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The Reproductive Biology of Arctica islandica

by

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SUMMARY

Arctica islandica is a large pelecypod that occurs in European waters from the White Sea to Spain and in American coastal waters from Newfoundland to Cape Hatteras. A. islandica supports an active fishery in the Middle Atlantic Region; however, optimal management of the fishery is hindered by a lack of adequate knowledge of the biology of the species. A summary is given of recent work on the reproductive biology of A. islandica. On the Southern New England Shelf the adult clams spawn from May through November, spawning being most intense from August through November. Multiple annual spawnings at both the individual and population level are evident. A. islandica is dioecious and oviparous. Attempts to stimulate adult clams to spawn in the laboratory have generally been unsuccessful. Stripped ova have an outer membrane which must be removed to effect a high percentage of fertilization in laboratory cultures. The larvae have been reared to metamorphosis in 32-35 days at 13°C and 53 days at 9°C. Post larval forms rapidly develop the characteristic shape and colored periostracum of the adult form.

INTRODUCTION

Arctica islandica L. (= Cyprina islandica) is a large pelecypod that occurs on the inner continental shelves of Europe and the east coast of North America from Newfoundland to Cape Hatteras (Nicol 1951, Merrill and Ropes 1969, Ropes 1978). A. islandica was first fished commercially in 1943 (Merrill and Tubiash 1970); however the fishery remained small and for many years was centered in the State of Rhode Island. The last decade has been notable for a marked increase in the size of the fishery for A. islandica. In turn this has stimulated research efforts directed towards the provision of data adequate for formulation of a fishery management plan. Several recent reports have described the growth rate and advanced age of sexual maturity in A. islandica (Thompson et al. 1980a and b, Ropes and Murawski 1980). The present manuscript describes recent field studies of the gonadal cycle of adult A. islandica on the Southern New England Shelf and laboratory studies of the growth and development of the larval forms of A. islandica.

A. islandica occupies a bathymetric range in the Middle Atlantic Bight that corresponds approximately to that of the seasonal "cold pool" of water described by Bigelow (1933), and Ketchum and Corwin (1964). This "cold pool" extends from approximately 30 m depth to in excess of 100 m and is bounded in shallower water by an intense seasonal thermocline that persists from May until September. The annual temperature range experienced by benthic fauna in the "cold pool" (2-13°C) is considerably less than that above the thermocline (2-25°C). The objectives of the field study were to document the seasonal gonadal cycle of adult A. islandica, to infer from this data the period of most intense spawning activity, and to examine possible relationships between the periodicity of spawning and seasonal changes in water temperature. The results of the field study facilitated design of subsequent laboratory experiments to both describe larval development in A. islandica and examine the influence of temperature on rate of larval growth.

METHODS

Field Studies:

During the period September 1978-May 1980 14 collections of A. islandica were made at intervals of 4-8 weeks at stations in the depth range 27-50 m in the vicinity of Block Island, Rhode Island. A commercial hydraulic dredge (blade width 1.54 m, pump pressure 5.63-7.0 kg/sq cm, 7.5 cm diameter ring size) was used during the period September 1978-August 1979. A non-hydraulic dredge (blade width 0.62 m, 5.0 cm diameter ring size) was used during September 1979-June 1980.

The clams were opened on board the vessel and the gonadal tissue removed and fixed. Histological preparation of the fixed tissue (Humason 1962, Mann 1979) included imbedding in paraffin, sectioning, and

Hematoxylin-Eosin staining. Slide preparations were examined microscopically for evidence of gametogenesis and spawning using the report of Loosanoff (1953) for comparative purposes, and subsequently classified into one of five categories of gonadal condition using the criteria developed by Holland and Chew (1974) for Tapes japonica (i.e., early active, late active, ripe, partially spent and spent).

At each station on each collection date a vertical profile, from surface to bottom at 5 m intervals, was made of temprature and conductivity. The latter values were subsequently converted to salinity.

