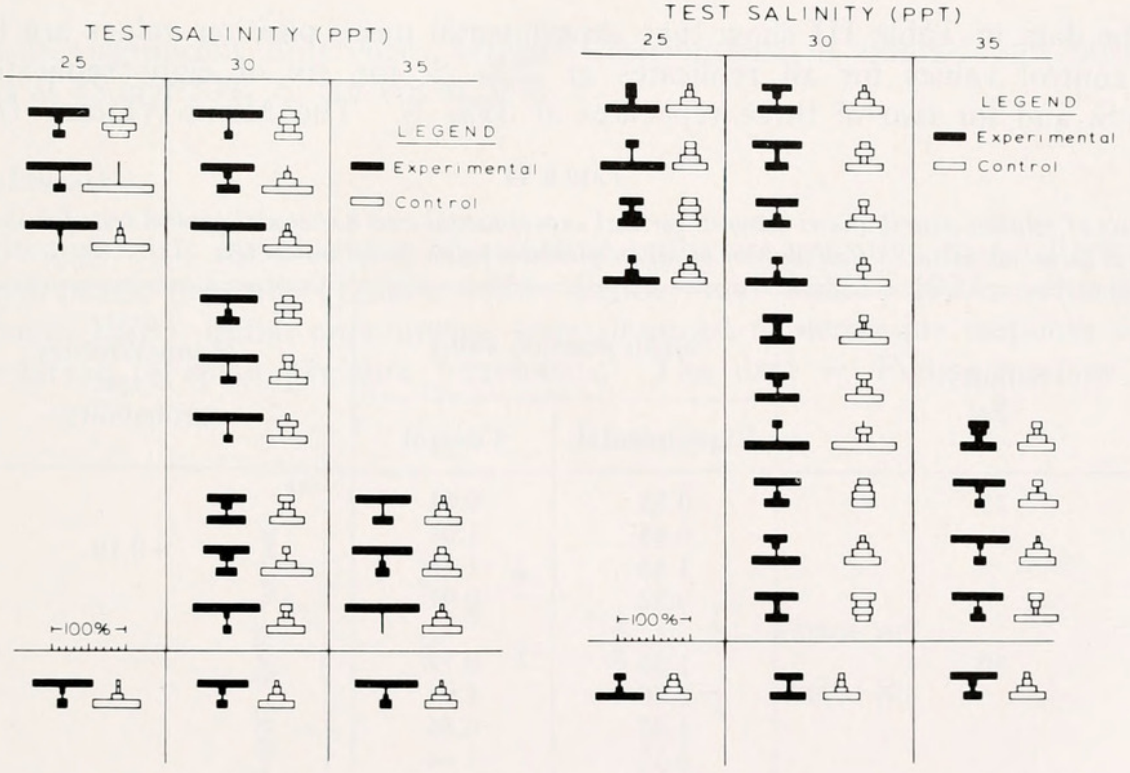

FIGURE 3. (Left.) Geotaxis in *Callinectes sapidus* zoeal stage I. Proportional distributions of larvae among the four sections of experimental and control tanks 30 min after initiation of experiments for all replicates tested at each salinity. The diagrams below the bottom horizontal line represent the mean distributions of all replicates at each salinity. Experimental design described in text.

FIGURE 4. (Right.) Geotaxis in *Callinectes sapidus* zoeal stage IV. Proportional distribution of larvae among the four sections of experimental and control tanks 30 min after initiation of experiments for all replicates tested at each salinity. The diagrams below the bottom horizontal line represent the mean distributions of all replicates at each salinity. Experimental design described in text.

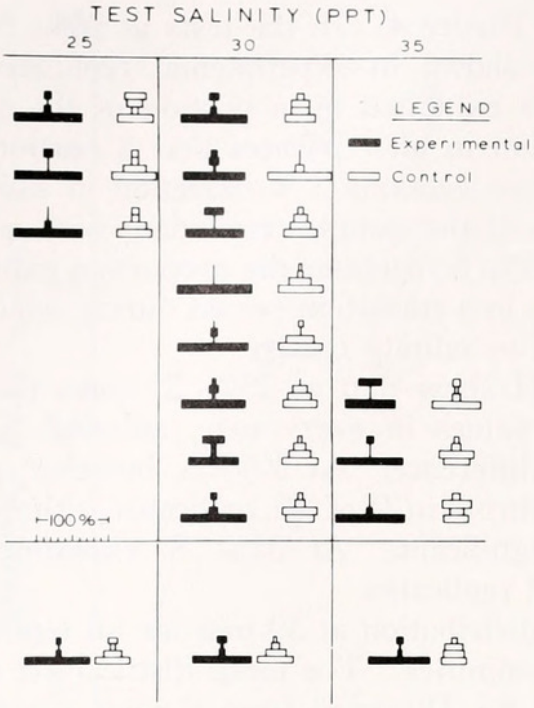

FIGURE 5. Geotaxis in *Callinectes sapidus* zoeal stage VII. Proportional distribution of larvae among the four sections of experimental and control tanks 30 min after initiation of experiments for all replicates tested at each salinity. The diagrams below the bottom horizontal line represent the mean distributions of all replicates at each salinity. Experimental design described in text.

