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## SEASONAL CHANGES IN THE DEPTH-DISTRIBUTION OF BIVALVE LARVAE ON THE SOUTHERN NEW ENGLAND SHELF

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**ABSTRACT** A limited survey was made of the seasonal change in occurrence, depth distribution, size distribution, and species composition of bivalve larvae at a single station on the southern New England shelf during the period April-December 1981. The data were related to temperature structure of the water column and chlorophyll *a* distribution. Bivalve larvae were most abundant during late August and September at depths greater than 10 m, in water temperatures of 14 to 18°C, and chlorophyll *a* concentrations of  $< 2 \mu\text{g}\cdot\text{l}^{-1}$ , and at the surface in October in a temperature of 15.5°C and chlorophyll *a* concentrations of  $\sim 3.0 \mu\text{g}\cdot\text{l}^{-1}$ . Larvae  $> 200 \mu\text{m}$  length consisted predominantly of the species *Modiolus modiolus* (Linné), *Arctica islandica* (Linné) and *Spisula solidissima* (Dillwyn). *Modiolus modiolus* was present in the depth range 10-40 m from late July through December with highest concentrations in August through October. *Arctica islandica* was present at 1 to 30 m depth in May and from 20 to 40 m from late July through November. Larvae of *A. islandica* that were captured in May possibly originated from spawning in late 1980; those that were captured in November were first shelled veligers of 110  $\mu\text{m}$  length. Those larvae may form the basis of an overwintering larval population. Larvae of *S. solidissima* were present from late July through October and extended into shallower, warmer waters than larvae of either *M. modiolus* or *A. islandica*.

**KEY WORDS:** Bivalve larvae, New England Shelf, *Arctica islandica*, *Modiolus modiolus*, *Spisula solidissima*

### INTRODUCTION

Franz and Merrill (1980) described the bivalve molluscs of the Middle Atlantic Bight as a mixture of southern and northern species. The southern or Transhatteran species reach their northern limit at Cape Cod and are generally limited to the shallower depths inshore of the seasonal thermocline. The northern species, a mixture of arctic-boreal and boreal species, generally exhibit submergence south of Cape Cod, (i.e., their distribution follows colder isotherms to increasing depth with more southerly latitudes). Recently, one member of this Boreal fauna, the ocean quahog *Arctica islandica* (Linné), was the subject of considerable attention. Mann (1982) and Jones (1981) described the seasonal cycle of gonadal production on the southern New England shelf and offshore New Jersey, respectively. Lutz et al. (1982) expanded the previous work of Landers (1976) to give a comprehensive description of larval and early postlarval development. Mann and Wolf (1983) described the swimming behaviour of the larvae in response to temperature and pressure stimuli. Based on a consideration of an earlier description of seasonal temperature structure of the waters of the Middle Atlantic region by Bigelow (1933) and the data of Landers (1976), Mann (1982) hypothesized, despite the presence of morphologically ripe specimens from March through October, that "larval survival is probably greatest during the months of October and November, which is the time of breakdown of intense seasonal thermocline and precedes the onset of low winter seawater temperatures." The data of Lutz et al. (1982) and Mann and Wolf (1983) support this hypothesis.

Early in 1981 the opportunity arose to make a limited survey of seasonal occurrence, species composition, and depth distribu-

tion of bivalve mollusc larvae at a station on the southern New England shelf during the period April-December 1981. While this survey was of insufficient scale to examine both spatial and inter-annual variability, it nonetheless offered an opportunity to examine the hypothesis of Mann (1982) and to provide information on bivalve larvae occurrence on the continental shelf. This report describes the results of the survey.

### MATERIALS AND METHODS

During April-December 1981, 14 one-day cruises were made to a station in 43 m of water situated west-southwest 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 water temperature that is representative of southern New England shelf and Middle Atlantic Bight waters (Mann, unpublished data). Adults of *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, 10, 20, 30, and 40 m with a Clarke-Bumpus net (30-cm diameter, 5:1 aspect ratio, 53  $\mu\text{m}$  mesh, 10-min tow duration, 3.7  $\text{km}\cdot\text{h}^{-1}$  speed). Tows were not replicated. The volume of water that passed through the net was recorded by a vane rotor in the mouth of the net. Volume varied between 9.64 and 10.28  $\text{m}^3$  with a mean value of 9.96  $\text{m}^3$ . Collected material 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

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on a Leitz compound microscope fitted with an ocular micrometer. All larvae were grouped into three size classes: straight hinge or early umbo larvae of length  $< 150 \mu\text{m}$ ; umbo larvae in the length range  $150\text{--}200 \mu\text{m}$ ; and umbo or pediveliger larvae of length  $> 200 \mu\text{m}$ . Individuals of  $> 200 \mu\text{m}$  length were identified, where possible, to genus or species using the keys of Chanley and Andrews (1971), de Schweinitz and Lutz (1976), Lutz et al. (1982), and unpublished material kindly supplied by Prof. R. D. Turner (Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA).