Laboratory Studies:

Both Loosanoff (1953) and Landers (1976) were unable to induce spawning of A. islandica in the laboratory. Attempts to induce spawning using either temperature shock (Loosanoff and Davis 1963) or hydrogen peroxide stimulation (Morse et al. 1977) in the present study were generally unsuccessful. Consequently eggs were stripped from ripe females, pretreated with ammonium hydroxide as recommended by Landers (1976) (30 minutes exposure to a solution of 3 mls of 0.1 N NH_4OH per 100 ml of egg suspension) and fertilized with stripped spermatozoa.

Five separate groups of larvae were reared to metamorphosis. One (#1) was reared by the Wells-Glancy method at the Virginia Institute of Marine Science Laboratory at Wachapreague, VA, and four (#2-5) were reared by a modification of the methods of Loosanoff and Davis (1963) at Woods Hole Oceanographic Institution, Woods Hole, MA. Culture conditions for each larval group are summarized in Table 1.

Table 1. Culture conditions for rearing of larval Arctica islandica.

Group #	1	2	3	4	5
Culture volume (L)	40	4	50	12	12
Larval density (#/ml)	1-2	2	6	6	6
Temperature (°C)	12.7-13.0	12.0-14.5	11.0-13.5	13	8.5-10°C
Salinity (°/oo)	32-34	32	32	32	32
Food concentration	100 cells/µl mixed sp.	50 cells/µl Isochrysis galbana + 50 cells/µl Pavlova lutheri			
Frequency of (days) Water change	2	3	3	3	3

At frequent intervals (each water change with culture #1, every second or third water change with other cultures) a subsample of larvals was examined under a compound microscope equipped with a ocular micrometer and measurements of length, height and straight hinge length made. The total numbers of larvae measured for cultures one through five respectively were 450, 98, 91, 39 and 143. Length versus height regressions for larvae from each culture were compared using separate analyses of covariance.

Larvae in culture #1 metamorphosed in the larval culture vessel. Larvae in cultures #2-5 were, on the appearance of the pediveliger stage of development, transferred to plastic petri dishes where they subsequently metamorphosed. Following metamorphosis culture #1 was maintained at 12.5-13.0°C for five weeks before being transferred to running, coarsely filtered (50 μ) sea water for over winter growth (temperature range: 9°C in November 1980, to -1°C in January 1981, to 14.3°C in April 1981). In April 1981 juveniles from culture #1 were returned to a temperature controlled (12.5-13.0°C) laboratory system. Juveniles from cultures #2-5 were maintained at 12-13°C in closed systems (1 μ filtered sea water changed twice per week, fed on 50 cells/μl of Isochrysis galbana) for 16 weeks and subsequently transferred to running, temperature controlled (11-13°C) sea water. Measurements of length and height were made infrequently on all juveniles following metamorphosis.

RESULTS

Field Studies:

A. islandica is dioecious. Of the 667 individuals examined only two were hermaphrodite, these containing spatially separate developing male and female follicles. The sex ratio of the sample, omitting the two hermaphrodites, was 1♂: 0.91♀. This is not significantly different from a 1:1 sex ratio. The animals examined ranged in size from 62-110 mm in length, predominantly (>80%) in the size range 80-100 mm. No attempt was made to examine the relationship of sex ratio to size.

Serial sectioning of gonadal tissue suggested that gonadal maturation occurred initially in tissues at the dorsal extremity, and progressively later moving toward the ventral extremity. Multiple spawning in one animal during one annual cycle originating from tissues in a similar spacial sequence was evident. No evidence was found of a second maturation of spent gonadal tissue during one annual cycle.

Table 2 summarizes observed gonadal conditions in mid-ventral sections taken from A. islandica at all stations during the study. Differences observed between different stations on any one chosen date were small, therefore data has been pooled for simplicity. Early active development began in male clams in February. Most ripe males occurred from May through September. Partially spent male clams were found from May through November and in January 1979. Early active female development began in

Table 2. Number of A. islandica in each gonadal development stage by date for the period September 1978-May 1980. Stage description EA, early active; LA, late active; R, ripe; PS, partially spent; S, spent.

