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Arctica islandica (Linne) Larvae: Active depth regulators or passive particles?

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ARCTICA ISLANDICA (LINNÉ) LARVAE: ACTIVE DEPTH REGULATORS OR PASSIVE PARTICLES[1]

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ABSTRACT

The seasonal change in depth distribution of *Arctica islandica* (Linné) larvae at a station on the Southern New England Shelf for the period April-December 1981 is compared with the output of a numerical model designed to predict distribution in a scenario where active depth regulation predominates. Larvae in excess of 200 μm length were present in the field in May at 1-30 m depth and, at depths of 20-40 m from late July through November. The majority of larvae captured in November were shelled veligers of 110 μm length. Good agreement of the model with field data exists with respect to absence of *A. islandica* larvae in the warm (> 18°C) shallow (0-20 m) waters between July and early September, and the abundance of larvae throughout the depth range 20-40 m from July through October. The model predicts occurrence of larvae in June; however, they were not seen in the field. The discrepancy can be due to the combination of reduced spawning by adult *A. islandica* (which is not included in the model) and less than optimum conditions for larval development. The model predicts aggregation of the negatively geotactic larvae at the surface following decay of a seasonal thermocline. Such aggregations were not seen in the field indicating that vertical mixing of the water column in the fall months is sufficient to negate distribution patterns dominated by active depth regulation. Depending upon the nature, intensity and stability of stratification of the water column, it is evident that depth distribution of *A. islandica* larvae can be dominated by either active depth regulation or passive movement at the mercy of physical mixing. The conditions of transition from active to passively dominated dispersal and distribution are poorly defined.

The literature relating to swimming behavior and dispersal of bivalve larvae has been reviewed by Mann (1986). Opinions differ as to whether dispersal is predominantly a process of passive movement at the mercy of water currents or a combination of active depth regulation coordinated with horizontal stratification and flow. Resolution of the debate as to the relative roles of active versus passive processes is confounded by the nature of the data sets available. An historical emphasis on species of commercial importance dictated the focus of major efforts on field studies in shallow estuarine systems. Field studies in isolation are essentially observational and the type of the data collected allows only the inference of cause and effect from correlation. Definitive resolution of cause and effect can only be effected by controlled experiments. Furthermore, the physics of estuarine circulation are so complex and dynamic that they too remain only poorly understood. It is apparent then that ecologists have chosen to examine the problem of bivalve larval dispersal in

perhaps the most intractable of environments and with only a limited arsenal of approaches.

Recent work examining larval behavior in controlled laboratory systems has, when combined with modelling, provided a new and powerful tool with which to address the problem of larval dispersal. This approach has been used in studies of blue crab *Callinectes sapidus* (Rathbun) by Sulkin and Van Heuklem (1982) and red crab *Geryon quinquedens* Smith by Kelly *et al.*, (1982), but has not previously been adequately exploited for bivalve molluscs. In this study I compared the results of field observations of depth distribution of the larvae of *Arctica islandica* (Linné) with a numerical model, constructed solely from laboratory generated behavioral data and field collected physical data. The model was designed to predict *A. islandica* larval distribution in a scenario where active depth regulation predominates. In effect the comparison allows discussion of the relative roles of active and passive processes in dispersal. Field study data are extracted from a larger data set collected in 1981 during a limited survey of seasonal occurrence, species composi-

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tion and depth distribution of bivalve larvae at a station on the Southern New England Shelf (Mann, in press). While this survey was of insufficient scale to examine both spatial and inter-annual variability, it nonetheless permitted examination of larval distribution in the relatively (compared to an estuary) uncomplicated physical environment of the Southern New England Shelf.

MATERIALS AND METHODS

A complete description of the study from which these field data are extracted is given by Mann (in press). Only relevant details are repeated here.

