

THE SEASONAL CYCLE OF GONADAL DEVELOPMENT IN *ARCTICA ISLANDICA* FROM THE SOUTHERN NEW ENGLAND SHELF¹

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ABSTRACT

The seasonal cycle of gonadal development of the ocean quahog, *Arctica islandica*, on the Southern New England Shelf was investigated by collecting adult clams at regular intervals from September 1978 to May 1980 from a 36-50 m depth transect, preparing histological sections of the gonadal tissue, and examining these microscopically for stages of development. Hydrographic measurements made concurrently with the clam collections included temperature, conductivity, dissolved oxygen, and pH. Morphologically ripe specimens were present from March through October, but predominated from May through September. A prolonged spawning period from May through November is indicated, spawning being most intense from August through November. Multiple annual spawnings at both the individual and population level were evident. After an assessment of the hydrographic conditions in the area it was hypothesized that larval survival is probably greatest during the months of October and November, which is the time of the breakdown of the intense seasonal thermocline and before the onset of low winter seawater temperatures.

Ocean quahog, *Arctica islandica* (= *Cyprina islandica*), is a large pelecypod that occurs in European waters from the White Sea to Spain (Jensen 1902; Loven 1929; Zatsepin and Filatova 1961; Punin 1978) and in American coastal waters from Newfoundland to Cape Hatteras (Nicol 1951; Merrill and Ropes 1969; Ropes 1978). The species supports an active fishery in the Middle Atlantic region and has been the subject of much recent study (Murawski and Serchuk 1979; Thompson, Jones, and Dreibelbis 1980; Thompson, Jones, and Ropes 1980; Ropes and Murawski 1980). In the Middle Atlantic region the greatest concentrations of *A. islandica* are found in depths of 25-61 m with the mean depth of occurrence increasing from 39 m off Long Island to 52 m off Virginia and North Carolina (Merrill and Ropes 1969; Ropes 1978).

The seasonal temperature structure of the waters of the Middle Atlantic region was first comprehensively described by Bigelow (1933) and has subsequently been the subject of many investigations and reviews (Walford and Wicklund 1968; Colton and Stoddard 1973; Bumpus 1973; Beardsley et al. 1976; Williams and Godshall 1977). Two important features are evident: An intense summer thermocline that builds in May and persists until September, and a "pool"

of cold water (annual temperature range 2°-13°C), surrounded on both the inshore and offshore sides by warmer water, that develops on the continental shelf below the thermocline during the spring, summer, and early fall months (Ketchum and Corwin 1964; Bowman 1977). The cold pool of bottom water in the summer months overlies much of the depth range occupied by *A. islandica*. Maximum water temperatures on the sea floor in the depth range occupied by *A. islandica* occur in September and October (Bigelow 1933), and a strong relationship exists between the 16°C bottom isotherm for October and the inshore distribution limit of *A. islandica* (Bigelow 1933, figs. 49, 60; Merrill and Ropes 1969, fig. 2).

Loosanoff (1953) described the reproductive cycle of *A. islandica* based upon specimens collected regularly from commercial catches at Point Judith, R.I., from March to November (a complete annual cycle was examined but not reported). Following histological preparation and microscopic examination of the specimens, Loosanoff concluded that histological "Spawning begins near the end of June or early in July when the water temperature is approximately 13.5°C." The conclusion was based on temperature data inferred from earlier observations by Merriman and Warfel (1948). Loosanoff (1953) also concluded that spawning continued through August, and that approximately 50% of *A. islandica* examined were totally spent by early October. The larvae of *A. islandica* have been reared

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to metamorphosis by Landers (1976) and Lutz et al. (in press). Landers (1976) reported that fertilization and early cleavage were obtained at 10°, 15°, and 20°C; however, embryos only survived to the veliger stage at the two lower temperatures, and to metamorphosis at 10°-12°C. The cultures reared by Lutz et al. (in press) were maintained to metamorphosis at temperatures ranging from 9° to 13°C; but none of these investigators defined the maximum temperature at which metamorphosis could be effected.

After reviewing data on seasonal water temperature structure in the Middle Atlantic Bight and the reproductive biology of *A. islandica* reported by Loosanoff (1953) and Landers (1976), certain inconsistencies were evident. It has long been suspected that bivalve larvae can partially control their position in the water column by swimming (Carriker 1961; Wood and Hargis 1971; Cragg and Gruffydd 1975). If *A. islandica* spawn in July, then larvae swimming upwards to the regions of highest primary productivity, and hence phytoplankton food, would encounter both an intense thermocline at 20-30 m depths and surface temperatures in excess of 20°C. Both temperature conditions would be either deleterious to growth or even lethal according to Landers (1976). Therefore, it would appear appropriate to hypothesize that spawning in October or November would be more congenial to larval survival because, after the fall thermocline breakdown and subsequent vertical mixing of the water column, vertical movement of the larvae would not be limited by an intense thermocline. Furthermore, any temperature stratification that did exist at this time would have widely spaced vertical isotherms and thus form only weak barriers to horizontal dispersion.