The data in Table III show that experimental mean position values are lower than control values for all replicates at 25‰ S, for six of eight replicates at 30‰ S, and for two of three replicates at 35‰ S. The Mann-Whitney *U* test

TABLE II

Analysis of relative distributions between vertical experimental and horizontal control tests for stage IV larvae at three salinities. Calculation of mean position value described in text.

Salinity (‰)	Mean position value		Mann-Whitney *U* test probability
	Experimental	Control	
25	0.55	0.61	
	0.48	1.04	
	1.33	1.36	=0.10
	0.32	0.91	
30	1.30	0.72	
	2.00	1.03	
	1.82	0.84	
	0.37	1.64	
	1.44	0.64	
	0.92	0.90	>0.10
	0.40	0.25	
	1.87	1.26	
	1.04	0.84	
	1.95	1.70	
35	1.26	0.90	
	2.65	0.78	
	2.48	0.72	=0.05
	2.20	0.95	

TABLE III

Analysis of relative distributions between vertical experimental and horizontal control tests for stage VII larvae at three salinities. Calculation of mean position value described in text.

Salinity (‰)	Mean position value		Mann-Whitney *U* test probability
	Experimental	Control	
25	0.19	1.25	
	0.25	0.55	<0.05
	0.06	2.38	
30	0.33	1.05	
	0.42	0.10	
	0.67	0.94	
	0	0.56	
	0.08	0.48	<0.05
	0.39	0.75	
	0.94	0.80	
	0.25	0.86	
35	1.00	0.72	
	0.30	0.86	>0.05
	0.05	1.24	

indicates significant differences between distributions in vertical and horizontal tanks at 25 and 30‰ S, but not at 35‰ S.

Barokinesis

Because early larval stages of estuarine crabs are sensitive to small increases in hydrostatic pressure (Sulkin, 1973; Bentley and Sulkin, 1977; Wheeler and Epifanio, 1978), initial experiments were designed to determine response of blue crab larvae to small pressure increments. The data in Figure 6 show mean

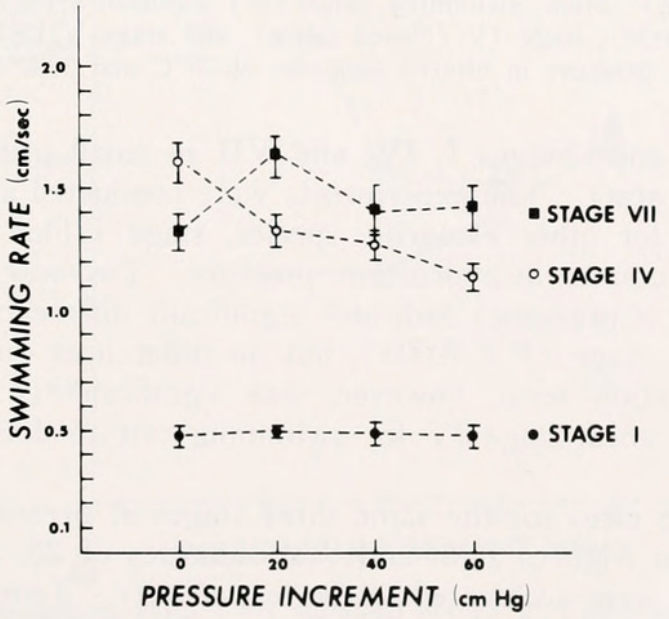

FIGURE 6. Mean swimming rates (± 1 standard error) of *Callinectes sapidus* zoeal stages I, IV, and VII in pressure increments up to 60 cm Hg (0.78 atm), in seawater of 25°C and 30‰ S.