During the period April 13-December 14, 1981 (Julian days 113-348), 14 one-day cruises were made to a 43 m deep station WSW of Cuttyhunk Island, MA; west of Gay Head, Martha's Vineyard, MA; and east of Block Island, RI (lat. 72°02'W, long. 41°14'N). The water column at this station exhibits an intense seasonal stratification in temperature that is representative of Southern New England Shelf and Middle Atlantic Bight waters (Mann, unpublished data). Adult Arctica islandica are abundant in this area (Merrill and Ropes, 1969; Ropes, 1978; Fogarty, 1981). Depth specific plankton tows were made, always during the hours of 1030-1430, at 1 m, 10 m, 20 m, 30 m, and 40 m with a Clarke-Bumpus net (30 cm diameter, 5:1 aspect ratio, 53 μm mesh, 10 minute tow duration, 2 knots speed). Tows were not replicated. Volume of water passing through the net was recorded using a vane rotor in the mouth of the net. Volume sampled varied between 9.64 and 10.28 m³ with a mean of 9.96 m³. The collected sample was stained with Rose Bengal and fixed with 10% v/v buffered formalin in sea water. Bivalve larvae were subsequently separated under a low power dissecting microscope. During periods of peak abundance plankton samples were split using the apparatus of Drinnan and Stallworthy (1979). Individual larvae were measured in length (anterior-posterior axis) and height (dorso-ventral axis) at 100 x or 400 x on a Leitz compound microscope fitted with an ocular micrometer. Larvae of 200 μm length were identified to species where possible. Larvae of A. islanica were identified using the key of Lutz et al., (1982). On each sampling date temperature and conductivity were recorded at 5 m depth intervals. Time-depth contour diagrams of each were constructed by linear interpolation.

The four sets of data used for model development were obtained as follows. A daily water temperature matrix at 5-meter depth intervals from surface to 45 meters was generated from the previously described contour diagram. Temperature specific growth rates of larval Arctica islandica, expressed as daily increase in length at 9°C and 13-15°C, were derived by linear interpolation of points given in Lutz et al., (1982, Fig. 2). These points were fitted to pass through an origin corresponding to 90 μm length (equal to the egg diameter) at day 0 and mean length at metamorphosis of 260 μm. Growth rate at 9°C was 3.09 μm/day. Growth rate was considered to be constant in the range 13-15°C at 5.31 μm/day. Recent attempts to culture A. islandica larvae under conditions identical to cultures 2-5 of Lutz et al., (1982) but
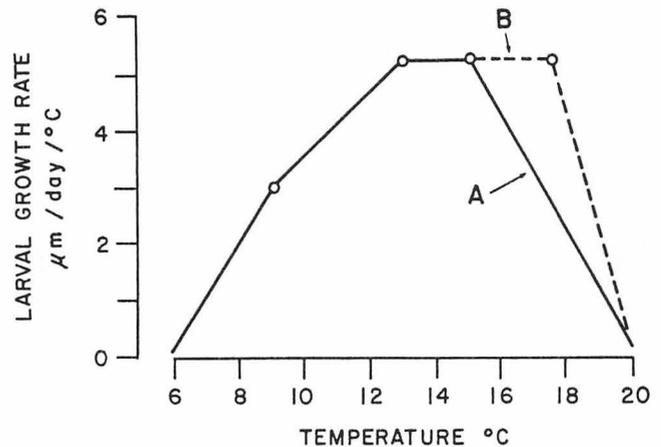

Fig. 1. Temperature specific growth rate model input data for Artica islandica. The curve is developed from linear interpolation of growth rate data taken at 6°C (Mann, unpublished), 9°C and 13-15°C (Lutz et al., 1982) and 20°C (Landers, 1976). Curve type A and B differ in point of inflexion between 15 and 20°C (see text).

at a lower temperature of 6°C, indicated that growth was arrested at the onset of the shelled veliger stage and, despite active feeding of the larvae, no larvae in excess of 120 μm length were recorded by 17 days after fertilization, when the culture was terminated (Mann, unpublished data). Therefore, growth for the present model was assumed to cease at 6°C. The true shape of the growth curve between the aforementioned points is not known. Previous laboratory studies with bivalve larvae (Walne, 1965; Helm and Millican; 1977) indicated gradually increasing growth rate with temperature to a maximum followed by a rapidly decreasing growth rate above this optimum temperature. For the present study, temperature specific growth rate was assumed to increase linearly at 1.03 μm/day/°C between 6 and 9°C, and then at 0.55 μm/day/°C between 9 and 13°C (Fig. 1). Landers (1976) stated that A. islandica larvae will not survive metamorphosis at 20°C. Lutz et al., (1982) did not examine the growth and survival of A. islandica larvae above 15°C. If temperature specific growth rate decreases linearly between 15 and 20°C to a value of zero at 20°C, the decrease in rate with increasing temperature would be 1.06 μm/day/°C; however, Mann and Wolf (1983, Fig. 4) indicated that the larval swimming temperature optima for A. islandica are in the range 15-18°C. These latter data suggested that optimal growth may occur between 15 and 18°C. Therefore, the model was run with two different forms of temperature specific growth rate versus temperature relationship (Fig. 1). In the first instance, hereafter termed type A, temperature specific growth rate was assumed to be constant between 13 and 15°C with a subsequent linear decrease in rate to zero at 20°C. In the second form, type B, temperature specific growth rate was assumed constant between 13 and 18°C with a subsequent decrease to zero at 20°C.