A need was evident to simultaneously assess the reproductive cycle of the adult *A. islandica* and hydrographic conditions affecting it and larval survival. This study describes the gametogenic cycle of adult *A. islandica*, based on microscopic examination of histological preparations from individuals collected regularly from several depths over a 2-yr period, and concurrent physical data collected during the same period.

METHODS AND MATERIALS

Fourteen collections of *A. islandica* were made at intervals of 4-8 wk from September 1978

to May 1980 at depths ranging from 27 to 50 m in the vicinity of Block Island, R.I. Stations at 27-30 m depth (Station A) were north and east of Block Island (lat. 41°19'N, long. 71°34'W and lat. 41°13'N, long. 71°32'W, respectively). Stations at 36, 42, and 48-50 m (Stations B-D, respectively) were on a transect directed due south at long. 71°31'W at lat. 41°11'N, 41°03'N, and 41°01'N, respectively. Specimens were collected with a commercial hydraulic clam dredge (blade width 1.54 m, pump pressure 5.63-7.0 kg/cm², 7.5 cm diameter ring size; tows of 5-min duration) during the period September 1978-August 1979 and with a nonhydraulic clam dredge (blade width 0.62 m; 5.0 cm diameter ring size; tows of 20-30 min duration) during September 1979-June 1980. Both dredges were selective for clams larger than the diameter of the rings.

The clams were opened on board the vessel and either the soft tissues removed whole, or a section of tissue approximately 1 cm² excised from the surface of the midventral region. The tissues were preserved in Bouins fixative for 24-48 h, rinsed in water for 6 h, and stored in 70% ethanol. Histological preparation of tissue sections included embedding in paraffin, sectioning at 7 μ , staining with Delafield's hematoxylin, and counterstaining with eosin Y by the procedure of Humason (1962). A minimum of 15 specimens was examined from the midventral samples collected on each collection date. An additional five specimens of whole animals from each collection date were examined in tissue excised from each of the dorsal, midventral, and ventral regions in order to assess the uniformity of development throughout the gonadal tissue. Slide preparations were examined microscopically for evidence of gametogenesis and spawning (Holland 1972), and each was classified into one of five categories of gonadal condition, by the criteria of Holland and Chew (1974) as follows:

Early active:

Male: Many follicles: spermatogonia and spermatocytes numerous, no spermatozoa.

Female: Oogonia arising from stem cells along the follicle; no free oocytes. Nuclei stain darker than cytoplasm.

Late active:

Male: Follicles contain predominantly spermatids and spermatozoa.

Female: Both free and attached oocytes present. Oocytes have nuclei that stain

lighter than cytoplasm and a distinct nucleolus.

Ripe:

Male: Follicles filled with spermatozoa in swirling patterns.

Female: Predominantly free oocytes with distinct nucleus and nucleolus.

Partially spent:

Male: Follicles disorganized and often empty. Some full follicles remaining.

Female: Follicles disorganized. Some mature ova remaining, some undergoing cytology.

Spent:

Male: Follicles disorganized and empty, few spermatozoa remaining.

Female: Follicles disorganized and empty, few ova remaining.

The report of Loosanoff (1953) was used for comparison throughout the procedure. The classification of gonadal development into stages is, by definition, qualitative. A quantitative option of describing female gonadal development as a function of mean ova diameter was considered inapplicable in the present study because ova were often elongated or otherwise nonspherical in shape, especially during development from oogonia to oocytes.

Hydrographic measurements were made at each station on each collection date. A vertical profile, from surface to bottom at 5 m intervals, was made of temperature and conductivity using either a model 6D or S8000 Hydrolab Water Quality Analyser (Hydrolab Corporation, Austin, Tex.)³ and the conductivity measurements were converted to salinity. On six occasions these data were supplemented by vertical profiles of dissolved oxygen content and pH measured with the same instrument.

RESULTS

Hydrographic Observations

Figure 1 depicts the seasonal temperature structure of the water column at Stations A-D. No marked differences were recorded between the 2 yr of the study; hence data have been pooled. An intense seasonal thermocline was initiated in April-May and reached a maximum intensity at

between 20 and 30 m depths in August. Surface waters cooled during the fall months of September and October. A uniform temperature structure throughout the water column was evident from November through April.

The intense nature of the thermocline and its relationship to depth at sample stations (A-D) is illustrated in Figure 2 for August 1979. Maximum bottom temperatures recorded at Stations A-D, respectively, were 15.4°, 14.0°, 12.9°, and 12.6°C, and they occurred earliest at the two shallower stations.

