

SIZE, AGE, SEXUAL MATURITY, AND SEX RATIO IN OCEAN QUAHOGS, *ARCTICA ISLANDICA* LINNÉ, OFF LONG ISLAND, NEW YORK

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ABSTRACT

Ocean quahogs, *Arctica islandica*, were collected off Long Island, New York, in 1978 for a determination of sexuality and gonadal condition. A microscopic examination of histologically prepared tissues of 133 clams, 19-60 mm in shell length, revealed that 36 were in an undifferentiated condition and could not be sexed. Sexual differentiation was evident in 97 clams; of the latter, 69 were in two types of intermediate development: those with sparse (20) and moderate (49) tubule development. Only 28 clams were fully mature. Age and growth were assessed from acetate peels of shell cross sections. Determinations of sex of these, and of specimens 57-103 mm in shell length collected from the same area in 1980, indicated that the smallest and youngest ocean quahogs were predominantly male, but the largest and oldest were predominantly female.

Ocean quahogs, *Arctica islandica*, like most other bivalves, lack external characteristics for a determination of sex, maturation, and gonadal condition. Sex determination has been made for other bivalves, such as the surf clam, *Spisula solidissima* (Ropes 1979a), from microscopic examinations of gametogenesis in histological preparations of gonadal tissues. Similar examinations were lacking for ocean quahogs. The resource has become an important fishery within the past half-decade (Ropes 1979b; Serchuk and Murawski 1980²).

In most bivalves that have been studied, sexual maturity occurs at a young age and small size, but species differences have been observed (Altman and Dittmer 1972). Thompson et al. (1980a, b) found that the ocean quahog is a slow growing, long-lived species which exhibits considerable variability in maturation with respect to size and age. The latter conclusion was based on examinations of 39 specimens, 87% of which were 40 mm or longer in shell length. The samples were collected in April-May, 3-4 mo before the spawning period reported for this species by Loosanoff (1953). It seemed reasonable to assume that mature, older quahogs in the sample would produce large num-

bers of sex cells, but it was not possible to determine whether most of the undifferentiated gonads in the sample would do likewise. Their contribution to the reproductive potential of the species was an enigma, and our knowledge of maturation was incomplete.

In late July and early August 1978, the National Marine Fisheries Service marked large numbers of ocean quahogs at a location near a site sampled in the study of sexual maturity reported by Thompson et al. (1980b). This was an opportunity to collect specimens for a reexamination of gonadal condition at about the time of maximum ripeness, as Loosanoff (1953) had reported finding many ocean quahogs in the partial spawning condition in mid-August. The time of collection, then, seemed favorable for obtaining sexually mature quahogs with fully developed, ripe gonads that could be clearly separated from immature quahogs with undifferentiated sex cells in the gonads.

METHODS

A commercial clam dredge vessel, MV *Diane Maria*, was chartered for the marking project during 25 July-5 August 1978. The hydraulic clam dredge had a 100-in (2.54 m)-wide knife and was modified by lining the inner surfaces with 1/2-in (12.7 mm) square-mesh hardware cloth to retain small clams. Sample tows were of 4-5 min duration and usually resulted in a dredge filled with clams, shells, and bottom substrata.

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²Serchuk, F. M., and S. A. Murawski. 1980. Evaluation and status of ocean quahogs, *Arctica islandica* (Linnaeus) populations off the Middle Atlantic coast of the United States. Woods Hole Lab. Ref. Doc. 80-32, 4 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

The sample site was 48 km SSE of Shinnecock Inlet, Long Island, N.Y., at lat. 40°21'N, long. 72°24'W, and 53 m deep. This location contained high densities and a wide size range of ocean quahogs and had a low probability of being disturbed by the fishery: criteria important for success in the marking experiment (Murawski et al. 1982). The wide size range of ocean quahogs found at and near the site included more small individuals for a study of maturity than elsewhere in the Middle Atlantic Bight.

Small quahogs (<65 mm shell length) were sorted from the catch during the marking operation, and the soft bodies were immediately removed from the shells for preservation in Bouin's fixative; shells were saved and coded for reference to corresponding tissues. Slides of the gonadal tissues were prepared for microscopic examination using standard histological techniques. The clam bodies were cut dorsoventrally through the mid-section, and the anterior and posterior pieces of each clam were embedded to produce two sections for examination. The 6 μ m thick sections were stained in Harris' hematoxylin and eosin. Recognition of gametogenic stages was based on previous studies of bivalve reproduction by Loosanoff (1953); Ropes and Stickney (1965); Ropes (1968a, b; 1971; 1979a); Thompson et al. (1980b); Jones (1981); and Mann (1982).

The shells were processed for observation of internal age/growth lines in acetate peels by methods similar to those reported in Thompson et al. (1980a, b) and reported more fully by Ropes (1982)³. A radial section was made from the umbo to ventral margin of left valves, since these contain a single prominent tooth that Thompson et al. (1980a, b) found had growth lines corresponding in number to those in the valve. Proper orientation of the valve for sectioning to retain the umbonal portion and broadest tooth surface in the anterior portion of the valve was a critical procedural step. The sections were made on a low-speed saw and by a 10.2 cm diameter by 0.03 cm thick diamond wafering blade. The cut edges were hand polished on wettable carborundum paper (240, 400, and 600 grits) to remove saw marks, polished to a high luster on a vibrating lap machine charged with aluminum oxide, then etched in a 1% HCl solution for one min. Peels were produced by flooding the

etched surfaces with acetone and applying 0.127 mm thick acetate film. After a 15-min drying period, the film was peeled off and sandwiched between glass slides. Peel images were enlarged on a microprojector to 40 \times . Age/growth lines were counted and the exit location of each at the external edge was marked on the peel for a comparison with the external bands by placing the anterior valve portion on the peel image. This procedure clearly demonstrated correspondence between the number and location of internal lines and external bands. It also delimited sequential increments between external bands for measurement to the nearest 0.1 mm with calipers.

Periodic age/growth phenomena in the shells of ocean quahogs have been called "bands" for increments of darker periostracum deposits on the external shell surfaces and "lines" for those accreted in the shells. The latter have been identified as prismatic microstructures that demark boundaries of growth increments (Ropes et al. in press); the external pigmented bands varied in intensity and width (from 0 to ~2 mm). A slight concentric depression often outlined the shell shape in the bands and corresponded to the location of internal lines. This and the method of marking the acetate peel aided in measuring increments of growth.

After completing the study of the gonadal tissues of small ocean quahogs, it was evident that the sex ratio of larger clams from the same area should be examined. Therefore, squashes of thawed gonadal tissues from 199 marked clams 57-103 mm shell length recaptured in August 1980 were examined microscopically at the laboratory for determination of sex.

RESULTS

Observations of Age

The shells and acetate peels of 137 clams were examined. Bands on the external shell surfaces were not equally distinct for all clams in the sample. The bands were widely separated for small clams, but crowded together at the ventral margin for large clams. A few shells had poorly defined bands, but lines in the peels aided in locating them. Age annuli formed during the earliest ontogeny of ocean quahogs are difficult to detect on the valve surface and must be carefully exposed in the sectioned shell. A quahog 20.0 mm in shell length had three barely detectable bands on the surface of its valves; the two most recent annuli in peels of the valve and hinge tooth were most obvi-

³Ropes, J. W. 1982. Procedures for preparing acetate peels of embedded valves of *Arctica islandica* for ageing. Woods Hole Lab. Ref. Doc. 82-18, 8 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

ous and the first was confounded by a secondary incomplete line that had formed slightly later (Fig. 1a, b). The formation of secondary lines is not typical at a young age. The formation of a complete line is, however, important in detecting annuli.