On each sampling date water temperature and conductivity were recorded at 5-m depth intervals using a Hydrolab S8000 instrument (Hydrolab Instruments, Austin, TX). During June-December, water samples were collected from the same depths as the plankton tows using a Niskin bottle, a subsample (250-1000 ml depending on concentration) was filtered through a preashed Gelman A/E glass fibre filter and the retained material assayed for chlorophyll *a* by the trichromatic method of Strickland and Parsons (1968). Vertical profiles for temperature and chlorophyll *a* for each date were used to construct, by linear interpolation, time-depth contour diagrams of each.

## RESULTS

### Hydrographic Observations

Figure 1 illustrates the temperature structure of the water column during the period April-December 1981. Thermal stratification began development in May and intensified through June and July. By the end of July a maximum surface temperature of  $20.3^\circ\text{C}$  contrasted with a bottom temperature of  $12.3^\circ\text{C}$  and an intense thermal gradient ( $0.5^\circ\text{C}\cdot\text{m}^{-1}$ ) was evident between 15 and 23 m. During August-September the depth of intense stratification increased as surface temperature gradually decreased. A maximum bottom temperature of  $15.0^\circ\text{C}$  was

recorded in mid-September. A well-mixed water column was again evident by late October.

Salinities in the range  $32.20$  to  $32.61 \text{‰}$  were recorded during the periods of vertical mixing of the water column; variation through the depth of the water column did not exceed  $0.15 \text{‰}$  on any one collection date. As thermal stratification intensified, surface salinity values decreased to  $31.40 \text{‰}$  by late August - early September. This lower salinity water extended to the approximate depth of the  $17^\circ\text{C}$  isotherm at 25 to 30 m (Figure 1) where it covered water of higher salinity ( $31.80$  to  $32.13 \text{‰}$ ). Bottom water typically maintained a slightly higher salinity (by  $0.30$  to  $0.70 \text{‰}$ ) than surface water during the summer thermal stratification.

### Chlorophyll Concentration

Figure 2 illustrates chlorophyll *a* concentration in the water column for June-December 1981. A weak chlorophyll *a* maximum in mid-June was observed at 20 m, immediately below the region of intense thermal stratification. Chlorophyll *a* was at a maximum ( $\sim 2 \mu\text{g}\cdot\text{l}^{-1}$ ) at 25 to 35 m depth by early August. This was below the region of most intense thermal stratification and corresponded to a thermal range of  $13$  to  $15^\circ\text{C}$  that decreased with depth. In contrast, the water column from 0 to 15 m had both the highest temperature ( $> 19^\circ\text{C}$ ) and lowest chlorophyll *a* content ( $< 0.5 \mu\text{g}\cdot\text{l}^{-1}$ ). Chlorophyll *a* was evenly distributed throughout the water column ( $\sim 0.4 \mu\text{g}\cdot\text{l}^{-1}$ ) in late September in spite of some minor thermal stratification from 30 to 43 m. A high concentration of chlorophyll *a* ( $> 3.0 \mu\text{g}\cdot\text{l}^{-1}$ ) extended to below 20 m ( $\sim 2.0 \mu\text{g}\cdot\text{l}^{-1}$ ) in early October following the breakdown of thermal stratification and mixing of the water column. After late October, little change was observed in chlorophyll *a* concentrations either temporally or through depth.