Salinity values recorded during the study agreed well with those reported previously by Ketchum and Corwin (1964). Surface to bottom salinities increased from 30.90‰ to 32.08‰ during July at Station A and from 31.59‰ to 32.85‰ at Station D. Salinities were highest but relatively stable throughout all depths and stations during the winter months (all values ranged from 32.30‰ to 33.52‰).

Dissolved oxygen data were in general agreement with those summarized for the Middle Atlantic region by Williams and Godshall (1977). Surface waters to 20 m depth were at or within 10% of saturation throughout the year. A gradual decline in percentage saturation was evident below the seasonal thermocline from April to late August (Fig. 3A). This was most obvious immediately adjacent to the sediment-water interface where a minimum dissolved oxygen level of 65% saturation was recorded at Station D in August 1979. Concurrently pH also decreased reaching a minimum of 7.9 (Fig. 3B) at the sediment-water interface at all stations in August 1979.

Gonadal Observations

Arctica islandica is dioecious. Out of 669 specimens, hermaphroditism was found in only 2 individuals which contained spatially separate developing male and female follicles (Fig. 4). Serial sectioning indicated that gonadal maturation occurred initially in tissues at the dorsal extremity of the gonadal mass and progressively later moving toward the ventral extremity (Fig. 5). Multiple spawnings in the same animal during one annual cycle, originating from tissues in a similar spatial sequence, were suggested by the presence of spent follicles in dorsal sections, while follicles in the ventral sections of the same specimen were in late active or ripe condition. No evidence was found of a second maturation of spent, dorsal gonadal follicles following spawn-

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

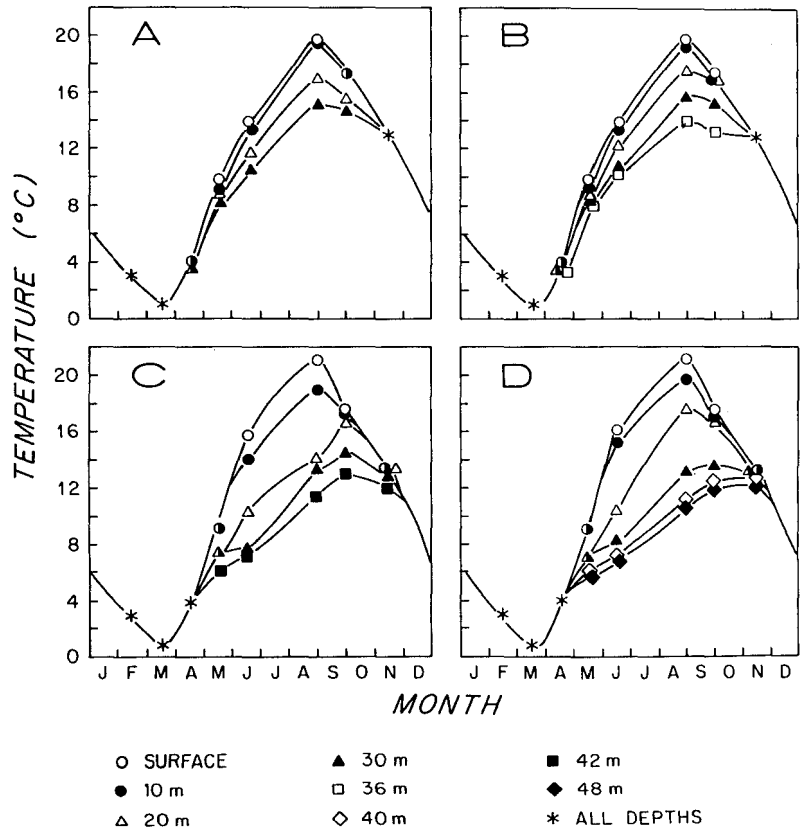


FIGURE 1.—Seasonal changes in seawater temperature at 10 m intervals at Stations A-D during September 1978-May 1980. For simplicity 2 yr of data have been pooled and are presented on a single annual cycle.