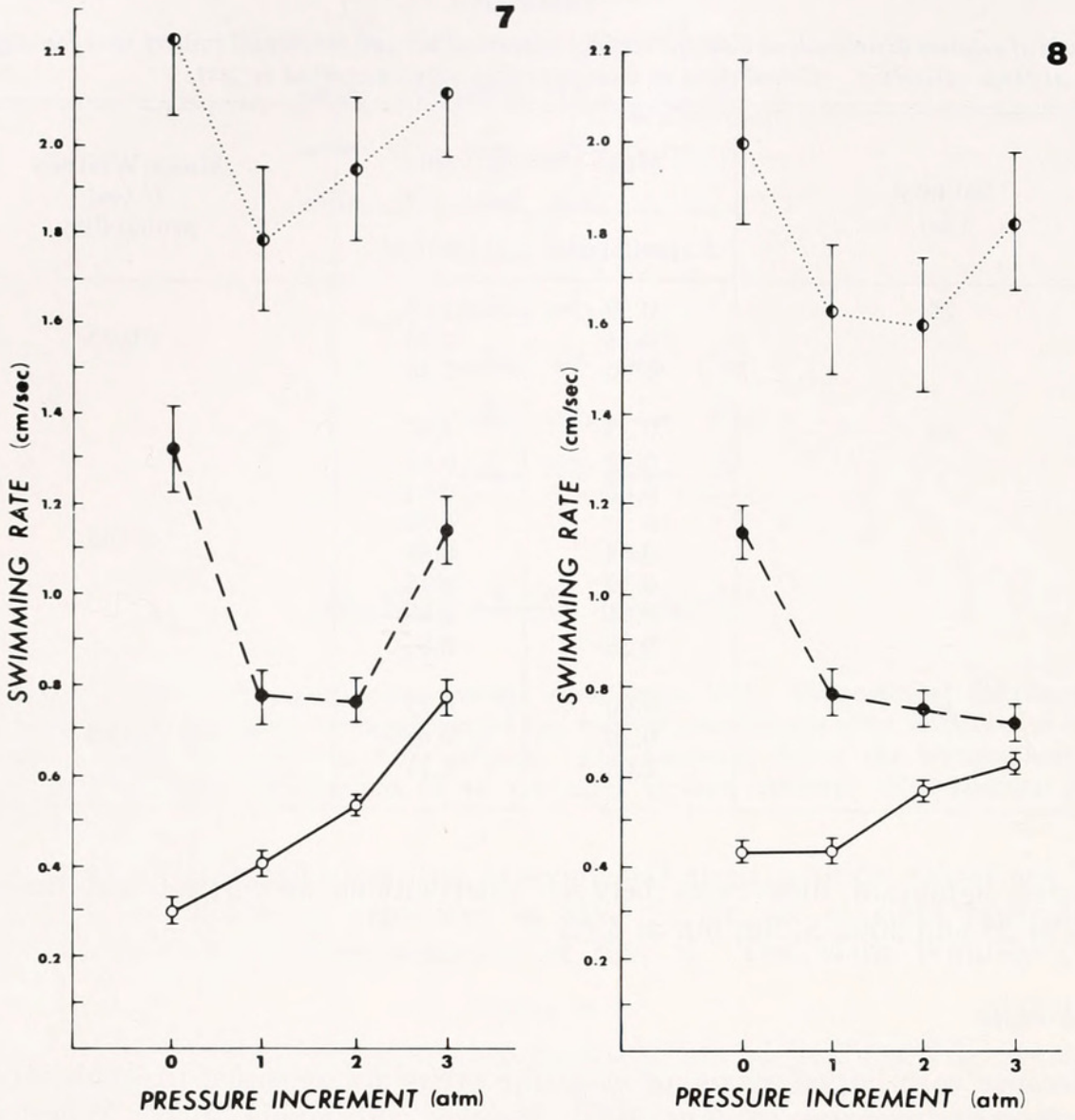

FIGURE 7. (Left.) Mean swimming rates (± 1 standard error) of *Callinectes sapidus* zoeal stage I (open circle), stage IV (closed circle), and stage VII (half-closed circle) as a function of hydrostatic pressure in filtered seawater at 25°C and 25‰ S.

FIGURE 8. (Right.) Mean swimming rates (± 1 standard error) of *Callinectes sapidus* zoeal stage I (open circle), stage IV (closed circle), and stage VII (half-closed circle) as a function of hydrostatic pressure in filtered seawater at 25°C and 30‰ S.

swimming rates of zoeal stages I, IV, and VII in small pressure increments up to 60 cm Hg (0.78 atm). The experiments were conducted at 25°C, 30‰ S. In contrast to results for other estuarine species, stage I blue crab larvae do not respond to small increases in hydrostatic pressure. Two-way analysis of variance (development stage × pressure) indicates significant difference in swimming rate due to development stage ($P < 0.005$), but no differences due to pressure ($P > 0.05$). The interaction term, however, was significant ($P < 0.005$), probably due to the trend in zoeal stage IV for swimming rate to decrease with increased pressure.