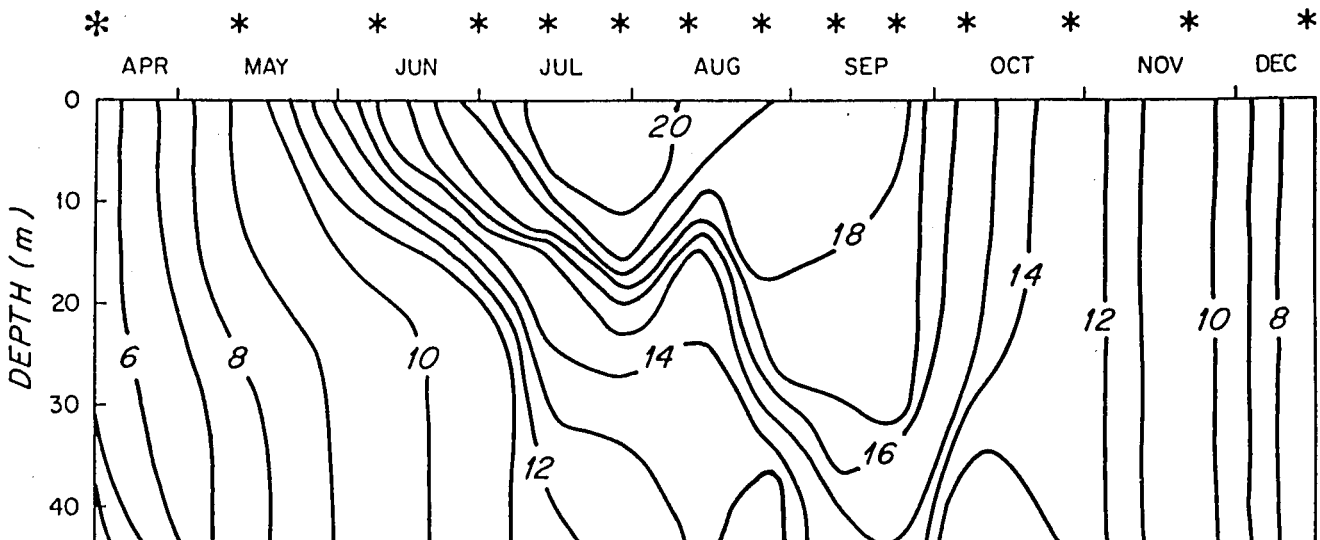


Figure 1. Depth-line isotherm diagram of temperature structure ( $^\circ\text{C}$ ) during the period April-December 1981 based on vertical profiles with a sampling interval of 5 m. (\*marks a sampling date.)

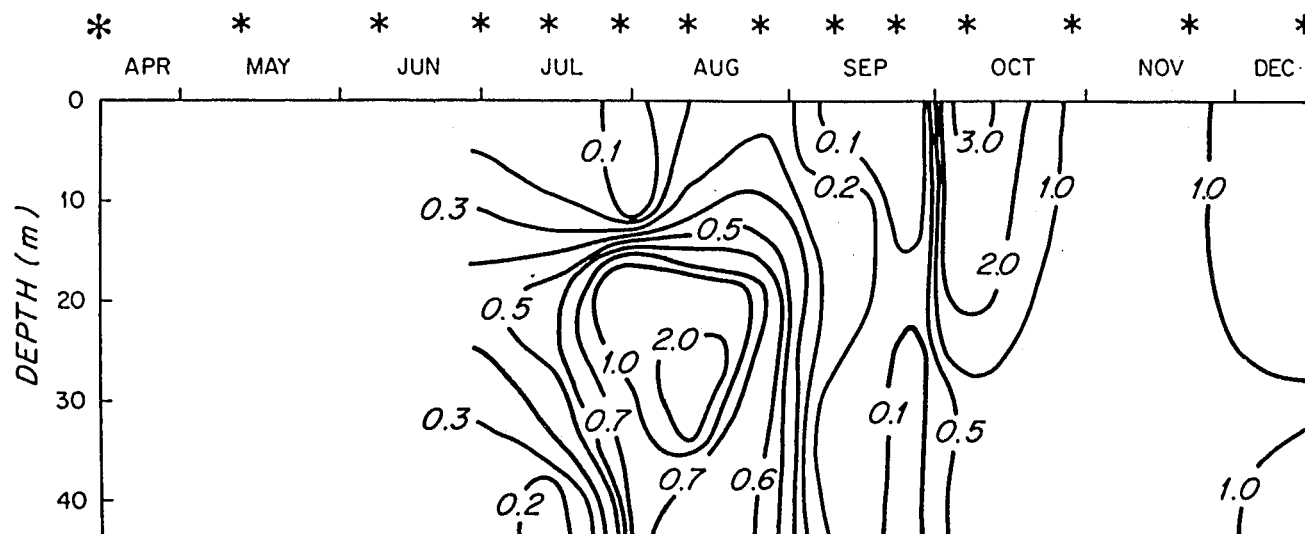


Figure 2. Depth-time contour diagram of chlorophyll *a* concentration ( $\mu\text{g}\cdot\text{l}^{-1}$ ) for the period June-December 1981 based on Niskin casts at 10 m depth intervals in the water column. (\*marks a sampling date.)

TABLE 1.

Seasonal changes in numbers, depth distribution, and size-class distribution of bivalve larvae on the southern New England shelf during April-December 1981. (ns: no sample collected due to net failure.)