Three clams had shell abnormalities related to an injury. An ocean quahog with six bands had a slight depression at the anterior end of the left valve that was not detected as unusual growth lines or increments in the peel of either the valve or tooth; the right valve showed no evidence of an injury (Fig. 2a, b). Another quahog had a deep indentation, and part of the ventral margin was missing in the left valve before band six had been formed, but the right valve showed a slight indentation and darkening as evidence of an injury (Fig. 3a, b). The peel of the left valve showed age lines before and immediately after the site of the injury (Fig. 3c). The sixth annuli in the hinge tooth was very prominent (Fig. 3d). The valve of a quahog with seven bands had definite surface indentations associated with annuli, and the hinge tooth showed regularly spaced growth increments (Fig.

4a, b, c). An injury was not clearly evident. The annuli in peels of all these clams were easily related to bands on the valve surface for measurements of growth.

For 9 clams (47.5-60.4 mm long), all annuli in the peels were counted, but only some bands were measured because those near the ventral margin were too crowded and poorly defined.

The shells of 3 clams (39.7-64.0 mm long) produced a confused pattern of lines in the ventral third of the peels and extensive ridging and poorly defined bands on the external valve surfaces (Fig. 5a, b, c). It was not evident that these clams had been injured, but they were omitted in analyses, since growth appeared to be aberrant. In all, 134 clams, 18.7-60.4 mm long and averaging 38.9 mm (S.D. \pm 8.65), were used.

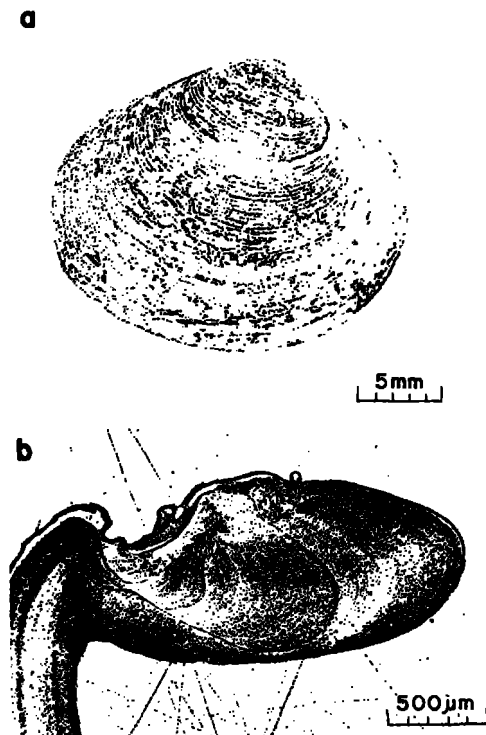


FIGURE 1.—(a) Right valve of a 3-yr-old ocean quahog, *Arctica islandica*, 20.0 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing three annuli.

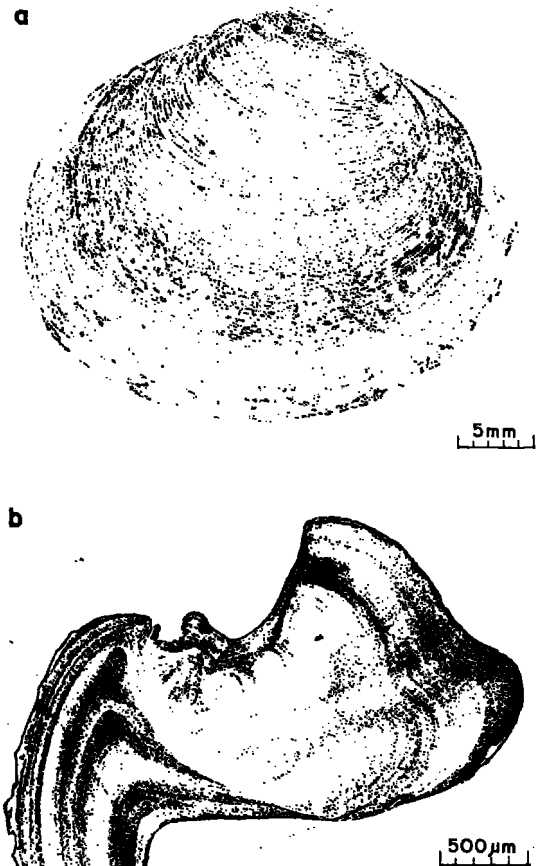


FIGURE 2.—(a) Right valve of a 6-yr-old ocean quahog, *Arctica islandica*, 31.1 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing six annuli.