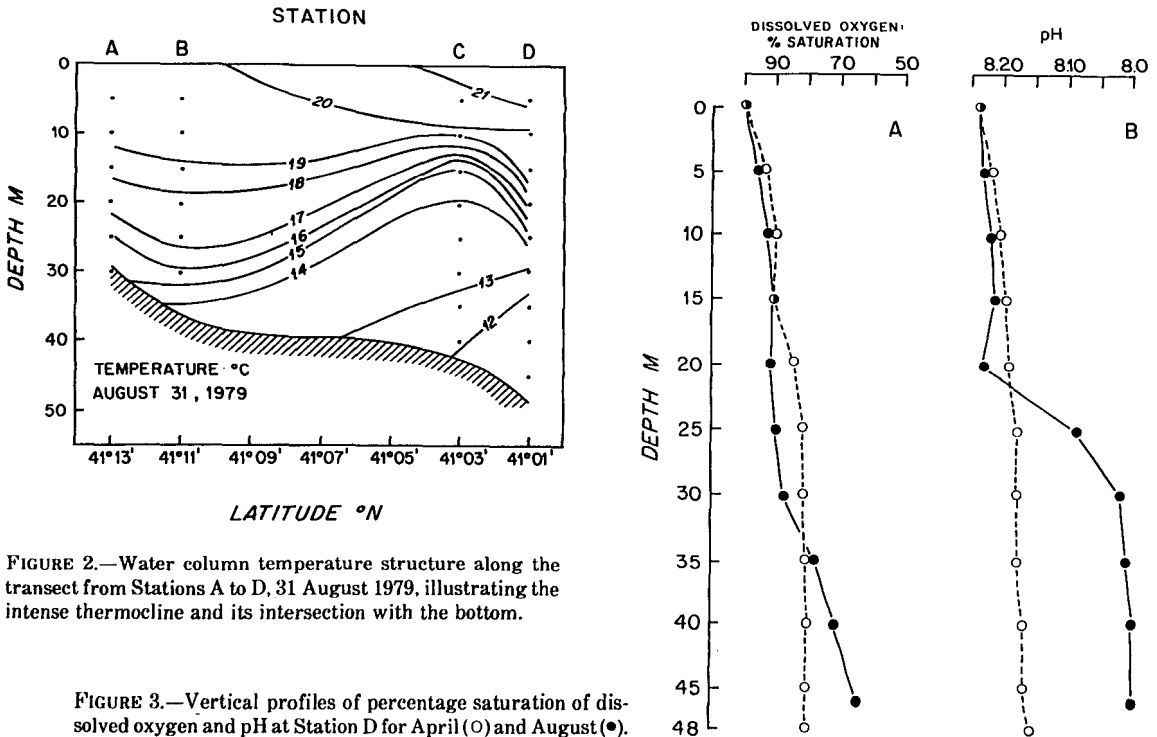


FIGURE 2.—Water column temperature structure along the transect from Stations A to D, 31 August 1979, illustrating the intense thermocline and its intersection with the bottom.

FIGURE 3.—Vertical profiles of percentage saturation of dissolved oxygen and pH at Station D for April (O) and August (●).