Depth (m)	Date (1981) Day Number	4/13 103	5/11 131	6/8 159	6/29 180	7/13 194	7/27 208	8/10 221	8/24 236	9/8 251	9/21 264	10/5 278	10/26 299	11/19 323	12/14 348
1	Larvae/m <sup>3</sup>	3	16	0	0.2	0.5	0.2	0.4	28	185	5.8	621	1645	547	0.1
	n measured	14	59		2	4	5	4	28	47	30	30	100	47	1
	% <150	58	0		100	100	100	75	17	70	100	100	98	92	0
	% 150-200	21	0		0	0	0	0	83	28	0	0	2	8	0
	% >200	21	100		0	0	0	25	0	2	0	0	0	0	0
10	Larvae/m <sup>3</sup>	0	74	0	0.4	0	170	71	320	270	129	2153	ns	272	52
	n measured		60		5		33	433	38	155	98	158		35	101
	% <150		0		100		0	99	24	71	98	95		90	0
	% 150-200		0		0		9	0	76	15	0	4		8	0
	% >200		100		0		91	1	0	14	2	1		2	100
20	Larvae/m <sup>3</sup>	5.7	2.2	0	0.3	0	1.2	677	330	3554	480	1843	ns	101	116
	n measured	19	11		4		6	30	30	90	128	56		46	272
	% <150	94	0		100		0	100	60	0	18	89		96	0
	% 150-200	0	18		0		0	0	40	10	11	10		4	0
	% >200	6	82		0		100	0	0	90	71	1		0	100
30	Larvae/m <sup>3</sup>	0.6	0.3	4.6	24	0.6	3.5	186	288	3025	639	2460	ns	311	83
	n measured	6	1	15	32	6	18	40	31	69	66	82		30	74
	% <150	100	0	67	67	100	0	69	9	2	6	7		100	0
	% 150-200	0	0	27	33	0	17	26	65	12	12	20		0	16
	% >200	0	100	7	0	0	83	5	26	86	82	73		0	84
40	Larvae/m <sup>3</sup>	0	1.5	0	9.3	0.7	26	7.4	69	416	109	4803	ns	59	0.3
	n measured		4		21	7	33	74	49	65	57	161		30	74
	% <150		0		19	28	0	16	6	9	0	0		100	0
	% 150-200		0		57	44	0	20	14	29	0	0		0	0
	% >200		100		24	28	100	80	70	65	91	100		0	100

*Bivalve Larvae*

Few larvae were evident until early August when a large concentration was recorded at 20 m (Table 1). This larval concen-

tration corresponded to both the 15°C isotherm (Figure 1) and a high chlorophyll *a* concentration (Figure 2). By contrast, low concentrations of larvae were recorded simultaneously in the

higher temperature ( $>19^{\circ}\text{C}$ ) surface water and at 40 m (Table 1). By early September very high ( $>3,000$  larvae $\cdot\text{m}^{-3}$ ) concentrations of larvae were recorded between the  $17^{\circ}\text{C}$  and  $18^{\circ}\text{C}$  isotherms at 20 to 30-m depth. Lower concentrations were again found at 1 to 10 m ( $<300$  larvae $\cdot\text{m}^{-3}$ ) and at 40 m (416 larvae $\cdot\text{m}^{-3}$ ). Intense vertical mixing of the water column began by early October and uniformly high concentrations of larvae ( $>1800$  larvae $\cdot\text{m}^{-3}$ ) were recorded at 10 to 40-m depths with only slightly lower concentrations at the surface. High surface concentrations of larvae were evident until late November. Data for depths in the range of 10 to 40 m were unavailable in late October due to net failure; however, larval concentrations (59-272 larvae $\cdot\text{m}^{-3}$ ) that were considerably below surface values ( $>547$  larvae $\cdot\text{m}^{-3}$ ) were recorded from 10 to 40 m in late November despite a well mixed, isothermal ( $10.5^{\circ}\text{C}$ ) water column. A decrease in water temperature in December coincided with lower larval concentrations (0.1-116 larvae $\cdot\text{m}^{-3}$  with greatest aggregation at 20 to 30 m) throughout the column.

Identification to the species level was attempted for 982 larvae; 922 of these were  $>200$   $\mu\text{m}$  in length (204 *Arctica islandica* (Linné), 207 *Spisula solidissima* (Dillwyn), 319 *Modiolus modiolus* (Linné), 89 *Anomia simplex* Orbigny, 163 unidentified). The remaining 60 larvae identified were *A. islandica* of approximately 110  $\mu\text{m}$  length.