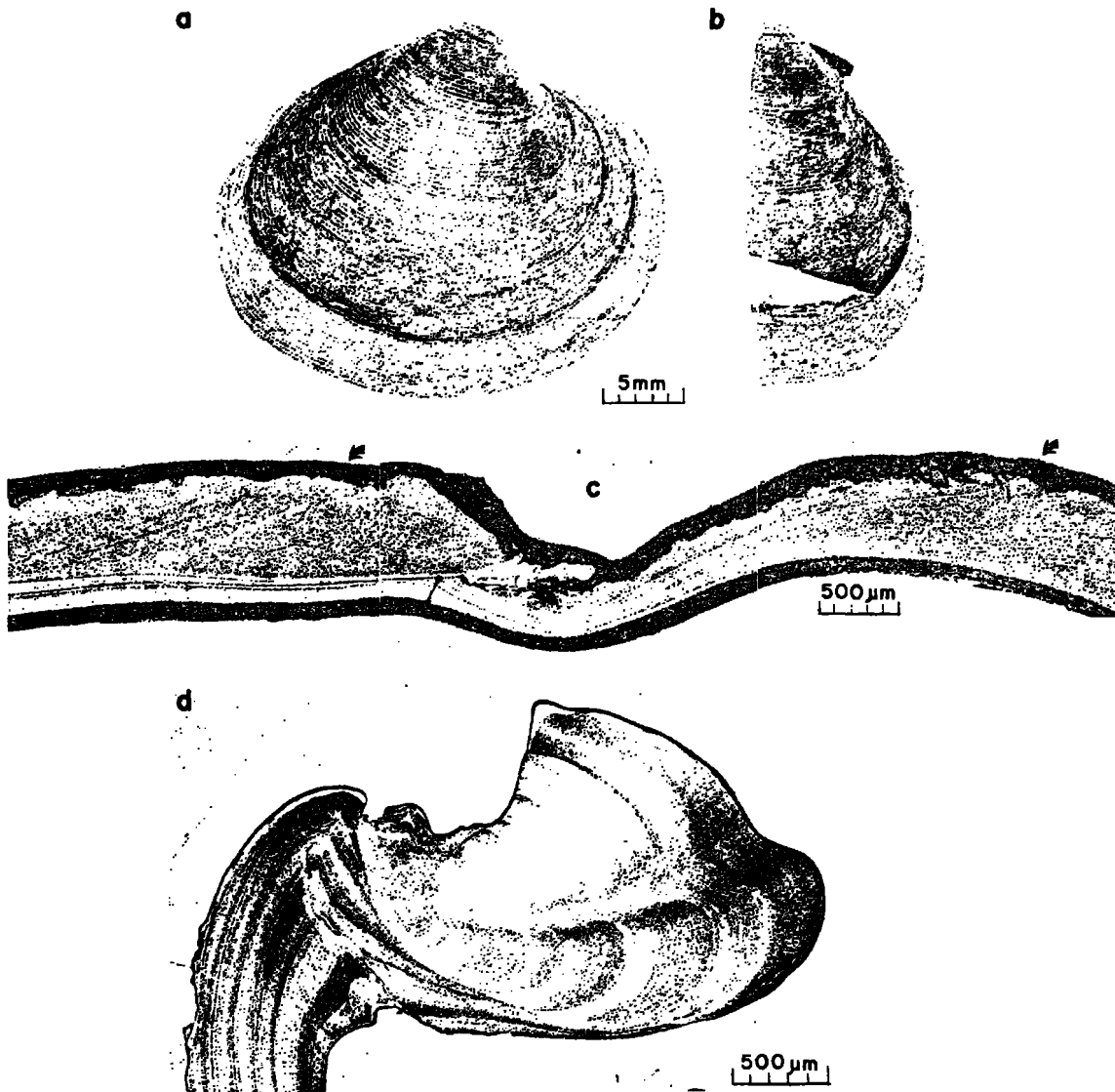


FIGURE 3.—(a) Right valve of a 6-yr-old ocean quahog, *Arctica islandica*, 33.1 mm shell length. (b) Sectioned anterior portion of the left valve showing injury. (c) Three serial photomicrographs of the acetate peel image. Arrows point to annuli formed before and after the injury. (d) Photomicrograph of the acetate peel image of the hinge tooth showing six annuli.

Size measurements at age of the clams are shown in Figure 6. The mean shell length, one standard deviation from the mean, and range are given for clams 3-8 yr old. The bands on the shells and lines in the peels indicated rapid growth through age 8. From age 3 and a mean size of 23.4 mm, the clams increased about 5 mm in shell length each year to age 8 and a mean size of 46.1 mm. Thereafter, growth seemed to decrease in rate. The bands were well separated to age 13. The

bands at the ventral margin of 14-yr-old and older clams were too indistinct for accurate measurements, but the growth lines in peels were clearly separated and easily counted. The oldest 14- to 18-yr-old specimens may have been the smallest and slowest growing individuals in their year classes, but mean lengths were not progressively smaller than means for clams 9-13 yr old. Thus, a significant bias was not clearly indicated in the selection of older specimens.

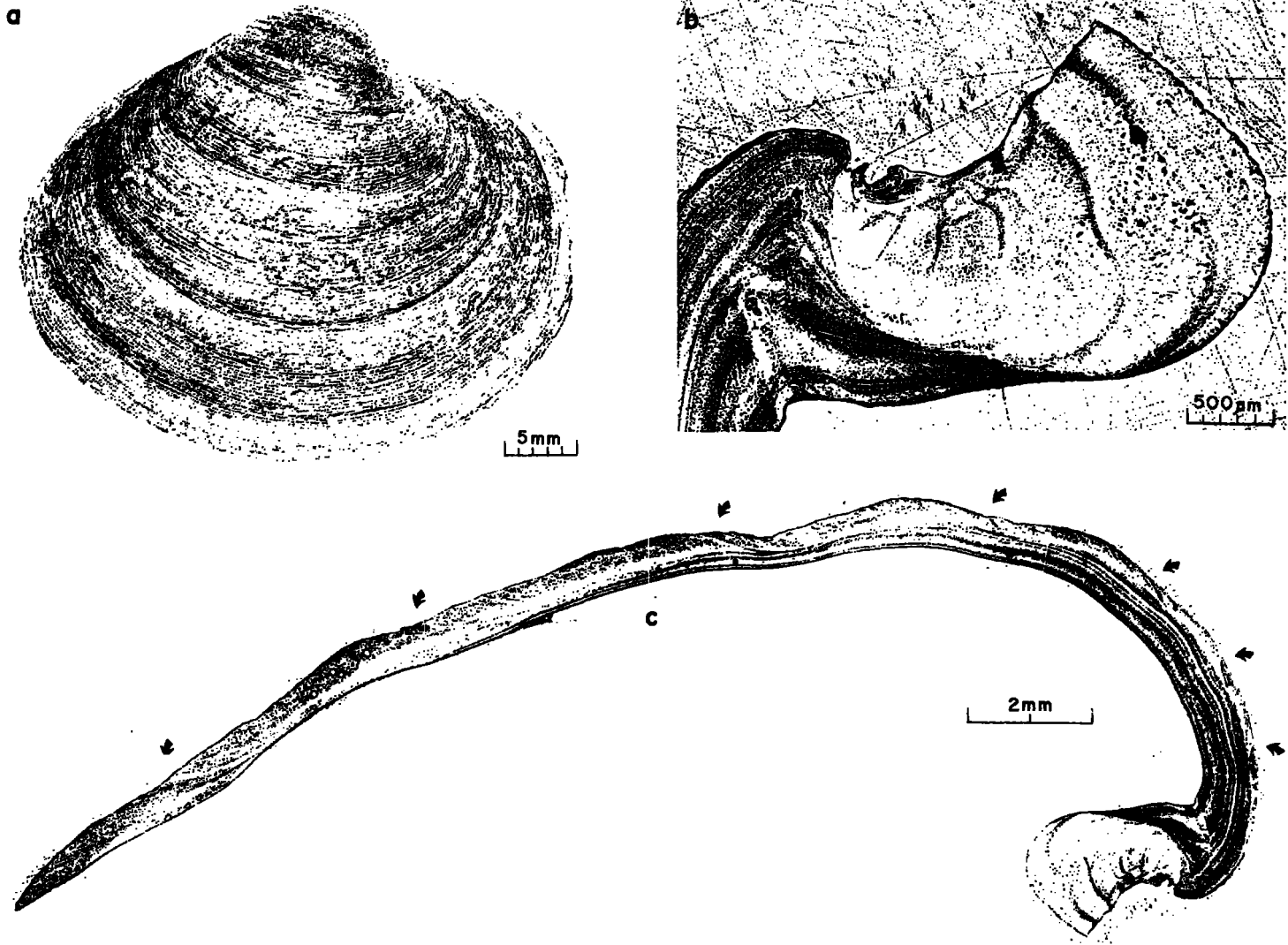


FIGURE 4.—(a) Right valve of a 7-yr-old ocean quahog, *Arctica islandica*, 35.6 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing seven annuli. (c) Four serial photomicrographs of the sectioned left valve with arrows pointing to annuli in the valve.