Mean swimming rates for the same three stages at pressure increments up to 3 atm are shown in Figures 7, 8, and 9 at salinities of 25, 30, and 35‰ S, respectively. Larvae were acclimated to the test salinity. Temperature was kept at 25°C. Three-way analysis of variance showed significant differences due to development stage ($P < 0.001$), pressure increment ($P < 0.005$), and salinity ($P <$

0.001). The only significant two-way interaction was stage × pressure ($P < 0.025$). Higher salinities have little effect on stage I larvae, but depress swimming rate in zoeal stages IV and VII. As the significant interaction term suggests, the effect of increased pressure is stage dependent. There is an increase in swimming rate as pressure increment exceeds one atm in zoeal stage I (high barokinesis) and a reduction in swimming rate with pressure increase in zoeal stages IV and VII (low barokinesis).

To determine the effect of reduced temperature on barokinesis, swimming rates were measured at 15°C at ambient pressure and at 3 atm pressure increment (Fig. 10). A two-way analysis of variance was conducted for each stage, testing temperature against pressure. Appropriate data collected at 0 and 3 atm increments at 25°C, 30‰ S, were used in the analyses. For zoeal stage I, no significant dif-

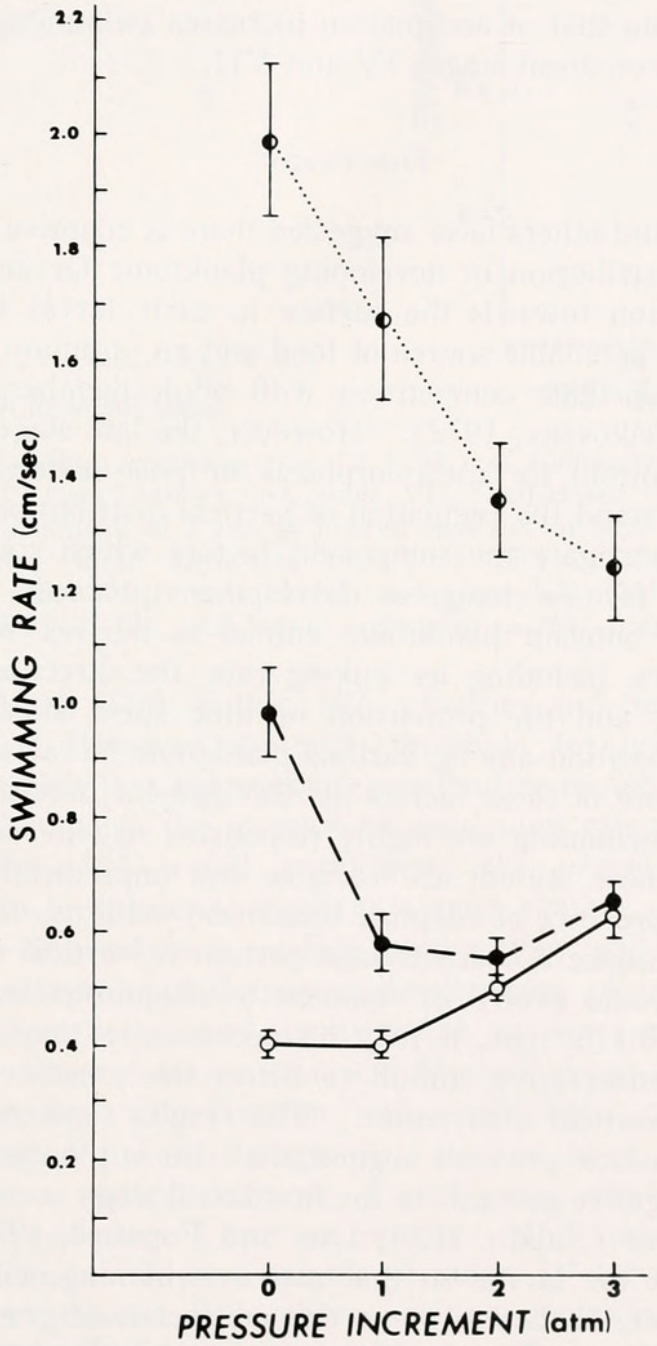

FIGURE 9. Mean swimming rates (± 1 standard error) of *Callinectes sapidus* zoeal stage I (open circle), stage IV (closed circle), and stage VII (half-closed circle) as a function of hydrostatic pressure in filtered seawater at 25°C and 35‰ S.

ferences were attributable to temperature ($P > 0.05$). Reduced temperature significantly reduces swimming rate only in zoeal stages IV ($P < 0.001$) and VII ($P < 0.001$), with significant interaction with pressure only in zoeal stage IV ($P < 0.01$). However, the reduction in temperature appears to moderate both high and low barokinesis to some degree in all developmental stages.