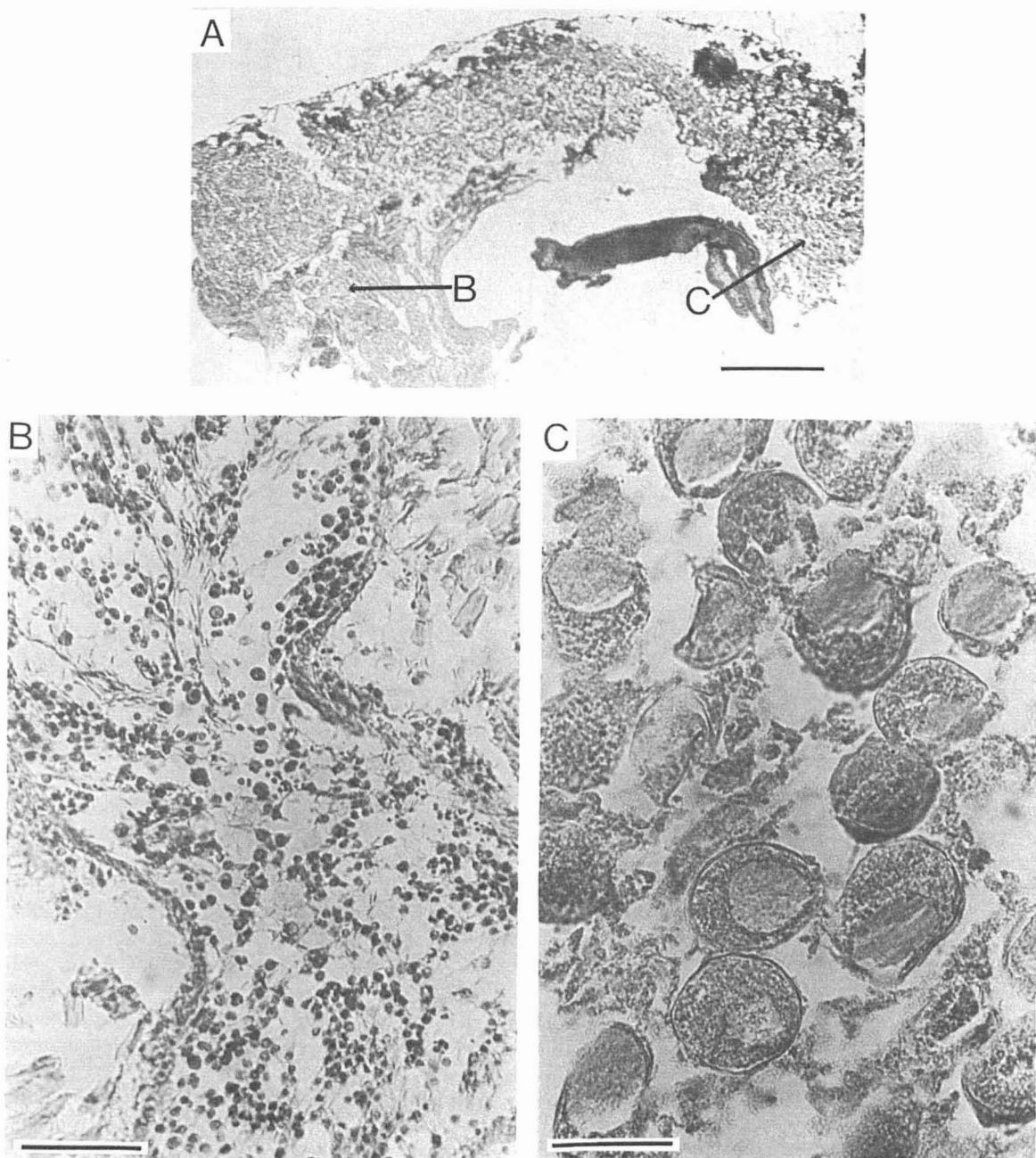


FIGURE 4.—Midventral sections of hermaphrodite *Arctica islandica* collected at Station A, 2 January 1980. A. Section illustrating spatially separate male (B) and female (C) gonadal tissue. Scale bar 1 mm. B. Expanded view of male gonadal tissue illustrating spent male follicle. Scale bar 50 μ . C. Expanded view of female gonadal tissue illustrating degenerating ova. Scale bar 50 μ .

ing during one annual cycle in either of the two years when observations were made. Gonadal maturation, then, probably occurs only once per year in each individual clam. The mean diameter of the ova taken from histological sections of ripe

female clams was 52.4 μ ($n = 59$ ova). This compares with a value of 66.3 μ ($n = 22$ ova) obtained from unfertilized eggs stripped from ripe, live animals. The disparity between preserved and live material in the present instance is probably