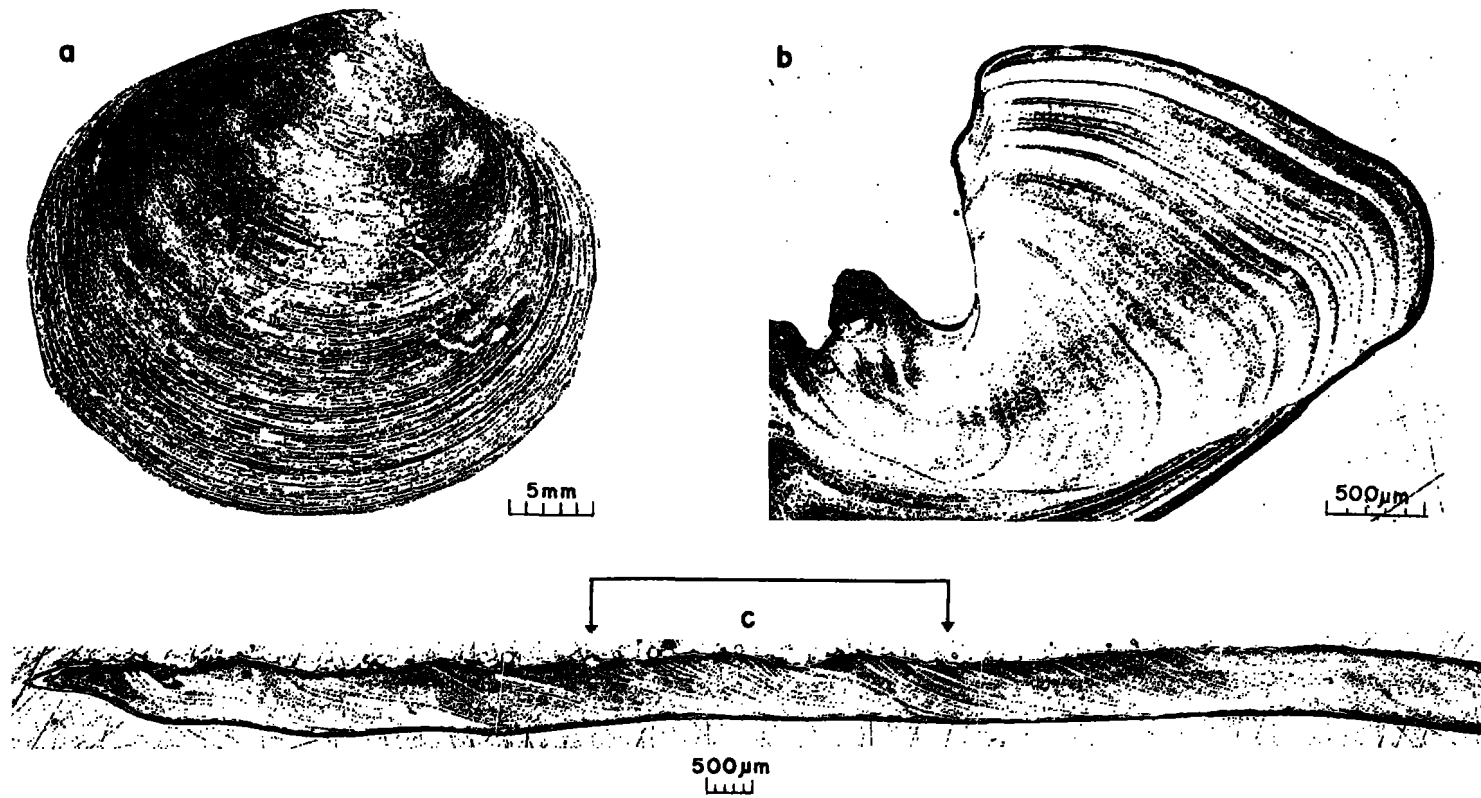


FIGURE 5.—(a) Right valve of a 40.0 mm shell length ocean quahog, *Arctica islandica*. (b) Photomicrograph of the acetate peel image of the hinge tooth. (c) Three serial photomicrographs of the acetate peel image of the sectioned valve at the ventral margin. Brackets show a zone of poorly defined and incomplete growth lines.

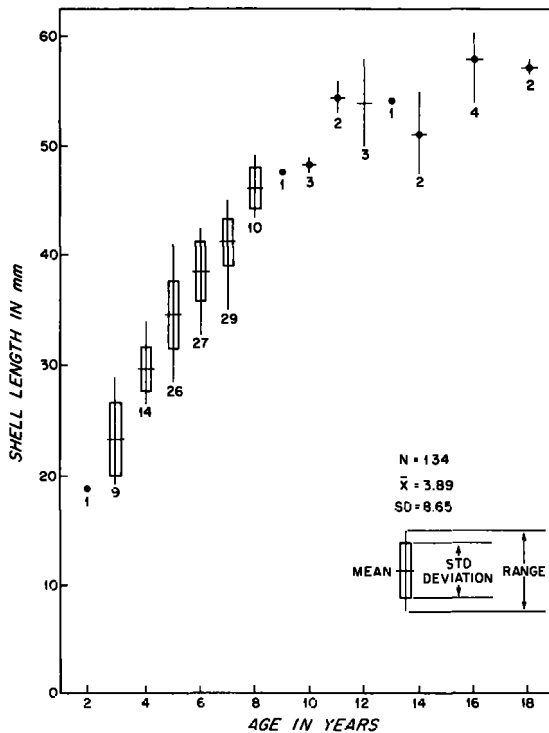


FIGURE 6.—Observed shell lengths at age of ocean quahogs, *Arctica islandica*, off Long Island, N.Y., late July-early August 1978.

Observations of Gonadal Condition

Gametogenesis

Gametogenesis in pelecypod molluscs exhibits similar basic characteristics. Each reproductive cycle begins with the production of the smallest, earliest cells at the basement membrane of follicles or alveoli. These infiltrate the lumina during maturation. Spermiogenesis through meiotic divisions is completed within male gonadal alveoli; oogenesis undergoes mitotic division of the oogonia and growth of the primary oocytes within the female gonadal alveoli. Oocytes may reach metaphase of the first meiotic division in the ducts of spawning females, but are blocked from completing maturation until after spawning and sperm penetration (Raven 1958). Most pelecypods expel the ripe cells into the surrounding environmental water where fertilization and larval development occur. A few pelecypods, and most notably female oysters of the genus *Ostrea*, are exceptions, since the eggs are held in the inhalent cavity during fertilization and initial developmental stages

(Yonge 1960). A reproductive cycle corresponds to the initiation and completion of gametogenic stages and spawning. Single annual cycles have been described for many pelecypods, including the ocean quahog, although biannual and continuous cycles have been described for others (Sastry 1979). In some species, such as the ocean quahog, successive reproductive cycles begin at or soon after spawning; in others, activation of a cycle is delayed and the gonads are considered to be in a quiescent or resting stage (Sastry 1979). The latter condition frustrates determination of sex, since secondary sexual characteristics are generally lacking in most pelecypods.

Spermiogenesis

Spermatogonia about $5.5 \mu\text{m}$ in diameter are the initial germinal cells produced by male *Arctica islandica* during a mitotic phase of spermiogenesis. Successive meiotic stages follow and include primary and secondary spermatocytes (~ 3.7 and $4.0 \mu\text{m}$ in diameter, respectively), spermatids ($\sim 2.2 \mu\text{m}$), and flagellated spermatozoa. The respective cells proliferate into the lumina of alveoli. Sperm have conical heads $\sim 4.8 \mu\text{m}$ long.

Oogenesis

Oogonia are the initial germinal cells produced by female *Arctica islandica* during oogenesis. These are embedded in the basement membrane and are comprised of cytoplasm and a conspicuous nucleus or germinal vesicle with a basophilic nucleolus surrounded by a network of loose chromatin. The distinction between oogonia, spermatogonia, and other cells in the basement membrane is not obvious. Primary oocytes begin protruding from the basement membrane into the lumina of alveoli and retain an attachment with it during the growth stage. The large spherical, vesicular nucleus of primary oocytes is surrounded by a coarse cytoplasm containing granules of the golgi apparatus and acidophilic granules of proteid yolk (Raven 1958; Kennedy and Battle 1964). The nucleolus differentiates into an amphinucleolus with maturation. Mature oocytes appear free in the lumina of alveoli and are often of irregular shape and have a distinct vitelline membrane. Measurements of the diameter of 50 clearly spherical oocytes that were sectioned through the nucleus and amphinucleolus ranged from 49.4 to $65.0 \mu\text{m}$ and averaged $56.6 \mu\text{m}$.