Data reported in Figures 8 and 9 indicated that acclimation to higher salinity reduces swimming rate in zoeal stages IV and VII. Shown in Figure 11 are the results of an experiment designed to determine the effect of a 10‰ S increase on larvae acclimated to the lower salinity. A two-way analysis of variance indicated significant interaction between development stage and salinity ($P < 0.005$) with stages significant ($P < 0.001$) and salinity not significant ($P > 0.05$). Because of the significant interaction, a series of one-way analysis of variance tests were conducted for each stage. The results indicated a significant difference in zoeal stage I ($P < 0.05$), but no significant differences in either zoeal stage IV or VII. Thus a 10‰ S increase from that of acclimation increases swimming rate in zoeal stage I, but has little effect on zoeal stages IV and VII.

Discussion

Thorson (1950) and others have suggested there is adaptive value in a changing pattern of vertical distribution in developing planktonic larvae of benthic species. For example, migration towards the surface in early larval stages may enhance dispersal, provide for a reliable source of food and an optimum of temperature and light, and reduce immediate competition with adult members of the population (Thorson, 1950; Mileikovsky, 1972). However, the late stages of benthic species must move to the bottom for metamorphosis or post-metamorphic development.

In order to understand the regulation of vertical distribution through ontogeny, it is necessary to investigate the component factors which control vertical movement and how these factors change as development proceeds. The vertical position of a negatively buoyant planktonic animal is the net result of a complex combination of factors, including its sinking rate, the direction of active orientation, swimming rate, and the proportion of time spent sinking and swimming. Changes in vertical position among various planktonic larval stages can be due to changes in one or more of these factors as development proceeds.

Orientation and swimming are highly responsive to external stimuli. Because in nature many of these stimuli are variable and unpredictable, it is difficult to generalize about the presence of adaptive behavioral patterns. However, behavioral adaptations which produce a characteristic pattern of vertical distribution through ontogeny probably would evolve in response to ubiquitous and predictable selective pressures. If this is true, it may be necessary to look only at behavioral responses to such conservative stimuli to detect the presence of a characteristic adaptive pattern of vertical distribution. The results reported here for response to gravity and hydrostatic pressure suggest that this is the case for *C. sapidus*.

The finding of negative geotaxis in the first larval stage is consistent with earlier reports for crab larvae (Sulkin, 1973; Latz and Forward, 1977). Negative geotaxis tends to orient the larvae so that active swimming will result in upward movement. Moreover, as larvae move deeper, increased pressure will result in increased swimming rate. The combination of negative geotaxis and high barokinesis thus produces a depth regulatory mechanism (Sulkin, 1973). Sensitivity to pressure change is common in early larval instars of crabs (Hardy and Bain-