Data describing optimum temperature for swimming in Arctica islandica larvae were taken from Mann and Wolf (1983, Fig. 4). Optimum temperatures for the lengths 90 μm

(trochophore stage), 110, 120, 145 and 204 μm were taken as 17.0, 15.0, 17.0, 15.0 and 18.0ºC. Optimum temperature was assumed to be constant at 18ºC for larvae between 204 and 265 μm length.

Data describing response to pressure changes were taken from Mann and Wolf (1983, Figs. 2 and 3). All developmental stages showed a negative geotactic swimming response that is enhanced under increased pressure such that the preferred depth of occurrence up to 202 μm in length is in the range 0-5 m. The swimming response to increased pressure and temperature optima of larvae in excess of 202 μm and 204 μm length, respectively, was not examined. The assumption is made that the swimming response of larvae in the length range 200-265 μm to both temperature and increased pressure is identical to that of smaller larvae, with the exception of the metamorphosing pediveligers which are assumed to exhibit a positive geotaxis that overrides a temperature optima response.

The growth model was not required to accommodate for diurnal fluctuations in light intensity and spectral quality because Arctica islandica larvae do not exhibit distinct phototaxis (Mann and Wolf, 1983). The swimming behavior of some other bivalve larvae is influenced by light (Mann, 1986).

The growth model used the four data sets (water temperature-depth matrix, temperature specific growth rate, optimum temperature and optimum pressure) to compute daily length increment and cumulative length at the prevailing temperature of a fertilized egg originating at 45 m depth on any specified day between April 13, 1981 (day 103 of the year and the day of first sample collection in the field program) and December 14, 1981 (day 346 of the year and the last sample date of 1981). After calculation of a daily length increment for a day, d, the temperature for the following increment, that is day (d + l), was made by selecting the appropriate value from the water temperature-depth matrix to correspond with the optimum temperature- optimum pressure combination for the larval size as determined by the appropriate inputs. The model therefore assumes active depth regulation by the developing larvae. Where temperature and pressure optima were not in agreement, that is an optimum temperature oc-

curring at depths greater than 5 m, the selection of optimum temperature was made in preference to that of optimum pressure, because the data of Landers (1976) suggested that prolonged exposure to temperatures of only slightly above the optima recorded here would be lethal. The depth value chosen from such considerations of temperature and pressure optima is a single deterministic value. In effect, it is actually the upper (shallow) limit of a vertical distribution range. Thus, the model never allowed larvae to experience water temperatures in excess of their optimum temperature. Results of the model consisted of a summary of daily length increments, cumulative length, a record of depth occurrence and accompanying temperature throughout development, and an estimate of days required to attain metamorphic length.

The sensitivity of the model to changes in shape of the growth curve was tested (type A and B as given in Fig. 1). Sensitivity to changes in the temperature optima was also examined by sequentially increasing the values from Mann and Wolf (1983, Fig. 4) by one degree increments up to a maximum value of 19ºC.

Both Jones (1981) and Mann (1982) have described the seasonal gonadal cycle of A. islandica for offshore New Jersey and southern New England Shelf populations. In both locations spawning appears to proceed from May through October with partly spawned individuals being most abundant in August-October; however, the essentially descriptive nature of these data make them somewhat intractable for quantitative modelling.