Thirty-six gonadal tissues were in an undif-

ferentiated condition (Table 1, Fig. 7a, b). Gonadal tubules were of small diameter, few in number, and surrounded by an abundant loose vesicular connective tissue. Gonia embedded in the germinal epithelium lacked definite cellular structures for sex determinations. The lumina of tubules were empty.

Sex determinations were possible for 97 quahogs, but in most (69) the gonads appeared to be in an intermediate stage and not fully developed. These latter tissues were separated into two categories: Those with either sparse or moderate tubule development.

Differentiated gonads with sparse tubule development were characterized by a limited number of gametogenic cells, as well as a limited number of tubules. The 16 male tissues examined were producing a few sperm; the 4 female tissues examined were producing a few oocytes. Abundant loose vesicular connective tissue occurred between the widely spaced gonadal tubules. In males, sper-

matogenic cells at the germinal epithelium were about one layer thick, but were absent in portions of the epithelium (Fig. 8a, b). Some sperm were in close contact with the spermatogenic cells and a few were scattered in the lumina of tubules. In females, the few small oocytes occurred at the germinal epithelium, none were in the tubule lumina, and all were in an early developmental stage (Fig. 8c, d).

For differentiated gonads with moderate tubule development, 39 males examined were producing sperm, while 10 females examined were producing oocytes. The gonadal tubules were more numerous than in gonads of sparse tubule condition, and some exhibited an expanded alveolar condition. Loose vesicular connective tissue clearly separated the tubules. In males, several layers of spermatocytes proliferated from the germinal epithelium with some sperm forming a fringe extending toward the empty lumina; however, portions of the germinal epithelium in some tubules

TABLE 1.—Gonadal condition relative to age, sex, and size of three categories of ocean quahogs, *Arctica islandica*—sexually immature, intermediate, and mature—off Long Island, N.Y., late July-early August 1978. M = male; F = female.

	No. clams (%)							Total no.
	Immature (undifferentiated)	Intermediate Tubule development				Mature		
		Sparse		Moderate		M	F	
		M	F	M	F			
Age (yr)								
2	1(0.8)							1
3	4(3.0)	2(1.5)		2(1.5)				8
4	7(5.3)	5(3.7)		2(1.5)				14
5	11(8.2)	4(3.0)	1(0.8)	9(6.7)		1(0.8)		26
6	9(6.7)	3(2.2)	1(1.5)	10(7.5)		2(1.5)	1(0.8)	27
7	3(2.2)	2(1.5)	1(0.8)	12(9.0)	9(6.7)	2(1.5)		29
8	1(0.8)			3(2.2)	1(0.8)	5(3.7)		10
9						1(0.8)		1
10				1(0.8)		2(1.5)		3
11						1(0.8)	1(0.8)	2
12						1(0.8)	2(1.5)	3
13						1(0.8)		1
14						1(0.8)	1(0.8)	2
15								
16							4(3.0)	4
17								
18						2(1.5)		2
Age range	2-8	3-7	5-7	3-10	7-8	5-18	6-16	2-18
Mean	5.03	4.63	6.00	6.08	7.10	9.79	13.22	6.71
Shell length (mm)								
<20	2	0	0	0	0	0	0	2
20-29	8	4	0	3	0	0	0	15
30-39	16	9	3	18	2	2	0	50
40-49	10	3	1	18	8	12	1	53
50-59	0	0	0	0	0	5	6	11
>59	0	0	0	0	0	0	2	2
Length range	19-46	21-44	36-42	20-48	39-45	36-58	41-60	19-60
Mean	34.4	33.8	38.4	37.2	41.8	47.1	55.0	39.0
Total no.	36(27.1)	16(12.0)	4(3.0)	39(29.3)	10(7.5)	19(14.3)	9(6.8)	1133

¹The tissues of a 21.1 mm, 3-yr-old clam were too poorly prepared for examination.

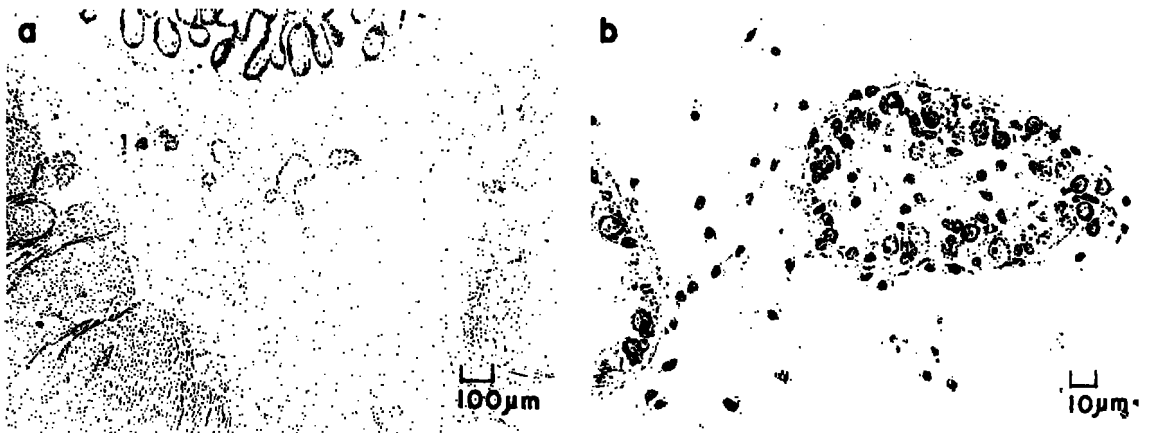


FIGURE 7.—(a) Undifferentiated gonadal tissue section from a 5-yr-old ocean quahog, *Arctica islandica*, 37.2 mm shell length. (b) Enlargement of a gonadal tubule from the same clam.