Only three larvae were identifiable to species from the samples collected on 13 April 1981 (day 103) and all were *S. solidissima* (Table 2). Although absolute numbers of larvae per tow collected on 11 May 1981 (day 131) were small; a large proportion of these were *A. islandica* at or approaching pediveliger stage of development (Table 2). These larvae were concentrated in the upper 20 m of the water column. A predominance of larvae  $>200$   $\mu\text{m}$  in length was not seen again until 27 July 1981 (day 208) when *S. solidissima* was evident between 10 and 40 m, including two pediveligers at 30 m, and *Modiolus modiolus* was present at 40 m. Larvae of *M. modiolus* were present in significant numbers in the  $>200$   $\mu\text{m}$  length

TABLE 2.  
Species composition of bivalve larvae of  $>200$   $\mu\text{m}$  length collected at specific depths on the southern New England shelf during the period April-December 1981. (ns: no sample collected due to net failure.)

Depth (m)	Date 1981 Day Number	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
		103	131	159	180	194	208	221	236	251	264	278	299	323	348
1	n identified	3	20	0	0	0	0	1	0	1	0	0	0	0	1
	<i>Modiolus modiolus</i>	0	0					0		1					0
	<i>Spisula solidissima</i>	2	0					0		0					0
	<i>Arctica islandica</i>	0	20					0		0					0
	<i>Anomia simplex</i>	0	0					0		0					0
	Other	1	0					1		0					0
10	n identified	0	60	0	0	0	30	1	0	14	2	0	ns	1	24
	<i>Modiolus modiolus</i>		0				1	0		9	0			0	24
	<i>Spisula solidissima</i>		0				21	0		1	0			0	0
	<i>Arctica islandica</i>		57				0	0		0	0			1	0
	<i>Anomia simplex</i>		0				0	0		0				0	0
	Other		3				8	1		4	2			0	0
20	n identified	1	11	0	0	0	6	0	0	82	73	0	ns	0	30
	<i>Modiolus modiolus</i>	0	0				0			45	20				30
	<i>Spisula solidissima</i>	1	0				0			15	32				0
	<i>Arctica islandica</i>	0	9				0			7	4				0
	<i>Anomia simplex</i>	0	0				0			0	0				0
	Other	0	2				6			15	17				0
30	n identified	0	1	1	0	0	5	30	32	61	76	48	ns	30*	16
	<i>Modiolus modiolus</i>		0	0			1	15	18	21	27	9			16
	<i>Spisula solidissima</i>		0	0			2	0	1	12	31	22			0
	<i>Arctica islandica</i>		1	0			0	0	3	12	6	5		30*	0
	<i>Anomia simplex</i>		0	0			0	4	3	0	1	6			0
	Other		0	1			3	12	7	16	11	6			0
40	n identified	0	4	0	5	1	33	41	15	74	45	70	ns	30*	3
	<i>Modiolus modiolus</i>		0		0	0	21	34	1	8	15	0			3
	<i>Spisula solidissima</i>		0		0	0	2	3	5	40	17	0			0
	<i>Arctica islandica</i>		0		0	1	1	3	0	9	3	2		30*	0
	<i>Anomia simplex</i>		0		0	0	0	1	2	1	3	68			0
	Other		4		5	0	9	0	7	16	7	0			0

\* Indicates identification of first shelled larvae at length of 110  $\mu\text{m}$ .

fraction throughout August and September, and smaller numbers occurred in October. *Modiolus modiolus* was the only species present in the  $>200 \mu\text{m}$  length fraction in the depth range of 10 to 40 m in the samples collected on 14 December 1981 (day 348). Smaller ( $<200 \mu\text{m}$  length) larvae predominated throughout August–November at all depths except during the period 8 September to 5 October 1981 (days 251–278) in the depth range 20–40 m. In the  $>200 \mu\text{m}$  length range *S. solidissima* showed continuing presence during late August, September, and early October. Larvae of *A. islandica* of comparable size were recorded, usually at depths of  $\geq 20$  m, throughout August, September, and early October.