RESULTS

Table 1 summarizes field data as estimated numbers of Arctica islandica larvae of > 200 μm length, which were present at specific depths on the Southern New England Shelf from April 13 through December 14, 1981 (Julian days 113-348). Note that these data deal predominantly with larvae of > 200 μm length, whereas model data are for a variety of lengths. The assumption is made that the responses exhibited by the size classes of larvae examined are generally representative of larvae throughout development. Arctica

Table 1. Numbers of Arctica islandica larvae of > 200 μm length m^{-3} collected at specific depths on the Southern New England Shelf during the period April-December 1981. ns: no sample collected due to net failure.

Date (1981)	4/13	5/11	6/8	6/29	7/13	7/27	8/10	8/24	9/8	9/21	10/5	10/26	11/19	12/14
Julian Day Number	103	131	159	180	194	208	221	236	251	264	278	299	323	348
Depth (m)														
1	0	16	0	0	0	0	0	0	0	0	0	0	0	0
10	0	70	0	0	0	0	0	0	0	0	0	n.s.	5.4	0
20	0	1.5	0	0	0	0	0	0	273	18.7	0	n.s.	101*	0
30	0	0.1	0	0	0	0	0	7	512	41.3	187	n.s.	311*	0
40	0	0	0	0	0.2	0.3	1.9	0	33	6.5	138	n.s.	59*	0
All depths	0	88	0	0	0.2	0.3	1.9	7	818	66	325	0	5.4	0

*indicates identification of first shelled larvae at length of 110 μm (modified from Mann, in press).
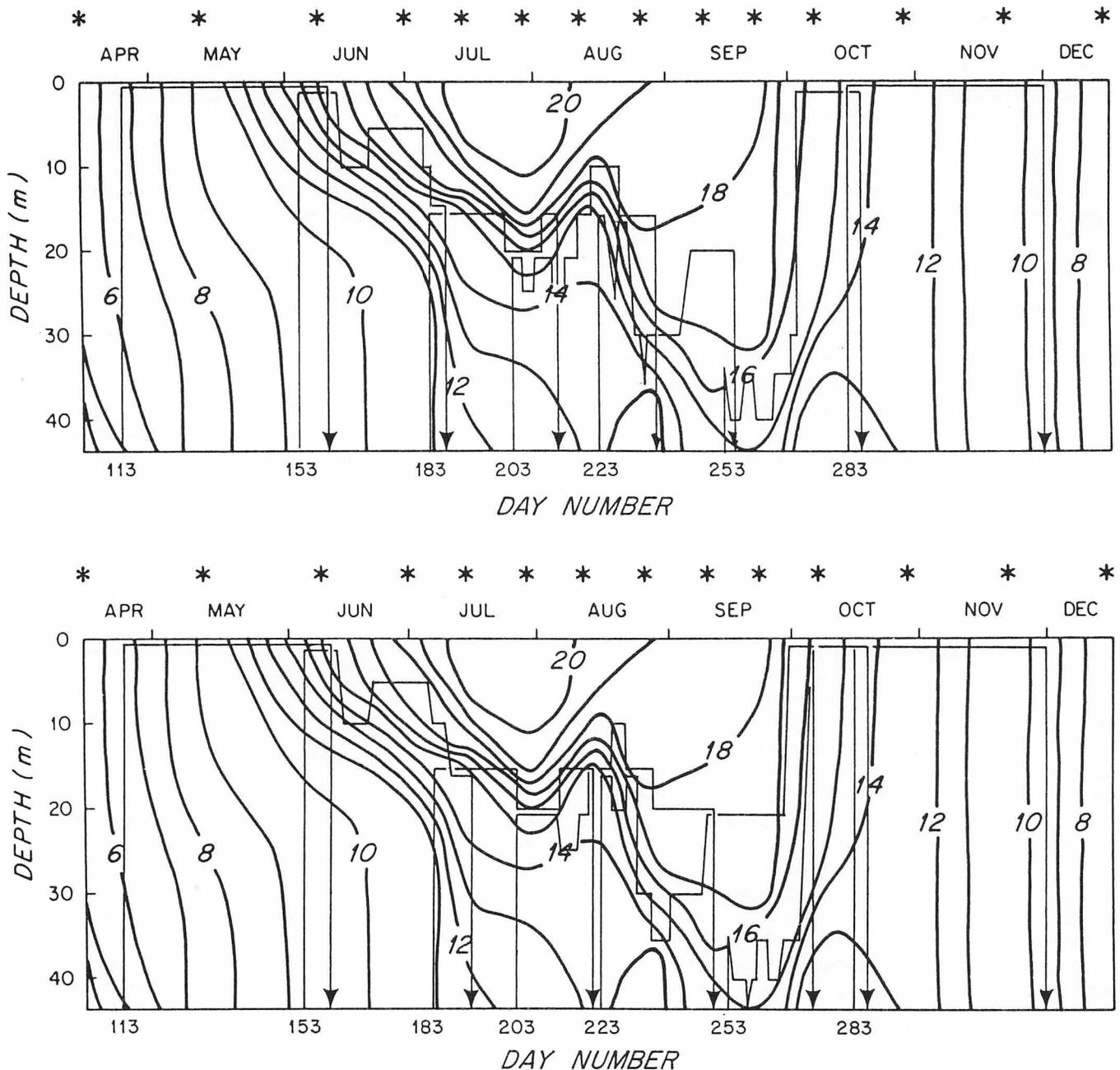
Fig. 2. Depth-time isotherm diagram of temperature structure during the period April-December 1981 based on vertical profiles with a sampling interval of 5 m. Heavy, curved lines labelled with even number values from 6 to 20 represent temperature in °C of isotherm. Superimposed on the isotherm diagram are light straight lines representing predicted depth of occurrence of *Arctica islandica* larvae originating from spawnings occurring on Julian days 113, 153, 183, 203, 223, 253 and 283. Where light lines terminate, arrows indicate predicted day of metamorphosis. Fig. 2A is model output for type A temperature specific growth rate input (see Fig. 1), Fig. 2B is for type B input (see Fig. 1). * Denotes dates on which field observations of temperature and larval abundance were made.