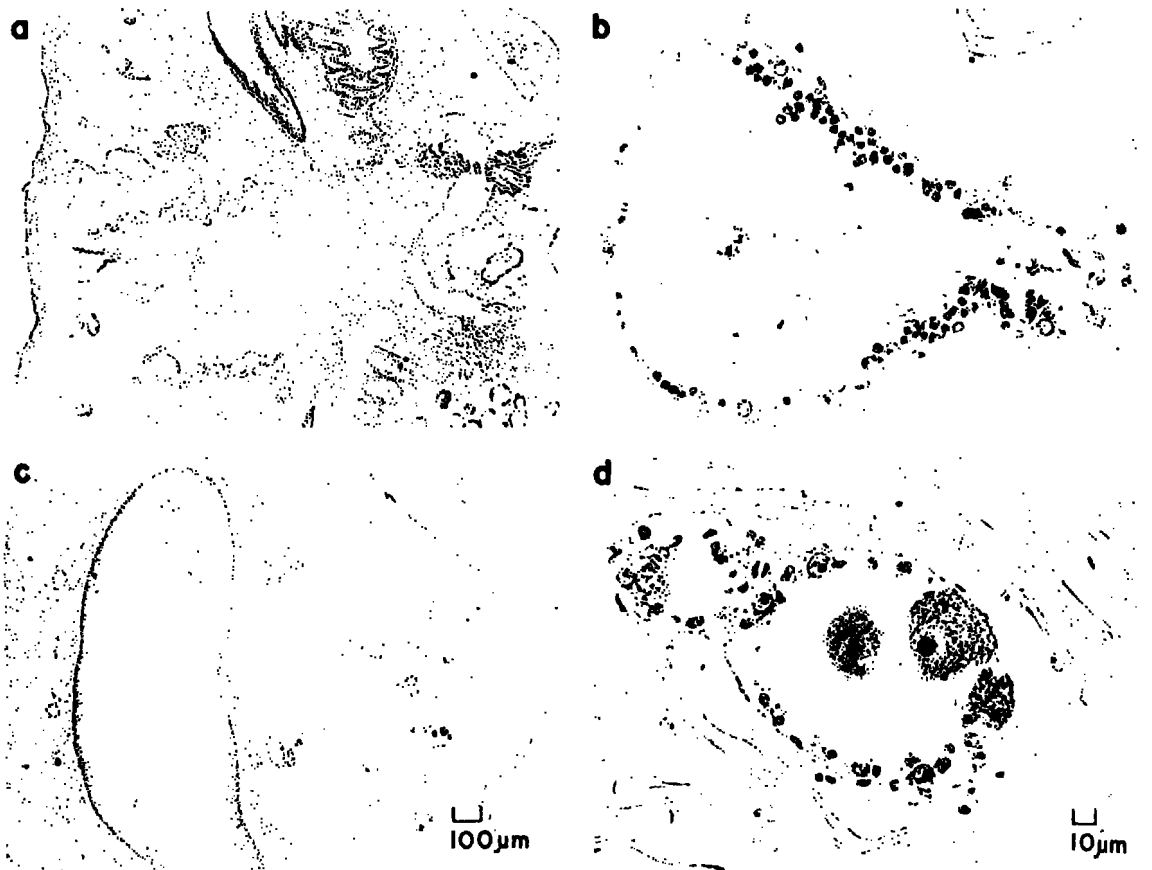


FIGURE 8.—(a) Differentiated gonadal tissue section in the sparse condition from a 3-yr-old male ocean quahog, *Arctica islandica*, 21.0 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the sparse condition from a 5-yr-old, 37.5 mm shell length, ocean quahog. (d) Enlargement of oogenesis in a gonadal tubule.

again lacked obvious spermatogenic cells (Fig. 9a, b). Oocytes in females were at the same stage of development as seen for females with sparse gonadal tubules, but more were growing from the germinal epithelium and some portions of the germinal epithelium lacked obvious oogenic cells (Fig. 9c, d).

The sexually mature condition was found in 19 males and 9 females. In these quahogs the tubules were greatly expanded and filled the gonadal area; little connective tissue occurred between adjacent tubules. Developmental stages similar to those described for other bivalves by Ropes and Stickney (1965) were recognized. Two males and one female were in an early gonadal condition. Spermiogenesis and oogenesis had cellular characteristics as in gonads of moderate tubule development, but the tubules were more numerous and

crowded together. Six males were in a late gonadal condition. Primary and secondary spermatocytes and spermatids were proliferating from the germinal epithelium, filling about half of the tubules and sperm crowded into the lumina. No females were found in the late gonadal condition, but 11 males and 2 females were in an advanced late stage. In males, spermatocytes and spermatids proliferated from the germinal epithelium and sperm predominated in the lumina of the tubules (Fig. 10a, b). In females, oocytes crowded into the lumina of tubules and a few seemed to be attached to the germinal epithelium. No ripe males and only six ripe females with numerous ripe oocytes crowding into the tubules were found (Fig. 10c, d). The potential for developing large numbers of germinal cells was most evident and indicative of full sexual maturity in all of these quahogs.

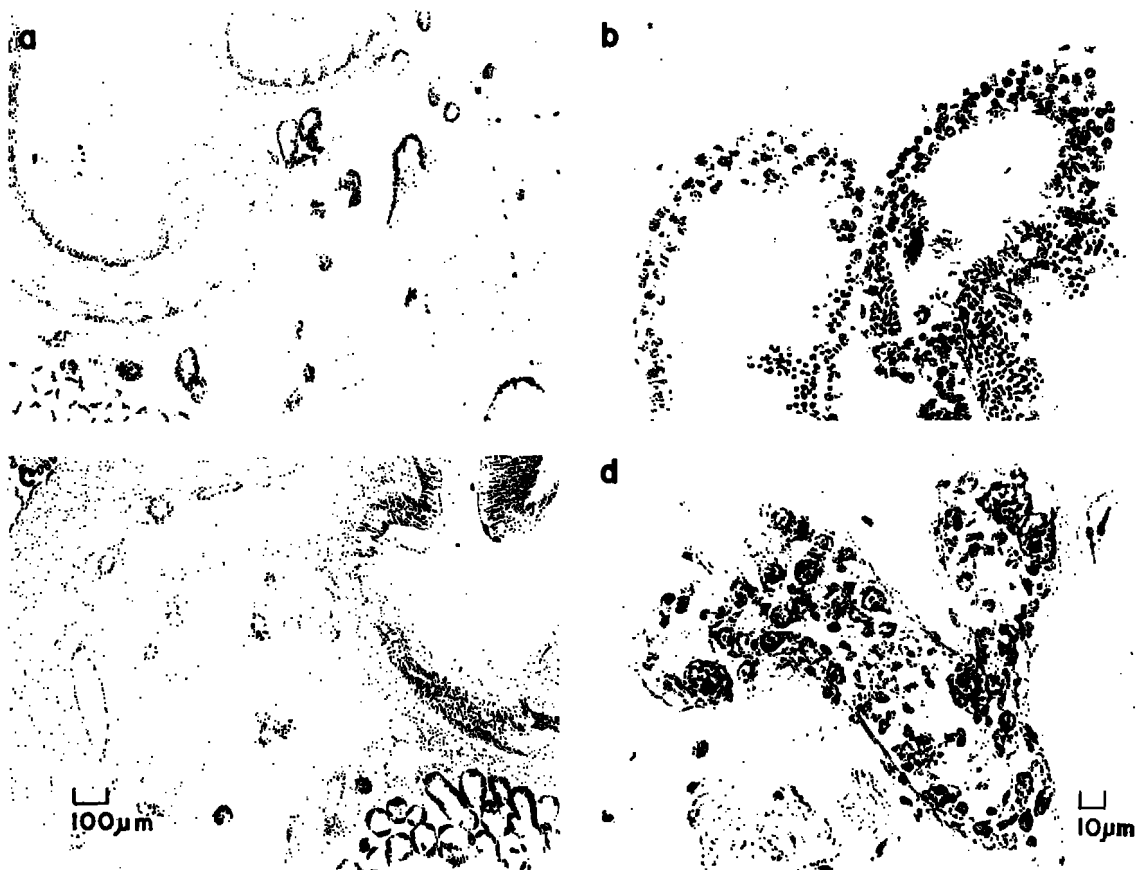


FIGURE 9.—(a) Differentiated gonadal tissue section in the moderate condition from a 7-yr-old ocean quahog, *Arctica islandica*, 42.9 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the moderate condition from an 8-yr-old female ocean quahog, 43.3 mm shell length. (d) Enlargement of oogenesis in a portion of a gonadal tubule.