The data in Tables 1 and 2 can be combined to estimate absolute numbers of larvae per  $\text{m}^3$  for each of the species listed in Table 2 for the length size range  $>200 \mu\text{m}$ . Highest concentrations of larvae of *S. solidissima* were recorded on 27 July 1981 (103 larvae· $\text{m}^{-3}$  at 10 m), 8 September 1981 (585, 512, and 138 larvae· $\text{m}^{-3}$  at 20, 30, and 40 m, respectively), 21 September 1981 (213 larvae· $\text{m}^{-3}$  at 30 m), and 5 October 1981 (149 and 823 larvae· $\text{m}^{-3}$  at 20 and 30 m, respectively). Highest concentrations of larvae of *M. modiolus* were recorded on 8 September 1981 (1,750 and 896 larvae· $\text{m}^{-3}$  at 20 and 30 m, respectively), 21 September 1981 (93 and 186 larvae· $\text{m}^{-3}$  at 20 and 30 m, respectively), and 5 October 1981 (337 larvae· $\text{m}^{-3}$  at 30 m). Highest concentrations of larvae of *A. islandica* were recorded on 11 May 1981 (70 larvae· $\text{m}^{-3}$  at 10 m), 8 September 1981 (273, 512, and 33 larvae· $\text{m}^{-3}$  at 20, 30, and 40 m, respectively), and 5 October 1981 (187 and 138 larvae· $\text{m}^{-3}$  at 30 and 40 m, respectively).

Identification of the smallest veliger stages ( $<150 \mu\text{m}$ ) was not generally attempted because of the large numbers present and the difficulty of making definitive identifications of such small larvae; however, the samples collected at 30 and 40 m during November were notable for the marked uniformity of the first shelled larvae present. Subsamples of 30 larvae per tow were examined and, based upon morphometry and measurements of length, height, and hinge length, they were identified as *A. islandica*. Larvae of *Anomia simplex* characterized by a notch in the ventral margin of one valve, were present throughout August, September, and October at depths in excess of 20 m.

## DISCUSSION

The limited spatial and temporal extent of this survey and lack of sample replication clearly restrict interpretation of the resultant data. Only one station was sampled intensively in this study. Consequently, the contribution of horizontal, advective processes to temporal changes in physical structure of the water column, chlorophyll concentrations, and number of larvae collected cannot be definitively measured. On the other hand, the fact that adult stocks of the species denoted in Table 2 are widespread throughout the southern New England shelf and Middle Atlantic Bight (Merrill and Ropes 1969; Ropes 1978; Fogarty 1981; Theroux and Wigley 1983) and that the seasonal

water temperature structure illustrated in Figure 1 is characteristic of the same area (Bigelow 1933; Ketchum and Corwin 1964; Beardsley and Boicourt 1981) suggests that larval data reported here may also be representative of that greater area.

In this study depth-specific plankton tows at intervals of 10 m were effected in preference to oblique tows predominantly because of equipment limitations. With such a protocol the possibility exists that significant numbers of larvae would not be representatively sampled because of aggregation caused by various environmental stimuli. Larval collections were made only between 1030 and 1430 hours. No examination of depths distribution were made at night. Mann (1986) reviews literature relating to phototactic behaviour in bivalve larvae. Only the data of Quayle (1952) for larvae of *Venerupis pullastra* (Montagu) provided any evidence of possible diurnal migration associated with changing light levels. (It was not possible to separate tidal and diurnal influences in Quayle's data.) Mann and Wolf (1983) reported that larvae of *Arctica islandica* exhibited little phototactic behaviour in laboratory systems. The larvae of *Modiolus modiolus* and *Spisula solidissima* have not been examined for phototactic behaviour. The influence of phototactically-induced, diurnal migration and aggregation on the distributions reported here cannot be definitively stated; however, the occurrence of larvae of *A. islandica*, *M. modiolus*, and *S. solidissima* over depth ranges greater than 10 m (see Table 2) argues against such aggregation.

The high concentrations of larvae recorded during late August and September were associated with water temperatures in the range of 14 to 18°C and decreasing chlorophyll content (Table 1; Figures 1 and 2). In contrast, the high concentration of larvae at the surface in October was associated with, but not necessarily related to, a higher chlorophyll *a* concentration that resulted predominantly from a bloom of the large diatom *Rhizosolenia* sp. It is relevant to ask whether or not chlorophyll concentrations are representative of food concentrations which are sufficient to sustain active feeding and growth of the larvae. Critical studies of bivalve larval feeding and growth have generally expressed food concentration in terms of cells· $\text{ml}^{-1}$  (e.g., review by Epifanio 1976) rather than chlorophyll *a*. Chlorophyll *a* values in the field study varied from 0.1 to 3  $\mu\text{g}\cdot\text{l}^{-1}$ . Chlorophyll *a* to particulate organic carbon (POC) ratios have been widely reported and vary considerably (Steele and Baird 1961a, 1961b; Harris and Riley 1956; Goldman and Mann 1980). These values will, of course, include POC from sources other than cells that contain chlorophyll *a*. If within this range (1:23 - 1:260) a chlorophyll *a*: POC ratio of 100 is arbitrarily assumed, then a corresponding range of POC values over the time course of this study of 10 to 300  $\mu\text{g}\cdot\text{l}^{-1}$  is obtained. Goldman and Stanley (1974, Table 4) gave conversion factors for POC: cell concentration in the range 0.54 to 2.29  $\text{mg}\cdot\text{l}^{-1}$ :  $10^5$  cells· $\text{ml}^{-1}$  depending upon the size of the algal cell. Application of maximum and minimum values to the present POC numbers resulted in a range of cell concentrations for the study period of  $5.4 \times 10^2$  to  $1.62 \times 10^4$  cells· $\text{ml}^{-1}$  and  $2.29 \times 10^3$  to