islandica larvae occur in significant concentrations in May (1 and 10 m) and from September to November (20-40 m). Salinity variation through the depth of the water column did not exceed 0.15 °/₀₀ on any one date; however, changes in both absolute temperature and temperature stratification were evident during the study (Fig. 2). The May occurrence of *A. islan-*

dica larvae coincided with temperatures of 9-10°C prior to thermal stratification. The 20-40 m depths during September corresponded to 15-18°C water which is overlayed by warmer water. During October and November temperature destratification occurred and the water column mixed from top to bottom. Water temperature decreases to 10°C by the

end of November.

Predicted shallow limit of depth of occurrence throughout development of growth types A and B larvae originating from spawnings on specific dates during day numbers 113 (April 13) through 283 (October 10) of the year are illustrated in Figs. 2A and 2B. Irrespective of growth type, larvae from spawnings prior to day 113 (April 13) experience low temperatures, remain in the depth range of 0-5 m throughout development, and reach metamorphic size, together with those spawned on day 113, and on day 153 (June 2). Larvae originating from spawnings on day 153 swim to the surface but soon encounter surface temperatures which are sufficiently high to encourage depth regulation in the range 5 to 15 m before metamorphic size is attained on day 192 (July 11) (type A) or 186 (July 5) (type B). The increasing surface temperature during days 180-210 (June 29-July 29) and the maintenance above 18°C until day 265 (September 22) restricts larvae spawned during days 173-213 (June 22-August 2) (type A) or 173-233 (June 22-August 22) (type B) to depths greater than or equal to 10 m. Larvae originating from spawnings on day 223 (August 12) rise to the depth range of 0-5 m during the final 7 days of development in type A growth. In type B growth larvae spawned on day 243 (September 1) rise to the surface for the final 17 days of development. Although surface temperatures decrease slowly after day 220 (August 9) the 17°C isotherms increase in depth during days 220-265 (August 9-September 22). Larvae originating from spawnings on day 223 (August 12) encounter these "sinking" isotherms and remain at depths below them during early development. Larvae originating from spawnings on day 253 (September 10) experience a similar depth limitation during early development; however, by day 283 (October 10) mixing of the water column has reduced thermal stratification to a point where no barriers to vertical movement of any of the developmental stages exist.