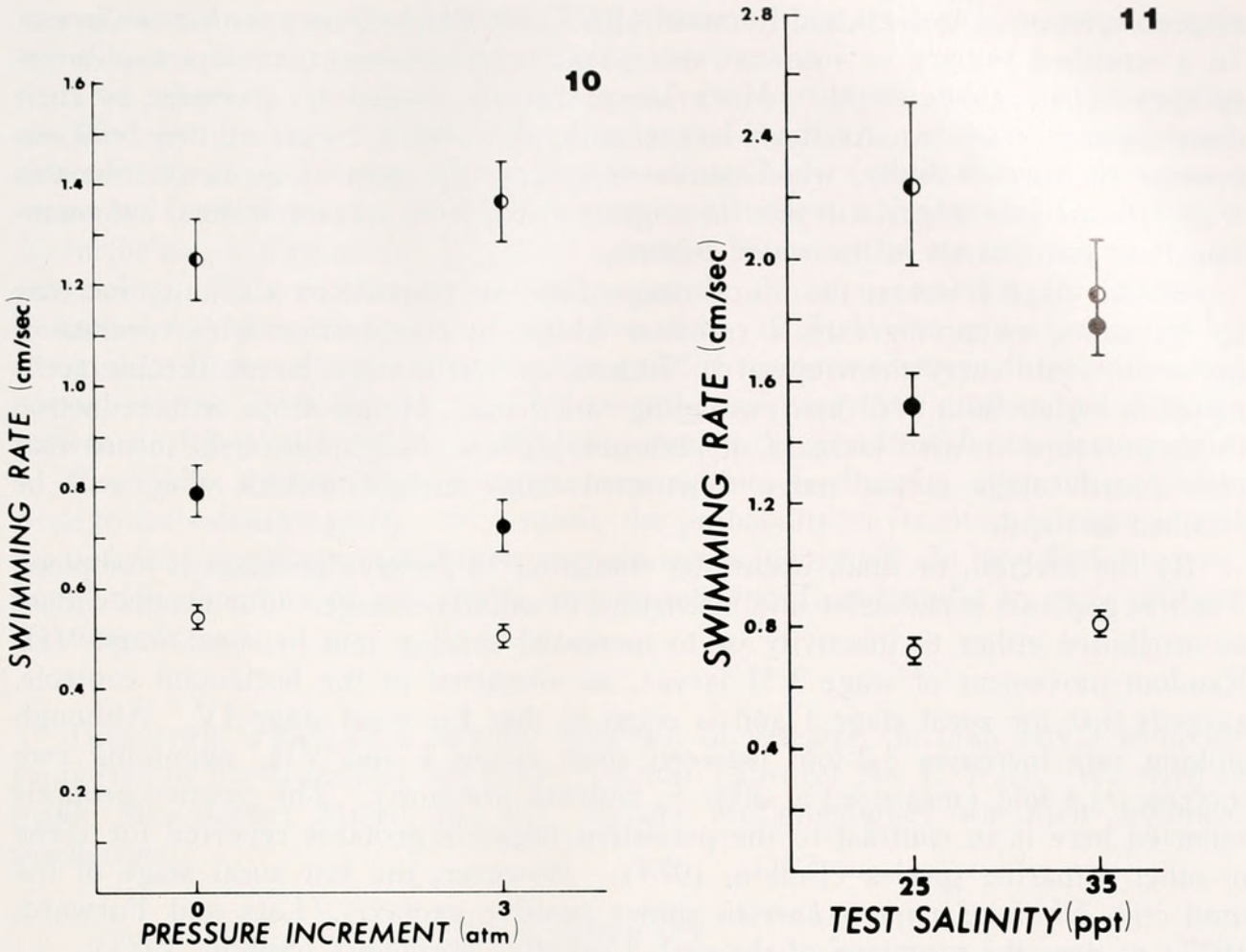

FIGURE 10. (Left) Mean swimming rate (± 1 SE) of *Callinectes sapidus* zoeal stage I (open circle), stage IV (closed circle), and stage VII (half-closed circle) at ambient pressure and at a pressure increment of 3 atm in filtered seawater at 30‰ S and 15°C.

FIGURE 11. (Right) Mean swimming rate (± 1 SE) of *Callinectes sapidus* zoeal stage I (open circle), stage IV (closed circle), and stage VII (half-closed circle) in test salinities of 25‰ and 35‰ (25°C). All larvae acclimated to 25‰ S and 25°C.

bridge, 1951; Rice, 1964, 1966; Sulkin, 1973; Bentley and Sulkin, 1977; Wheeler and Epifanio, 1978). However, the high threshold for pressure sensitivity in *C. sapidus* zoeae suggests that the pressure mechanism is not activated in shallow systems. On the other hand, the increase in swimming rate which occurs with a salinity increase (Fig. 11) would complement the pressure mechanism in a stratified, deep system or substitute for it in a more shallow one.

If stage I larvae descend from surface waters, they will encounter increased pressure, increased salinity, and decreased temperature. Zoeal stage I responds to gravity, pressure, salinity, and temperature in ways which will produce upward movement. Stage I larvae thus exhibit behavioral adaptations likely to promote maintenance of vertical position high in the water column.

By the fourth larval instar, changes in behavior have occurred which are likely to produce deeper vertical position. Fourth stage zoeae have a sinking rate greater than that of zoeal stage I and are in a period of transition between negative and positive geotaxis. In any sample of stage IV larvae, some individuals will exhibit negative geotaxis and others positive geotaxis. Furthermore, the sign of geotaxis in individual larvae is sensitive to salinity change. A 5‰ reduction in salinity induces increased incidence of positive geotaxis, whereas a 5‰ S increase induces increased incidence of negative response. This is similar to

responses reported by Latz and Forward (1977) for *Rhithropanopeus harrisii* larvae. In a stratified estuary or the near-shore marine environment, these complex responses help regulate depth. More larvae become positively geotactic as their development proceeds. As these larvae swim downward, however, they will encounter increased salinity, which tends to reverse the sign of geotaxis. In this way, intermediate stages will tend to migrate down from surface waters, but maintain their position up in the water column.