$6.77 \times 10^4$  cells·ml<sup>-1</sup>, respectively. Although grazing activity of molluscan veliger larvae decreases below  $10^4$  cells·ml<sup>-1</sup> (Gallager and Mann 1980, Figure 3), significant grazing can still be effected at the lowest estimate of cell concentration. Furthermore, these values are probably more than adequate to sustain larval growth in that larvae of *A. islandica* grow well in food concentrations of 5 to  $10 \times 10^4$  cells·ml<sup>-1</sup> (Lutz et al. 1982) and larvae of *M. modiolus* grow well at 3 to  $8 \times 10^4$  cells·ml<sup>-1</sup> (de Schweinitz and Lutz 1976). With respect to the large bloom of *Rhizosolenia* sp. in October it is relevant to note that this species is probably too large to be ingested by most bivalve larvae and POC estimates that were obtained from chlorophyll *a* values at that time represent an over-estimation of food available to bivalve larvae.

The spawning season of *Modiolus modiolus* is poorly documented (de Schweinitz and Lutz 1976). The presence of larvae from July through December in the present study suggests that, on southern New England shelf at least, the spawning season for this species is protracted. Ropes (1968, 1978) and Jones (1981) both examined the spawning cycle of *Spisula solidissima* on the Middle Atlantic Shelf off New Jersey. Ropes (1968) reported two spawnings, a major event in July and August, and a minor event in October and November during the years 1962, 1963, and 1964. In 1965, by contrast, water temperatures were lower and only one spawning event, which was delayed and of longer duration than in 1962-64, was reported (Ropes 1968). Jones (1981) collected larvae of *S. solidissima* from a location inshore of the summer thermocline and reported a single spawning period that extended from June through November with a major concentration from August through October. Larvae of *S. solidissima* were present from late July through October in this study suggesting that, in the more northerly location, the spawning season may be terminated slightly earlier in the year.

Mann (1982) recorded a prolonged spawning season for *Arc-tica islandica* on the southern New England shelf from May through November with most intense spawning from August through November. Previously, Loosanoff (1953) reported a spawning season for *A. islandica* from the same location from June through mid October with maximum activity from August through early October. Further south, Jones (1981) described peak spawning as being "an autumnal to early winter event rather than summer/early autumn." Larvae of *A. islandica* were recorded on each sampling date from mid-July through early October as members of the size fraction that exceeded 200  $\mu$ m in length. This observation is in agreement with the comments of Loosanoff (1953) and Mann (1982) on adult spawning periodicity. The occurrence of maximum numbers of >200  $\mu$ m length larvae of *A. islandica* in September and October suggests that the period of maximum survival may be slightly more protracted than the period of October to November suggested in the hypothesis of Mann (1982). The large number of early shelled larvae (<150  $\mu$ m length) of *A. islandica* recorded in mid-November probably arose from a spawning within the preceding two weeks based upon ambient seawater temperature

(10.7°C) and laboratory growth-rate data (Lutz et al. 1982, Figure 2). Again, this indication of active spawning in late October to early November is in agreement with the comments of Mann (1982). The presence of these larvae suggests that the hypothesis of Mann (1982) is reasonable concerning the end of the period during which maximum survival occurs; unfortunately, the lack of data for late October that resulted from equipment failure does not allow further statements on the last date of occurrence of large (>200  $\mu$ m) larvae of *A. islandica* in the water column.