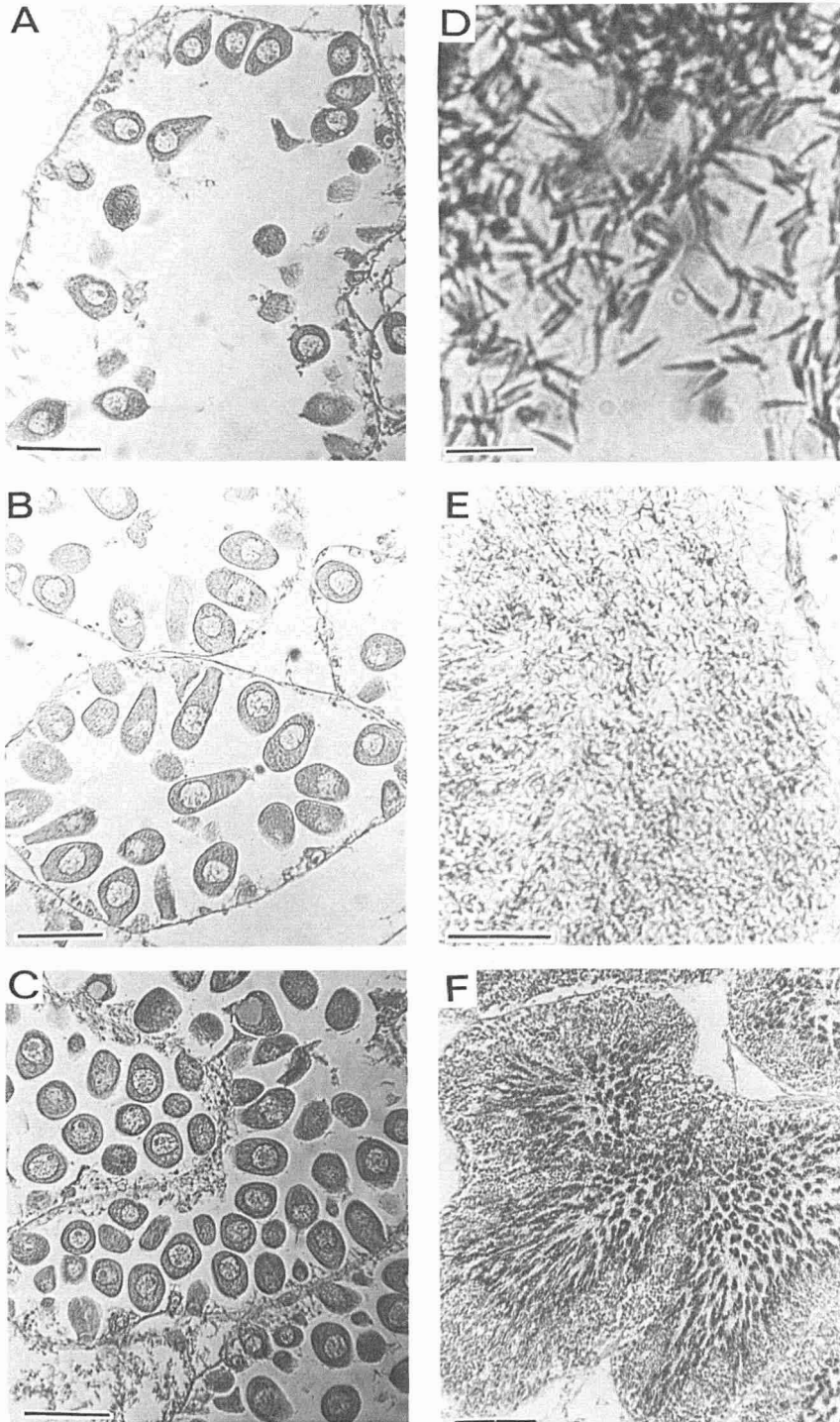


FIGURE 5.—Sequential development of gonadal material in the dorsal-ventral plane in *Arctica islandica*. A. Female, dorsal section, spent gonadal tissue. Scale bar 100 μ . B. Female, midventral section, partially spent gonadal tissue. Scale bar 100 μ . C. Female, ventral section, ripe gonadal tissue. Scale bar 100 μ . Preparations A-C from one clam. D. Male, dorsal section, ripe spermatozoa. Scale bar 10 μ . E. As for D except scale bar 50 μ . F. Male, ventral section, late active development. Scale bar 100 μ . Preparations E and F from one clam. Both clams from Station D, 15 June 1979.

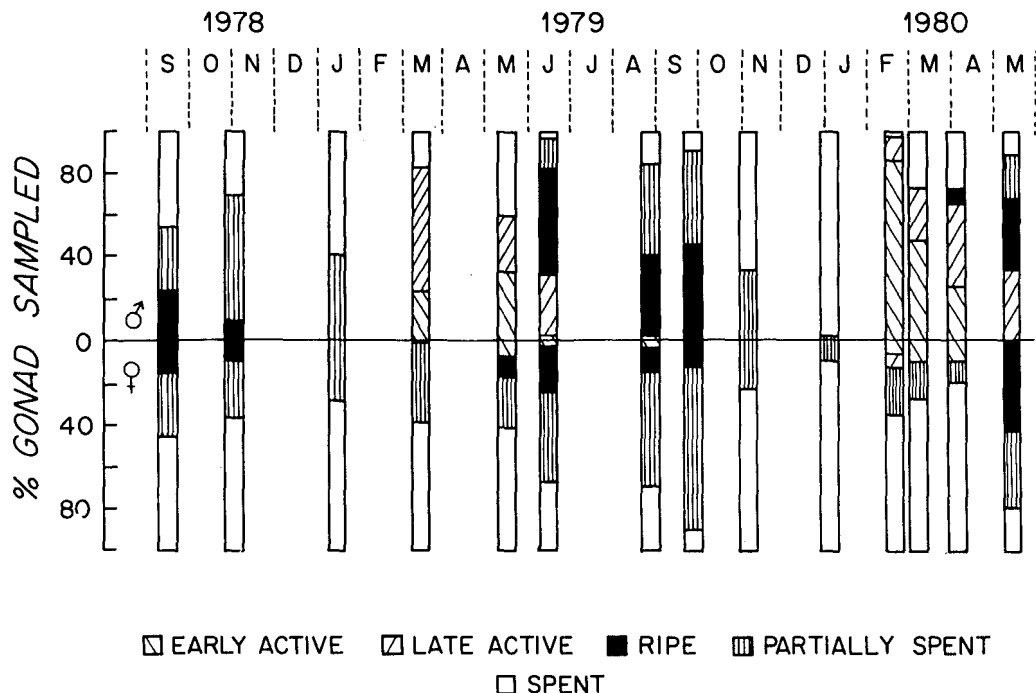


TABLE 1.—Numbers of *Arctica islandica* in each gonadal development stage by date for the period September 1978-May 1980: Data are pooled for shallow (A, B) and deep (C, D) stations, respectively. Stage description: EA, early active; LA, late active; R, ripe; PS, partially spent; S, spent.