	♂						♀					
Date	EA	LA	R	PS	S	n	EA	LA	R	PS	S	n
9/78	0	0	5	4	8	17	1	2	3	5	8	19
11/78	0	0	3	17	9	29	0	0	2	6	15	23
1/79	0	0	0	2	3	5	0	0	0	4	11	15
3/79	3	7	0	0	2	12	0	0	0	5	8	13
5/79	8	6	0	0	10	24	1	0	1	3	8	13
6/79	1	31	54	14	4	104	0	1	21	39	29	90
8/79	1	0	24	28	10	63	0	1	6	29	16	52
9/79	0	0	5	5	1	11	0	0	1	6	1	8
11/79	0	0	0	2	4	6	0	0	0	2	7	9
1/80	0	0	0	0	14	14	0	0	0	1	13	14
2/80	12	1	0	0	1	14	1	1	0	4	10	16
3/80	7	4	0	0	4	15	1	0	0	2	7	10
4/80	3	10	1	0	6	20	2	0	0	2	17	21
5/80	0	5	5	3	2	15	0	0	6	6	3	15
						349						318

May of 1979 and February of 1980. Ripe females were present from May through October. The onset of spawning was marked by a substantial increase in the proportion of partially spent animals that continued throughout the spawning period. A prolonged spawning season from May through November, with peak activity from August through November, was indicated.

An intense seasonal thermocline was initiated in April-May and reached a maximum intensity between 20 and 30 m depth in August (Figure 1). Surface waters cooled during the fall months of September and October, and, following the breakdown of the thermocline in November, uniform temperature structure throughout the water column was recorded through the winter months until the following April. Salinity values were slightly lower at the surface during the summer months (e.g., 31.59°/oo versus 32.85°/oo in July) but relatively stable throughout all depth and stations in the winter months (32.30% to 33.52°/oo range).

Laboratory Studies:

The "stripped" ova of A. islandica possess distinct egg capsules that frequently confine the developing embryo up to at least the 16 cell stage. The capsule confers some asymmetry on the fertilized egg, the diameter of which ranged from 75-90 µm. The mean length of the smallest shelled stage (prodissoconch I) was 107.1 µm (n = 50 s.d. = 5.3 µm). As shell length reached 150 to 165 µm the hinge line was obscured by the appearance of a low, rounded umbo. With subsequent growth the larvae assumed a distinctly circular appearance when viewed laterally being slightly more pointed at the anterior than posterior end. The pediveliger foot became functional at a length of 230 µm and metamorphosis occurred at a mean length of 259.3 µm (n = 100 s.d. = 13.1 µm).

No significant differences (5% confidence level) were recorded in either slope or elevation of the length versus height regressions for larvae from any of the individual larval cultures. A combination of all individual measurements was made and a common regression line calculated. This yielded the relationship.

$$\text{shell height } (\mu) = [1.02 \times \text{shell length } (\mu)] - 30.0 \quad (n = 821\ r = 0.99)$$

Larval growth rate appeared to be relatively independent of feeding regime, size of culture vessel, frequency of water change, and site and date of origin of parent stock; however, a strong influence of temperature was evident. Cultures #1-4, reared at mean temperatures of approximately 13°C, reached metamorphosis in 32-35 days; however culture #5, reared at a mean temperature of 9°C, required a minimum of 53 days to reach metamorphosis (Figure 2).