An explanation of the presence of larvae of *A. islandica* of length >200  $\mu$ m in May is problematic. At the ambient temperature on the day of sample collection (7.3°C at 0 m increasing to 9.5°C at 43 m) growth to >200  $\mu$ m length would probably take 6 weeks or longer (Lutz et al. 1982, Fig. 2), especially considering the fact that temperature was increasing at that time. The earliest that those larvae could have been spawned would, therefore, be late March-April, a period when water temperatures reach an annual low of ~1°C in this region and when very little spawning activity was noted by either Loosanoff (1953) or Mann (1982). The possibility exists that these larvae may have originated from a late autumn spawning during the preceding spawning season. This possibility is supported by the presence of large numbers of early veliger larvae of *A. islandica* in samples collected in November (Table 2); however, survival of larvae through the winter months would also necessitate a planktonic life of approximately 6 months, an ability to survive essentially arrested growth periods at low temperatures, and the good fortune not to be either lost to predation or washed out of a region in which recruitment may occur. A study of the effect of extended periods of low temperature on the development of larvae of *A. islandica* is required to evaluate the potential contribution of overwintering larvae to maintenance of this species on the New England shelf.

Franz and Merrill (1980) reported the bathymetric range of adults of *A. islandica* and *M. modiolus* in the Middle Atlantic Bight as 9 to 165 m and 1 to 146 m, respectively. Theroux and Wigley (1983) reported that *M. modiolus* occupies a bathymetric range of 13 to 256 m; the majority of their samples were taken between 25 and 49 m. Both *A. islandica* and *M. modiolus*, therefore, exhibit submergence south of Cape Cod; however, Mann and Wolf (1983) noted that in more northerly parts of its zoogeographic range *A. islandica* can be found in shallow, sublittoral depths. *Modiolus modiolus* also occurs in shallower depths in more northerly locations. Gosner (1971) reported that *M. modiolus* occurs from slightly below tide level to 81 m, whereas de Schweinitz and Lutz (1976) noted that the species can be "collected subtidally along the coast of Chamberlain, Maine." Cragg (1980) reported that selection favours a more sensitive depth regulation mechanism in the larvae of littoral species than in the larvae of sublittoral species. If this regulation translates as comparable depth regulation in species that occupy similar bathymetric ranges, then larvae of *A. islandica* and *M. modiolus* would be expected to control their depth within and occupy similar bathymetric ranges. Although this aspect

of the larval biology of *M. modiolus* has not been examined experimentally in the laboratory, the similarity of depth distribution of larvae in the field (Table 2) is notable.

Although *S. solidissima* occupies a shallower bathymetric range (Merrill and Ropes 1969) than *A. islandica* or *M. modiolus*, Franz and Merrill (1980) considered it a member of the boreal fauna. Theroux and Wigley (1983) stated that *S. solidissima* "inhabits the Boreal, Virginian and Carolinian provinces in the northwest Atlantic" and occupies "primarily inshore shallow waters." The depth regulation of larvae of *S. solidissima* have not been examined; however, these larvae are more tolerant of higher temperatures, reaching metamorphosis in 19 days at 22°C (Loosanoff and Davis 1963), than either *M. modiolus* (16-21.5°C, de Schweinitz and Lutz 1976) or *A. islandica* (<15°C, Landers 1976; Lutz et al. 1982). The larval development temperature of 22°C for *S. solidissima* is compatible with both the observation of larvae of *S. solidissima* at 20.3°C and 10 m depth on day 208 of this study and the temperature of the overlaying water during the period of spawning of adults of *S. solidissima* in the Middle Atlantic Bight (see Ropes [1968, 1978] and Jones [1981] for data on spawning; and Bigelow [1933] for water temperature data).

The southern range extension of such boreal species as *A. islandica* and *M. modiolus* on the shallow continental shelf south of Cape Cod appears to be made possible by the presence of the summer "cold pool" below the depth of the seasonal thermocline (compare zoogeographical data of Theroux and Wigley [1983] with the physical data of Bigelow [1933]). It would clearly be profitable to examine the seasonal occurrence and survival to metamorphic size of the larvae of these boreal species

in the water column of the southern New England shelf and Middle Atlantic Bight over a number of years. This option is particularly attractive in examining recruitment in *A. islandica*, a long lived species (Thompson et al. 1980) which, despite apparent regular spawning activity (Loosanoff 1953; Jones 1981; Mann 1982), exhibits a lack of representation in small (<20 mm longest dimension) size classes in the Rhode Island Sound region (Mann, unpublished data collected 1978-1981). The relative contributions of lack of recruitment and predation (see Franz and Worley [1982] for comments on predation on juveniles of *A. islandica*) to this observation have yet to be defined. This approach might also provide insight into the recruitment of *S. solidissima* on the southern shore of Long Island, NY, a process which according to Franz (1976) is "apparently dependent on massive settlements of larvae occurring irregularly and infrequently."

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