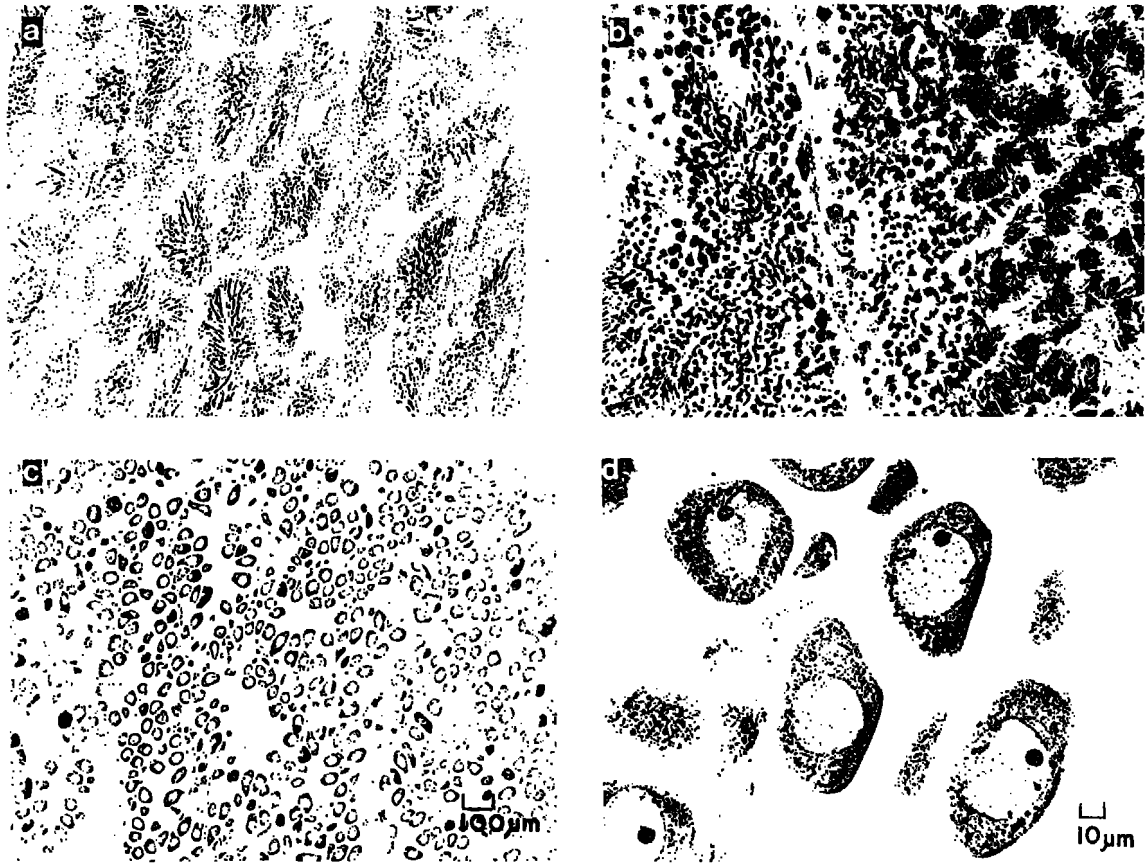


FIGURE 10.—(a) Differentiated gonadal tissue section in the mature condition from an 18-yr-old male ocean quahog, *Arctica islandica*, 57.8 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the mature condition from a 16-yr-old female quahog, 59.8 mm shell length. (d) Enlargement of ripe oocytes in a tubule.

Gonadal Condition vs. Size and Age

In an analysis of gonadal condition relative to age and size, quahogs in the undifferentiated, immature condition ranged from 2 to 8 yr old, averaged 5.0 yr old, and were from 19 to 46 mm long and averaged 34.4 mm (Table 1). This condition was found in 27% of the gonads in the sample.

For the three types of differentiated gonads, quahogs with sparse tubule development comprised 15% of the sample. Males ranged from 3 to 7 yr old, averaged 4.6 yr old, and were from 21 to 44 mm long and averaged 33.8 mm; females ranged from 5 to 7 yr old, averaged 6.0 yr, and were from 36 to 42 mm long and averaged 38.4 mm. This category contained the smallest and youngest female in the sample: 38 mm long and 5 yr old.

Quahogs with moderate tubule development

comprised 37% of the sample. Males ranged from 3 to 10 yr old, averaged 6.1 yr, and were from 20 to 48 mm long and averaged 37.2 mm; females ranged from 7 to 8 yr old, averaged 7.1 yr, and were from 39 to 45 mm long and averaged 41.8 mm. This category contained the smallest and youngest male in the sample, which was 20 mm long and 3 yr old (Fig. 1a, b).

Sexually mature quahogs comprised 21% of the sample. Males ranged from 5 to 18 yr old, averaged 9.8 yr, and were from 36 to 58 mm long and averaged 47.1 mm; females ranged from 6 to 16 yr old, averaged 13.2 yr, and were from 41 to 60 mm long and averaged 55.0 mm. The smallest mature quahog found was a male 36 mm long and 6 yr old, although a 5-yr-old, 41 mm long male was also mature; the smallest and youngest mature female found was 41 mm long and 6 yr old.

None of the gonads contained germinal cells

suggestive of ambisexuality. This is consistent with the conclusion of Loosanoff (1953) that the sexes are separate. The sex ratio, however, was particularly imbalanced in favor of males. In the 69 quahogs considered less than fully mature, 55 were males and 14 were females, while in the 28 sexually mature specimens, 19 were males and 9 were females; the observed ratios were 4:1 and 2:1, respectively. The data were subjected to goodness of fit tests under the hypothesis of a 1:1 ratio between the sexes; results indicated highly significant ($P < 0.01$) and significant ($P < 0.05$) differences, respectively.

Microscopic examinations of gonadal tissue squashes of the 199 clams collected in 1980 revealed an overall sex ratio of 96 males and 103 females. These results were not significantly different from parity (1 male:1.07 female), but by separating the data into 10 mm size groups, a significant difference ($P < 0.05$) in favor of males was indicated in the size group 80-89.9 mm, and a highly significant difference ($P < 0.01$) in favor of females was indicated in the 100-110 mm size group (Table 2).

Figure 11 shows the combined observations of clam size and sex obtained from the 1978 and 1980 samples. In these samples, males tended to decrease in occurrence relative to females with increasing shell size.

TABLE 2.—Occurrence of male and female ocean quahogs, *Arctica islandica*, within 10 mm size groups off Long Island, N.Y., August 1980.

Size group (mm)	Number	
	Males	Females
50-59	4	0
60-69	44	32
70-79	12	21
80-89	16	5
90-99	19	33
100-109	1	12
Total	96	103

DISCUSSION

The time of sampling, sample size, and capture of small quahogs provided a basis for detection of the differentiated and sexually mature stage at younger ages and smaller sizes as compared with the study of Thompson et al. (1980b). In the present study, 5- and 6-yr-old quahogs 41 and 36 mm long, respectively, were considered sexually mature; the youngest mature quahog reported by Thompson et al. (1980b) was a 42 mm male 11 yr old. The intermediate gonadal condition was

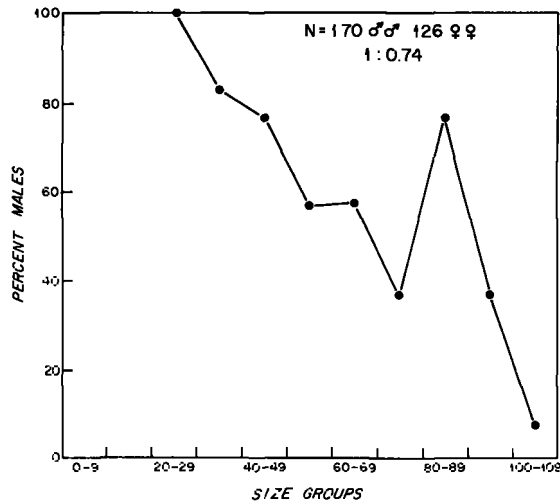


FIGURE 11.—Sex of ocean quahogs, *Arctica islandica*, relative to shell length (mm) in collections off Long Island, N.Y., 1978 and 1980.

found to occur at lower ages and smaller sizes than by Thompson et al. (1980b), and slightly smaller sizes were found for sexually mature quahogs. Variability in attainment of sexual maturity at age/size was observed in both studies.