Shortly after metamorphosis the valves became an opaque white and a large exhalant siphon began to form. At 1 mm length the exhalent siphon was partially surrounded by the developing tentacles of the tentacular

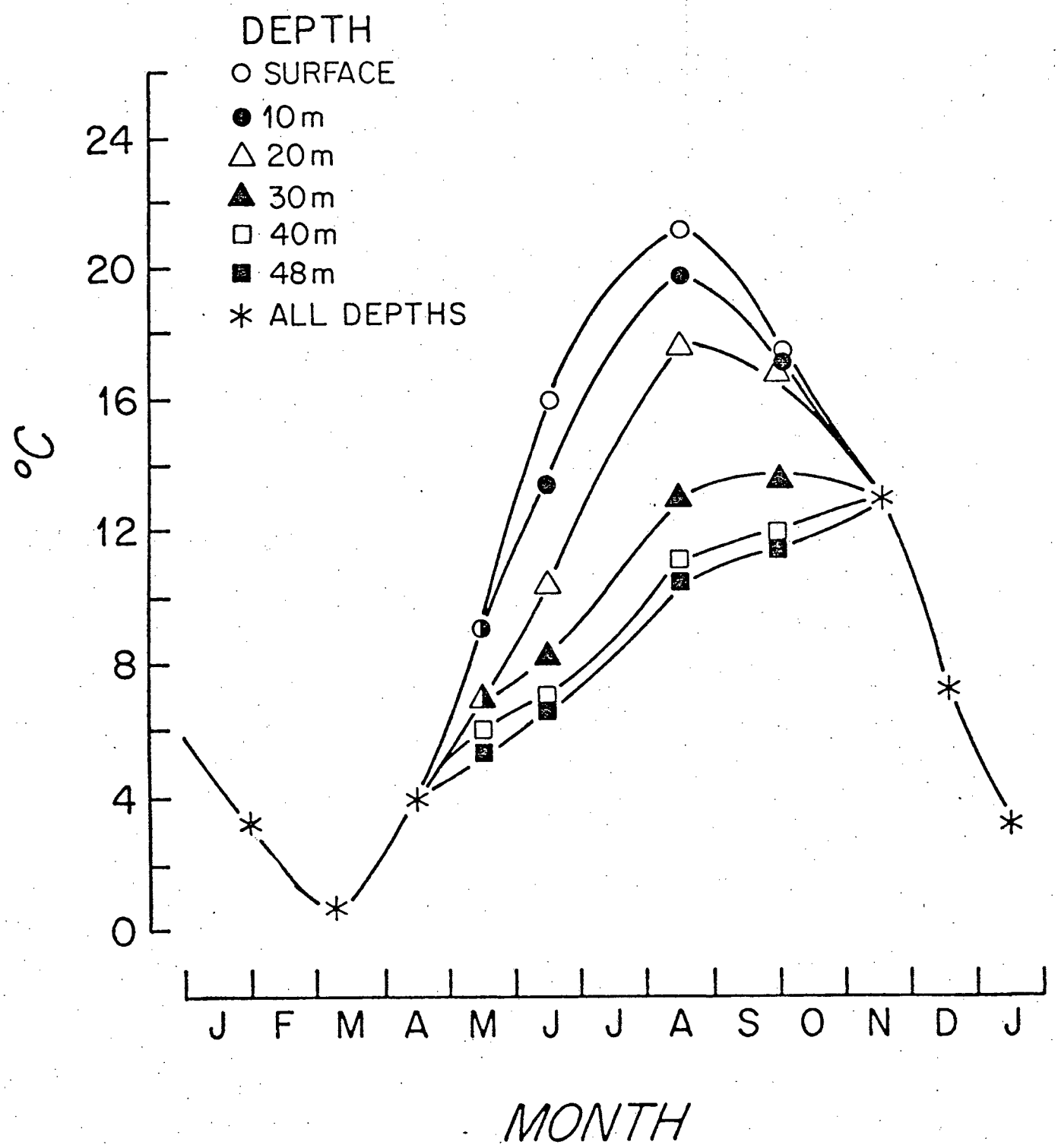

Figure 1. Seasonal changes in sea water temperature at 10 m intervals at one of the adult collection sites during September 1978-May 1980. For simplicity data have been pooled and are presented on a single annual cycle. Data are considered representative of all collection sites.