Date	Station	♂						♀					
		EA	LA	R	PS	S	n	EA	LA	R	PS	S	n
9/78	A + B			2		2	4	1	2	1	1	1	6
	C + D			3	4	6	13			2	4	7	13
11/78	A + B					8	4	12		2	5	10	17
	C + D			3	9	5	17			1	5	6	6
1/79	A + B					2	3	5					
	C + D	(¹)									4	11	15
3/79	A + B						2	12					
	C + D	(¹)	3	7							5	8	13
5/79	A + B						10	24	1		1	3	8
	C + D	(¹)	8	6									13
6/79	A + B		1	11	27	11	4	54			11	16	17
	C + D			20	27	3		50	1	10	23	12	46
8/79	A + B					14	14	8	36		5	8	10
	C + D		1		10	14	2	27	1	1	21	6	29
9/79	A + B					1	4	1	6		1	3	5
	C + D					4	1		5		3		3
11/79	A + B						2	4	6			2	7
	C + D	(¹)											9
1/80	A + B						14	14			1	13	14
	C + D	(¹)											
2/80	A + B		12	1			1	14	1	1		4	10
	C + D	(¹)											16
3/80	A + B		7	4			4	15	1			2	7
	C + D	(¹)											10
4/80	A + B												
	C + D	(²)	3	10	1		6	20	2		2	17	21
5/80	A + B			1	3	3		7			2	3	5
	C + D			4	2			2	8		4	3	10
Total								349					318

¹Dredging prevented by bad weather.

²No collection due to gear failure.

A total of 667 *A. islandica* were of separate sexes and the observed ratio of this sample was 1:0.91. These data are not significantly different from a 1:1 sex ratio. This analysis omits the two hermaphrodites. Recently, Thompson et al. (1980b) have described the advanced age for sexual maturity in *A. islandica*, and Ropes and Murawski (1980) have examined the size and age at sexual maturity of *A. islandica* collected from a depth of 53-55 m south of Long Island, N.Y. They found that individual *A. islandica* as large as 47 mm in length had undifferentiated gonads and males began producing germinal cells at a smaller size and younger age than females. Small individuals were rare in the present study. *Arctica islandica* caught with the hydraulic dredge ranged from 70 to 110 mm in shell length, but were predominantly (84% of total) from 80 to 100 mm. The smallest specimen caught in the nonhydraulic dredge measured 62 mm in length, but most specimens (80% of total) were 80-100 mm. A record relating the length of each clam examined to its gonadal development was not kept in the present study; therefore a relation-

ship between sex and length cannot be described. The present data on sex ratio differ from those of Jones (1980), who observed a sex ratio of 1:0.72 in a sample of 320 *A. islandica* of >75 mm individual length which were collected from offshore New Jersey during the period April 1977-March 1979.

DISCUSSION

Data describing water column physical characteristics are in general agreement with previous work in illustrating the seasonal, intense thermocline, and indicate that mixing across this phenomena is small during the summer months. Partial oxygen depletion below the thermocline during the summer is probably strongly related to biological activity.

The minor differences in gonadal development in *A. islandica* between stations is, at first, surprising considering the fact that the inshore, shallower stations (A and B) were consistently warmer than the offshore, deeper stations (C and D) (Figs. 1, 2, 6); however, an assessment of go-

nadal condition is subject to the following inherent inadequacies. First, a continuous gametogenic process is being described in discrete stages. Second, it is difficult to consistently obtain a midventral section that is a representative mean of the cline of gonadal developmental stages within one animal. Third, sample collections were relatively infrequent considering the small differential in bottom temperatures between the stations and the comparatively high rate of change of bottom temperature during the summer months (Fig. 1). It is probable that these three factors effectively combined to mask any depth-dependent difference in gonadal development.

Morphologically ripe specimens were present from March through October, but predominated from May through September. Although no morphologically ripe specimens were found in December or January—in contrast to the data of Loosanoff (1953)—the presence of partially spawned animals at this time, followed by the first appearance of early gametogenic stages in February and March, supports Loosanoff's hypothesis that no significant "resting" or "indifferent" period occurs in the annual gametogenic cycle. The sequential ripening of gonadal follicles from the hinge (dorsally) towards the foot (ventrally), in a manner similar to that described for *Mya arenaria* by Coe and Turner (1938), was not described by Loosanoff (1953). No examples of the "atypical" sperm development described by Loosanoff (1953) were observed in the present study. The present data are, however, not in complete agreement with the recent statement in Thompson, Jones, and Dreibelbis (1980), with respect to *A. islandica*, that "All individuals spawned once and once only in each of the two years studied." Jones (1980) is quoted as the source of documentation substantiating this statement. This is somewhat surprising in that, like the present study, Jones (1981) found some sequential gonadal 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 these observations support the conclusion that individual specimens spawn at least once per annual reproductive cycle.

It is relevant to speculate on the nature of the proximal stimuli (*sensu* Baker 1938) of gametogenesis and spawning in *A. islandica*, given the present physical and biological data, based on the extensive discussion of the subject by Baker