The onset of sexual maturity at young ages has been reported for several bivalves. The bay scallop, *Argopecten irradians*, attains maturity at 1 yr; the hard clam, *Mercenaria mercenaria*, soft clam, *Mya arenaria*, and blue mussel, *Mytilus edulis*, matures at 1-2 yr (Altman and Dittmer 1972). Surf clams, *Spisula solidissima*, from an inshore habitat showed precocious sexuality in a few post-larvae or juveniles; they spawned at 1 yr, but reached full maturity at 2 yr (Ropes 1979a). Sea scallops, *Placopecten magellanicus*, spawned at about 1.5-2 yr after forming the first growth ring (Naidu 1970). In apposition to more mature gonadal conditions, some scallops in his collections were considered undifferentiated and differentiated male and female immature specimens. Lucas (1966) observed precocious sexuality in a scallop (*Chlamys varia*) and two clams (*Glycymeris glycymeris* and *Venus striatula*) from waters off France. The development of the reproductive potential during the early life history of these several bivalves seems consistent with estimates of their life span, which are as short as 2 yr for the bay scallop and as long as 30 yr for the surf clam (Belding 1906; Ropes 1979a). In contrast, the present study revealed that ocean quahogs attain maturity at 5-10 yr of age, and Thompson et al.

(1980a) reported a longevity of about 150 yr. They found that growth was vigorous at old age and that there were no obvious indications of reproductive senility. A small abyssal nuculoid bivalve, *Tindaria callistiformis*, studied by Turekian et al. (1975) seems most exceptional with regard to age and size at sexual maturity. They found a longevity of about 100 yr for a large specimen (8.4 mm shell length) by radiometric techniques and counts of shell growth bands, but gonadal development was not recognized until the clams were about 4 mm long and 50-60 yr old. The attainment of sexual maturity about midway in the life span of *Tindaria* sets it apart from other species that reproduce at a younger age. Nevertheless, all have the potential to reproduce for many years. Reproduction during a long life span of a species may be an evolutionary strategy in response to uncertain larval and juvenile survival (Krebs 1972). Reproduction during a particularly long life span is most obvious for *Arctica islandica*.

For the 69 gonads containing sexually differentiated germinal cells and sparse-to-moderate tubule development, some morphologically ripe sperm were present. In contrast, oogenesis never exceeded an early developmental state. Jones (1981), Loosanoff (1953), von Oertzen (1972), and Mann (1982) reported that mature ocean quahogs spawn each year. Thus, the sperm may be spawned, but the fate of the oocytes remains an enigma. In American oysters, *Crassostrea virginica*, germinal cells remaining in the gonads after spawning are reabsorbed (Galtsoff 1964), but viable, nearly ripe, or ripe germinal cells may be retained by hard clams throughout the fall, winter, and into the following spring (Loosanoff and Davis 1951). Thus, bivalves appear to differ greatly in this respect. No conclusion can be drawn relative to retention of germinal cells after spawning for ocean quahogs which were intermediate between the immature and mature condition in the absence of collected data.

Gonadal development in 28 mature clams suggested that many (46%) were approaching ripeness or were ripe (21%). Later development probably resulted in a spawning which was begun in late August-September. This seems reasonable based on observations by Mann (1982) of the reproductive cycle of *Arctica islandica* from sample locations in Block Island Sound. At the beginning of his study in September 1978, most (69%) were in the partially spent or spent condition and spawning was indicated until mid-November. An exact correspondence of the time and duration of spawn-

ing may be a hazardous assumption, since the two sample sites are about 110 km apart and some of the samples taken by Mann (1982) were at shallow depths (36 m).

A disparity in the initiation of gametogenesis was observed between the sexes. Male ocean quahogs began producing germinal cells at a smaller size and younger age than females. This suggests that females require a longer period of development and growth. The later development of female sexuality is a probable explanation for the highly significant difference obtained in tests of the sex ratio of quahogs in the intermediate gonadal condition. The significant difference observed for fully mature quahogs may be due to the small number in the sample (Dixon and Massey 1957), but Jones (1981) observed a similar disparity ($P = 0.008$) for quahogs > 75 mm from offshore New Jersey. In his collections 184 were males and 136 were females, a ratio of 1:0.74. Mann (1982) examined ocean quahogs that were mostly 80-100 mm long and found 185 males and 169 females, a ratio of 1:0.91. These observations suggest that spatial variation may occur in the sex ratio of ocean quahog populations, but that males are more numerous than females.

Pelseneer (1926) investigated the sex ratio of several mollusc species, including bivalves. He found more females among the older individuals of some populations and the converse among younger individuals. Coe (1936) recognized the existence of such disparities in molluscs and proposed the following hypotheses as possible explanations: 1) That males have a shorter longevity than females, because of a differential mortality rate or less resistance to unfavorable environmental conditions; 2) that the development of alternative sexual conditions is environmentally determined; and 3) that sex change may occur. Loosanoff (1953), von Oertzen (1972), Thompson et al. (1980b), and Jones (1981) all considered the species to be strictly dioecious, as did Mann (1982), although he found two hermaphrodites. These are anomalous, "accidental functional hermaphrodites" by the terminology of Coe (1943). Although Sastry (1979) hypothesized that a failure in the genetic sex-differentiating mechanism may produce some hermaphrodites, he found no evidence of a phenotypic or genetic basis for sex determination in pelecypods.

It is unlikely that ocean quahogs are protandric. This condition in a typically hermaphroditic species is characterized by the development of male organs or maturation of their products before

the appearance of corresponding female products. In *Ostrea lurida*, for example, spermatogonia are proliferated first throughout the follicles, but before the sperm mature oogonia have developed into numerous oocytes in the same follicles and the gonad has a definite intersexual character (Coe 1932). More than 90% of the young oysters exhibit the bisexual condition and no strictly male or female specimens occur. Old oysters in the female phase retain sperm balls and spermatogonia, and those in the male phase retain large and small oogonia. The two anomalous ocean quahogs found by Mann (1982) were examples of bilateral hermaphroditism, i.e., the germinal cells for each sex were in separate follicles. None of the investigators of the reproductive cycle in ocean quahogs suggested finding ambisexual conditions (Loosanoff 1953; von Oertzen 1972; Jones 1981; Mann 1982). Thus, the characteristic germinal cell development for protandry is lacking in ocean quahogs.

Sex reversal in some molluscs has been linked to castration from parasites invading the gonads, but evidence of causality was considered inconclusive by Noble and Noble (1961) and Malek and Cheng (1974). Except for the occurrence of the commensal nemertean, *Malacobdella grossa*, in ocean quahogs (Gibson 1967; Jones 1979), parasites in the species have not been reported (Ropes and Lang 1975)⁴. The causality of hermaphroditism in ocean quahogs, then, remains uncertain and evidence is unavailable that sex may be environmentally determined.

The hypothesis that female ocean quahogs may live longer than males has some support from determinations of the sex of specimens recovered from the marking site in August 1980. Based on predicted ages of ocean quahogs at the marking site reported by Murawski et al. (1982), the largest and oldest notched ocean quahogs were predominantly female. Since this may be atypical for the extensive population of ocean quahogs inhabiting the Middle Atlantic Bight, samples from other locations are being examined to determine possible spatial variations.

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