Examination of the sensitivity of this data in relation to increasing temperature optima suggests that larvae spawned in the early part of the year remain in or near the surface waters slightly longer and return to them slightly sooner following the thermocline decay. The suggested depth range of occurrence of larvae during the mid year period still "sinks" below the 19°C isotherm but remains above the 15°C isotherm.

Figure 3 illustrates the relationship of predicted time in days to attain metamorphic length versus day of spawning for spawnings originating at ten day intervals during the period day 103-303 (April 13-October 30) under growth types A and B. The type A growth-temperature relationship predicts two periods when growth rate is high and metamorphosis is reached in less than 35 days. These periods coincide with spawnings on days 163 (June 12) and 263-283 (September 20-October 10). Prior to day 163 (June 12) growth rate is low due to low temperature whereas between days 163 and 263 growth rate is again low due to temperatures in excess of 15°C. Decreasing water temperatures throughout the water column in late October-December result in increasing time to metamorphosis and is associated with spawnings after day 283 (October 10). Spawnings on or after day 303 encounter
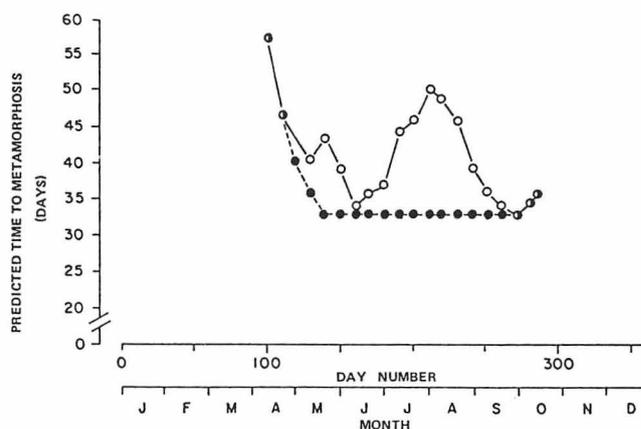

Fig. 3. Predicted time to metamorphosis (days) under growth types A (O) and B (●) of *Arctica islandica* larvae originating from spawnings which occur at 10-day intervals during the period day 103-303 versus day of spawning.

temperatures of 6°C or below during larval development and fail to metamorphose. When the type B growth-temperature relationship is used a time to metamorphosis of 33 days is predicted for all spawnings from day 143 (May 23) to day 273 (October 1).

Increasing temperature optima resulted in greater depression of growth rates during the mid summer period with growth type A, but only marginally depressed growth rate during days 190-220 (July 9-August 9) with growth type B when temperature optima were fixed at 19°C.

DISCUSSION

The extent to which active depth regulation contributes to the observed variation in distribution of *Arctica islandica* larvae in the field can, in part, be estimated from the degree of agreement of the model output and actual observations. There is good agreement between the field data (Table 1) and the predictive model output (Figs. 2A and 2B) on the absence of *A. islandica* larvae in the depth range 0-10 m between days 180 (June 29) and 270 (September 27). The model predicts aggregation of larvae at 10-25 m during days 180-213 (June 29-August 3), however, very small numbers are seen in the field at this time. The model output agreed well with field records of the presence of *A. islandica* larvae of > 200 μm length throughout the 20-40 m depth range from days 194 to 278 (July 13-October 5). In contrast the prediction of aggregation of *A. islandica* larvae in the 0-5 m depth range following the breakdown of the seasonal thermocline was not substantiated in that field data (Table 1) indicated both large (> 200 μm length) and small (< 150 μm length) *A. islandica* larvae at 20-40 m depth in November (day 323). Clearly, the negative geotactic behavior of *A. islandica* larvae observed in the unstratified water column of laboratory containers by Mann and Wolf (1983) is not the predominant force influencing vertical distribution in the field during the fall period when there is active mixing throughout the depth of the water column.