Unlike stage I larvae, the fourth stage does not respond to a salinity increase by increasing swimming rate, a response which, in combination with reversal of geotaxis, would carry them upward. Indeed, as fourth stage larvae become acclimated to higher salinities, their swimming rate drops. It also drops with reduction in temperature or with increase in pressure. These adaptations help insure that once fourth stage larvae move downward from surface waters, they will be retained at depth.

By the seventh, or final, instar the transition to positive geotaxis is complete. Positive geotaxis is pervasive and insensitive to salinity change. Our results cannot be attributed either to inactivity or to increased sinking rate in zoeal stage VII. Random movement of stage VII larvae, as measured in the horizontal controls, exceeds that for zoeal stage I and is equal to that for zoeal stage IV. Although sinking rate increases 3.2-fold between zoeal stages I and VII, swimming rate increases 4.4-fold (measured at 30‰ S, ambient pressure). The positive geotaxis reported here is in contrast to the persistent negative geotaxis reported for zoeae of other estuarine species (Sulkin, 1973). However, the last zoeal stage of the mud crab *Rhithropanopeus harrisii* shows positive geotaxis (Latz and Forward, 1977) as does the megalopa of the crab *Leptodius floridanus* (Sulkin, 1973).

The same factors which reduce swimming rate in stage IV larvae as they move deeper are operative in zoeal stage VII. Swimming rate does not change with an increase in salinity, but does decrease as larvae become acclimated to higher salinity, or are subjected to increased pressure or reduced temperature. These responses are likely to produce a deep vertical position in zoeal stage VII.

Thus behavioral response to pressure and gravity, as modified by temperature and salinity, provide the basis for differential vertical distribution during larval development of *C. sapidus*. Early stage larvae that enter surface waters, either by hatching in shallow areas or by migrating upward, are likely to stay near the surface. Changes in behavioral response will stimulate larvae in later zoeal stages to move deeper. Behavioral evidence that suggests a prevalence of early stages in surface waters and late stages in deep water is consistent with field evidence (Sandifer, 1975; Goy, 1976).

This adaptive pattern of vertical distribution has predictable conseqences to larval dispersal in an estuarine and near-shore marine environment. The proximity of spawning grounds to the estuary mouth and the complementary behavioral adaptations which insure the presence of early stages in seaward-flowing surface waters will result in tremendous losses of larvae from the estuarine habitat. However, a mechanism for recruitment back to the estuary exists. Deep waters of the continental shelf along the Atlantic coast of North America drift landward (Bumpus, 1965; Harrison *et al.*, 1967; Beardsley *et al.*, 1976), with particularly noticeable landward components at the mouths of major estuaries (Harrison *et al.*, 1967). Scheltema (1975) suggests that larvae positioned in this deep, landward-flowing drift would be carried shoreward and perhaps into an estuary. Offshore

recruitment thus may be particularly significant in highly stratified estuaries with significant upstream non-tidal drift along the bottom.

The adaptive vertical distribution pattern reported here will, of course, be modified by the vagaries of the environment. Furthermore, the megalopa stage undoubtedly is also important in recruitment and may exhibit different behavioral responses from those reported here for late zoeal stages (Naylor and Isaac, 1973). Nevertheless, a mechanism for larval exhange between the estuary and the open sea exists. This mechanism is fundamentally the same as that for retention, described for other estuarine species (Bousfield, 1955; Wood and Hargis, 1971), and results from a combination of hydrographic features common in estuarine and coastal marine environments and behavioral responses that produce an adaptive pattern of differential vertical distribution during the period of larval development.

C. sapidus differs from other estuarine species in that its offspring originate close to the estuary mouth. As a result, the probability of retention is reduced and the potential significance of offshore recruitment is increased. In stratified estuaries, population dynamics of *C. sapidus* may be influenced profoundly by such offshore recruitment.

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Summary

1. The first zoeal stage of *Callinectes sapidus* shows negative geotaxis unaffected by salinity changes of 5‰; 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*.

LITERATURE CITED

Beardsley, R. C., W. C. Boicourt, and D. V. Hansen, 1976. Physical oceanography of the Mid-Atlantic Bight. American Society of Limnology and Oceanography; *Special Symposium*, 2: 20–34.