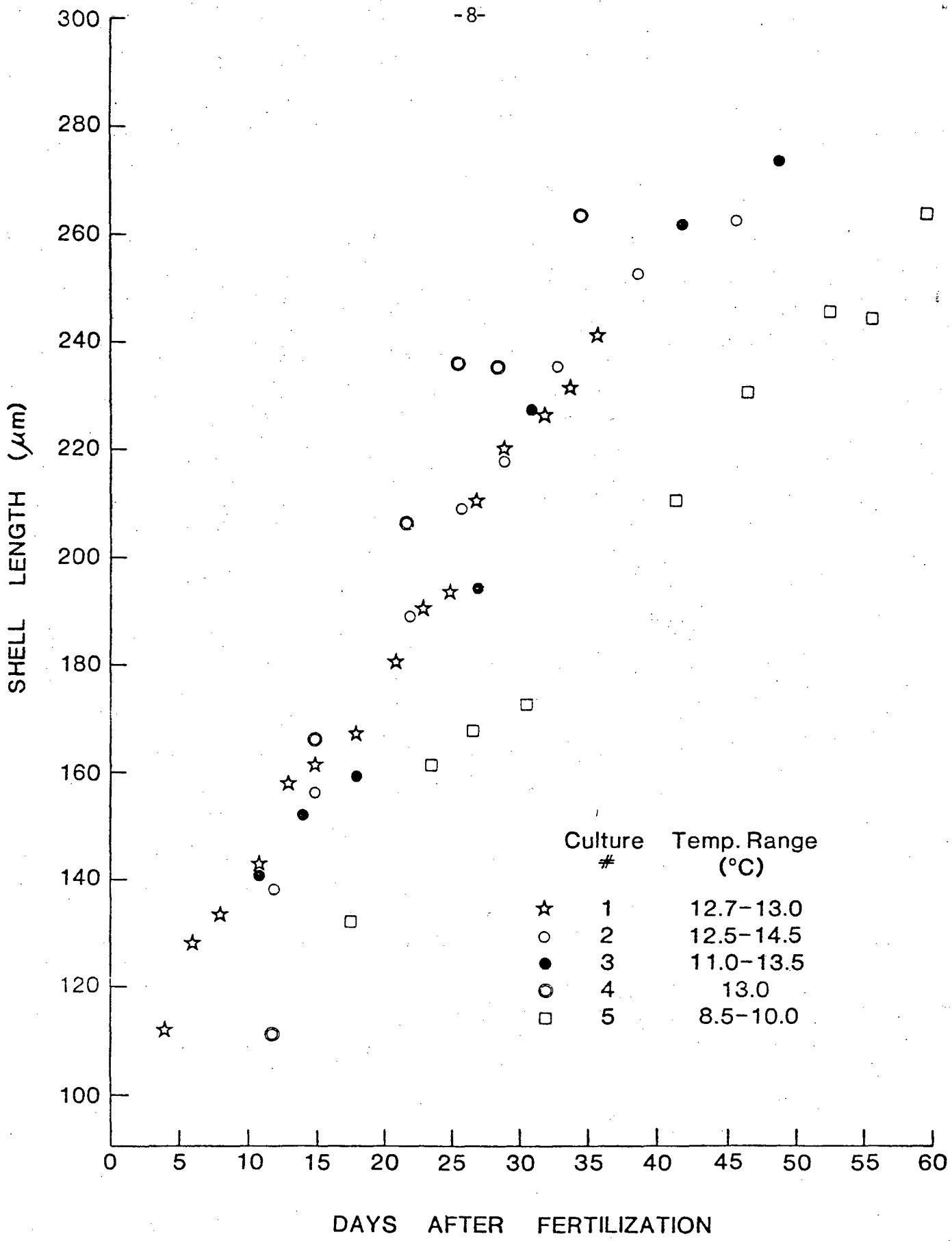

Figure 2. Growth of five groups of A. islandica larvae under various culture conditions (see Table 1). All values are mean of 10-30 individual measurements.