Further discrepancies between model results and field data are probably due to factors which are not represented in the model. These include larval mortality rate from starvation and/or predation in the field, larval loss from advection and, as mentioned earlier, variation in spawning intensity. Larval survival is probably inversely related to the time required to reach metamorphosis. A combination of less than maximal spawning activity and, if type A growth is inferred, greater than minimum predicted time to metamorphosis would contribute to an explanation of lack of large larvae in the field before day 236 (August 24). Such reasoning also suggests that the occurrence of highest concentrations of larvae will coincide with highest spawning activity (probably in August-October) and shortest time to metamorphosis. Irrespective of whether growth type A or B is inferred, application of this reasoning suggests the occurrence of highest larval concentration between day 243 (August 31) and 303 (October 30). The peak of abundance of large *A. islandica* larvae recorded in the field occurred between days 251 and 278 (September 8 and October 5 - see Table 1 and Fig. 2B). Net failure on day 299 (October 26) prevents further statements as to the end of this period of abundance of > 200 μm larvae; however, the presence of considerable numbers of small (< 150 μm) veliger larvae on day 323 (November 19 - see Table 1) suggests that it may continue past day 278 (October 5). The model predicts that the large numbers of small larvae present on day 323 (November 19) will not metamorphose due to decreasing temperature. It does not examine the option suggested and discussed by Mann (in review) that these larvae form the basis of an over-wintering population that ultimately gives rise to large (> 200 μm) larvae in May of the following year.

Despite the limitations of the relatively small data set used to construct the present model, a reasonably good agreement is seen between model results and field data. The model is simplistic in that it is only two dimensional and does not include an advective component; however, this development is hindered by a lack of current data (temporally, spatially and with depth) for the study site (R. C. Beardsley, personal communication). The general application of the model to other sites in the Middle Atlantic Bight is probably not unreasonable in that the spawning stock of *A. islandica* is widespread (Merrill and Ropes, 1969; Franz and Merrill, 1980; Theroux and Wigley, 1983) and roughly synchronous in time and intensity of spawning activity (Jones, 1981; Mann, 1982). Additionally, the thermal structure, especially the development and decay of the seasonal thermocline, is a relatively constant conservative feature throughout the Southern New England Shelf and Middle Atlantic Bight regions (Bigelow, 1933; Beardsley et al., 1976; Williams and Godshall, 1977; Beardsley and Boicourt, 1981).

The comparison of field collected and laboratory generated data sets presented here utilizes only one common data set, the time versus depth temperature matrix. In all other respects the data are independent of one another. The periods of agreement in the two final data sets strongly suggest that active depth regulation occurs in *Arctica islandica* larvae; however, the periods of discrepancy indicate that active depth regulation does not always predominate. The physical regimes corresponding to the transition from active depth regulation to passive movement are poorly understood, yet of obvious value. From a theoretical standpoint certain quantitative aspects are well documented. The relative positions of the ciliated velum and the valves combined with the pattern of ciliar beating dictate that bivalve larvae can only swim in vertically oriented helices. Rates of vertical excursion (i.e. change in actual depth, not absolute velocity) range from < 1 to 10 mm/sec depending upon size of the larva and water temperature. Bivalve larvae are flattened elipsoids that rarely exceed 300 μm in greatest dimension and have specific gravity of approximately 1.3. If the changes in velocities of water movement over discrete distances (be this centimeters, meters or kilometers) were known, the application of a purely mathematical approach to the problem of active versus passive processes in depth regulation and dispersal might be possible. This option becomes even more pressing when estuarine systems and other bivalve species are considered. Estuaries exhibit salinity stratification with depth, a salinity gradient along their length, and even the possibility of salinity gradients across their width. Salinity stratification is minimal on the New England Shelf. Estuarine circulation and stratification are influenced by tidal, neap-spring tidal and gravitational flow. Clearly, the physics of estuarine circulation are more complex and dynamic than those of the shelf system described here. Furthermore, larvae of estuarine bivalve species may exhibit a far less conservative repertoire of behavioural responses to environmental stimuli than do *A. islandica* larvae. For example, the larvae of *Ostrea edulis* L. (Cragg, 1980) and *Mytilus edulis* L. (Bayne, 1964) exhibit distinct phototaxis. Nonetheless the present study demonstrates for bivalve larvae, just as Sulkin and Van Heuklem (1982) and Kelly et al., (1982) have done for blue and red crab larvae respectively, the power of laboratory generated data and numerical models in elucidating factors controlling distribution and dispersal in stratified coastal systems. The application of such models to estuarine species is clearly warranted.

ACKNOWLEDGMENTS

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