BENTLEY, E., AND S. D. SULKIN, 1977. The ontogeny of barokinesis during the zoeal development of the xanthid crab *Rhithropanopeus harrisii* (Gould). *Mar. Behav. Physiol.*, **4**: 275–282.

BOUSFIELD, E. L., 1955. Ecological control of the occurrence of barnacles in the Miramichi Estuary. *Nat. Mus. Can. Bull.*, **137**: 1–69.

BUMPUS, D. F., 1965. Residual drift along the bottom on the continental shelf in the middle Atlantic Bight area. *Limnol. Oceanogr.*, **10** (Supplement): R50–53.

CARRIKER, M. R., 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. Monogr.*, 21: 19–38.

DUDLEY, D. L., AND M. H. JUDY, 1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. *NOAA Tech. Report*, NMFS, *Special Scientific Report, Fisheries*, **637**: 1–10.

FORWARD, R. B., JR., AND J. D. COSTLOW, JR., 1974. The ontogeny of phototaxis by larvae of the crab *Rhithropanopeus harrisii*. *Mar. Biol.*, **25**: 27–33.

GOY, J. W., 1976. *Seasonal distribution and retention of some decapod crustacean larvae within the Chesapeake Bay, Virginia.* Masters thesis, Old Dominion University. 334 pp.

HARDY, A. C., AND R. BAINBRIDGE, 1951. Effects of pressure on the behavior of decapod larvae. *Nature*, **167**: 354–355.

HARRISON, W., J. J. NORCROSS, N. A. PORE, AND E. M. STANLEY, 1967. Circulation of shelf waters off Chesapeake Bight—surface and bottom drift of continental shelf waters between Cape Henlopen, Delaware and Cape Hatteras, North Carolina. June 1963–December 1964. *United States ESSA Professional Papers*, **3**: 1–82.

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.

LATZ, M. I., AND R. B. FORWARD, JR., 1977. The effect of salinity upon phototaxis and geotaxis in a larval crustacean. *Biol. Bull.*, **153**: 163–179.

MILEIKOVSKY, S. A., 1972. The "pelagic larvaton" and its role in the biology of the World Ocean, with special reference to pelagic larvae of marine bottom invertebrates. *Mar. Biol.*, **16**: 13–21.

NAYLOR, E., AND M. J. ISAAC, 1973. Behavioral significance of pressure responses in megalopa larvae of *Callinectes sapidus* and *Macropipus* sp. *Mar. Behav. Physiol.*, **1**: 341–350.

NICHOLS, P., AND P. M. KENEY, 1963. Crab larvae (*Callinectes*) in plankton collections from cruises of M/V Theodore N. Gill. South Atlantic coast of the United States, 1953–1954. U. S. Fish and Wild. Serv. *Spec. Sci. Rep. Fish.*, **448**: 1–14.

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.

PRITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Mar. Res.*, **11**: 106–123.

RICE, A. L., 1964. Observations on the effects of changes in hydrostatic pressure on the behavior of some marine animals. *J. Mar. Biol. Assn. U. K.*, **44**: 163–175.

RICE, A. L., 1966. The orientation of pressure responses of some marine crustacea. Proceedings of Symposium on Crustacea, Part III, *Mar. Biol. Assn., India*, **1966**: 1124–1131.

SANDIFER, P. A., 1973. Distribution and abundance of decapod crustacean larvae in the York River Estuary and adjacent lower Chesapeake Bay, Virginia, 1968–1969. *Chesapeake Sci.*, **14**: 235–257.

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

SCHELTEMA, R. S., 1975. Relationship of larval dispersal, gene-flow, and natural selection to geographic variations of benthic invertebrates in estuaries and along coastal regions. *Estuarine Research*, 1: 372–391.

SULKIN, S. D., 1973. Depth regulation of crab larvae in the absence of light. *J. Exp. Mar. Biol. Ecol.*, **13**: 73–82.

SULKIN, S. D., 1975. The influence of light in the depth regulation of crab larvae. *Biol. Bull.*, **148**: 333–343.

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., 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.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev. of Camb. Philos. Soc.*, **25**: 1–45.

Van Engel, W. A., 1958. The blue crab and its fishery in Chesapeake Bay. I. Reproduction, early development, growth, and migration. *Comm. Fish. Rev.*, 20: 6–17.

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

Wood, L., and W. J. Hargis, 1971. Transport of bivalve larvae in a tidal estuary. Pp. 29–44 in D. J. Crisp, Ed., *Fourth European Marine Biology Symposium*, Cambridge Univ. Press, Cambridge, England.