(1938) and Giese and Pearse (1974). *Arctica islandica* initiated gametogenesis in February when water temperature is lowest. This is in contrast to the more intensively studied intertidal species which either cease gametogenesis during the period of lowest temperature, e.g., *Mytilus edulis* in Northern Europe (Chipperfield 1953), or initiate gametogenesis only with rising water temperatures and at the time of the phytoplankton spring bloom, e.g., *Ostrea edulis* and *Crassostrea gigas* (Walne and Mann 1975). Ansell (1974), Gabbott (1975), and Mann (1979a, b) found that the initiation of gametogenesis in bivalves is often preceded by a period of accumulation of carbohydrate reserves which are subsequently used as a predominant respiratory substrate during gametogenesis and that this period of accumulation usually coincides with a period of high primary productivity and food availability. The author can find no data on seasonal phytoplankton productivity for the region immediately east and south of Block Island; however, substantial data are available for the lower Narragansett Bay (Hitchcock and Smayda 1977; Pratt 1965; Smayda 1957), Block Island Sound (Riley 1952b), and Long Island Sound (Smayda 1976). Lower Narragansett Bay is characterized by an intense winter (January to March) diatom bloom and a smaller, late summer to autumn (July to October) bloom (Smayda 1976). Block Island and Long Island Sounds exhibit a more classical spring and autumn bloom (Hitchcock and Smayda 1977; Smayda 1976). It is not unreasonable to suggest that phytoplankton from the autumn and winter blooms in Narragansett Bay are washed into Block Island Sound (Riley 1952a), and that, because of the vertically well-mixed nature of the water column at this time, both they and the phytoplankton from the classical spring and autumn blooms become available to *A. islandica*. Phytoplankton was probably made available by wind and storm events similar to those which effect the mixing and distribution of chlorophyll in the New York Bight and Georges Bank, as described by Walsh et al. (1978). In turn these blooms may be a potential food source for storage metabolism in *A. islandica* during the late fall, winter, and early spring months prior to and coincident with the initial stages of gametogenesis. Specimens collected throughout this period had both bright green digestive glands and a well-developed crystalline style indicative of active feeding on phytoplankton.

The precise nature of the spawning stimulus to *A. islandica* remains open to discussion. Loosanoff (1953) suggested that spawning was initiated at a water temperature of approximately 13.5°C; however, the data of Figures 1 and 6 indicate that absolute temperature per se is probably not the ultimate spawning stimulus. Furthermore, laboratory experiments to induce spawning by temperature shock alone have proved both inconsistent and usually unsuccessful (Loosanoff 1953; Landers 1976; Lutz et al. in press). Indeed, *A. islandica* has proven to be a very difficult species to spawn in laboratory systems. It also fails to respond to salinity and pH changes, the addition of suspension of sex products (Loosanoff 1953; Landers 1976), and the more recent method of Morse et al. (1977) involving exposure to alkaline seawater (pH = 9.1) and hydrogen peroxide (range of concentrations $2.5 - 5 \times 10^{-3}$ M) (Lutz et al. in press). While these methods of stimulating spawning have generally been very successful with many intertidal and shallow water species (Loosanoff and Davis 1963; Morse et al. 1977) which experience short-term (e.g., tidal) environmental fluctuations, their inapplicability to *A. islandica* is, perhaps, not surprising considering the fact that the deep, infaunal habitat of the species is comparatively well damped from short-term environmental fluctuations. Spawning occurred from May through November in field populations of *A. islandica*, and was heaviest during late August to October and at the time of the fall thermocline breakdown. Changes in bottom temperature coincidental with spawning occurred, but the rate and magnitude were small (Fig. 1). Clarke⁴ recorded a prolonged spawning season for *A. islandica*. His studies of *A. islandica*, which were collected from a similar temperature regime to the present study in depths of 20 m off Seabrook, N.H., indicated some spawning from June through October with the greatest intensity from August to October. The prolonged nature of the spawning season in field populations reinforces the conclusion that while a specific, absolute temperature may be an important spawning stimulus, it is probably effective only in conjunction with changes in other stimuli, such as increases in percentage saturation of oxygen, pH, and food availability.

Spawning stimuli other than temperature

have been reported by Ansell et al. (1978), who found a close correlation in the Clyde Sea area between an abrupt increase in bottom dissolved oxygen levels following a seasonal thermocline breakdown and spawning activity in the infaunal bivalve *Nuculana minuta*.

The fate of larval *A. islandica* spawned prior to the thermocline breakdown also remains open to discussion. The observations of Landers (1976), Wood and Hargis (1971), and Cragg and Gruffydd (1975) suggest that larvae in the early stages of development swim upwards and that substantial larval mortalities are probable from early spawnings, since, at least, temperatures too hot for survival would be encountered. To complete development successfully larvae spawned in June would have to remain below an intense thermocline through which little mixing occurs. This appears improbable. The inference is that a period exists during which the survival of larvae is limited by hydrographic events and that the larvae of *A. islandica* do not freely move throughout the entire depth of the water column until after the breakdown of the summer thermocline. Furthermore, the low winter water temperatures recorded in the Middle Atlantic Bight may also effectively depress continued development of larval stages spawned late in the fall months. Therefore the period during which the larvae of *A. islandica* survive to metamorphosis may be considerably shorter (approximately 2 mo, October and November) than that during which the adults are capable of spawning (7 mo, May to November).

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