ring that completely surrounds both inhalant and exhalant siphons of the adult form. The inhalent region was marked by a juxtaposition of the mantle edges ventral to the exhalant siphon. The foot was extendable to a length equal to at least that of the shell length. At 2-3 mm the inhalant siphon had formed but, unlike the exhalant siphon, it was not extensable. The number of tentacles in the ring surrounding the siphons continued to increase. At 6 mm length the perostracum has assumed the characteristic dark yellow coloration common in smaller adults collected from the field. The active foot was still present. Some reduction in the size of the exhalant siphon had occurred and surrounding tentacular ring was fully formed. The characteristic lunule of the adult was present, and both valves exhibited regular external ridges.

DISCUSSION

The field data of the present study on the gonadal cycle of A. islandica are generally in agreement with those of Loosanoff (1953), who examined A. islandica from commercial catches at Point Judith, Rhode Island during the months of March to November, with respect to both the period of spawning and the lack of a significant "resting" or "indifferent" period in the annual gonadal cycle. The sequential ripening and spawning of gonadal tissue in a dorsal to ventral direction was not reported by Loosanoff (1953). The occurrence of multiple spawning conflicts with the statement of Thompson et al. (1980a) with respect to A. islandica that "All individuals spawned once and only one in each of the two years studied." Jones (1980) is quoted as the source of the documentation substantiating the quoted statement. This is somewhat surprising in that Jones (pers. comm. 1980) also found sequential development and the presence of a large proportion of partially spent individuals of both sexes in samples collected in the late summer and fall months. Both of Jones' observations add further support to multiple spawning at the individual level during each annual cycle.

The nature of the spawning stimulus in A. islandica remains open to discussion. Loosanoff (1953) suggested that spawning was initiated at a water temperature of 13.5°C; however, Table 2 and Figure 1 indicate that spawning can occur over a range of temperatures from 8-13°C suggesting that absolute temperature per se is probably not the ultimate spawning stimulus. Furthermore, the unsuccessful use of temperature stimuli in spawning A. islandica in laboratory studies is probably not surprising considering the fact that the deep, infaunal habitat of this species is comparatively well damped from short term environmental fluctuations.

The coincidence of the period of maximum spawning activity (August-October) with the decline and breakdown of the seasonal thermocline may be of considerable significance to the reproduction of A. islandica. A marked increase in percentage oxygen saturation in bottom water occurs at this time (Williams and Godshall 1977). Changes in dissolved oxygen levels have been invoked as spawning stimuli in deep water pelecypods

elsewhere (Ansell et al. 1978) and may be of significance, in conjunction with small changes in water temperature (Figure 1) and pH (R. Mann, unpublished data) in stimulating spawning in A. islandica in Southern New England waters. Also, absolute water temperatures at this time are both conducive to relatively fast growth of the larval forms (Figure 2), and remain sufficiently high throughout September and October to insure that the majority of larval forms are not prevented from reaching metamorphosis by temperature alone. The question remains as to the fate of larvae spawned prior to the period of thermocline breakdown in that the data of Landers (1976) suggests that the larvae of A. islandica cannot survive to metamorphosis at temperatures in excess of 15°C, and that of Mann and Wolf (1981, unpublished observations) suggests that A. islandica veligers will not swim through thermoclines in laboratory systems where absolute water temperatures in excess of 18-20°C are encountered. The possibility of A. islandica veligers maintaining station below a seasonal thermocline by means of a pressure (i.e., depth) modulated behavioral response cannot be discounted (see also Carriker 1961, Wood and Hargis 1971, and Cragg and Gruffydd 1976). Both laboratory experimental programs to examine the pressure response of A. islandica veligers and field programs to investigate seasonal depth distribution of A. islandica larvae are in progress at this time with the specific objective of providing further information on how the larval biology of A. islandica is related to the seasonal spawning activity and hydrography of the Middle Atlantic Bight.

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