GROWTH OF THE OCEAN QUAHOG, *ARCTICA ISLANDICA*, IN THE MIDDLE ATLANTIC BIGHT

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ABSTRACT

In situ growth rate of the ocean quahog, *Arctica islandica*, was investigated at a site 53 m deep off Long Island, New York, during 1970-80. Specimens notched during summer 1978 and recaptured 1 and 2 calendar years later yielded information on shell growth and the periodicity of supposed annual marks. Growth of specimens recaptured after 1 year at liberty ($n = 67$, 59-104 mm shell length) was described by $SL_{t+1} = 2.0811 + 0.9802\, SL_t$, where SL is shell length in millimeters at age t. Average shell length of marked specimens recaptured during summer 1980 increased 1.17 mm ($n = 200$), approximately twice that of ocean quahogs recaptured in 1979 (0.56 mm). Band formation on the external surface of small ocean quahogs (less than about 60 mm) was apparently an annual event since small specimens recaptured in 1979 formed one such mark during the interval between release and recapture. Small specimens sampled during summer exhibited relatively wide marginal growth from the last external mark to the shell edge, while winter samples had formed new annuli at the shell margin, thus, external bands were formed during early autumn-early winter. Internal banding in shell cross sections of small ocean quahogs correlated in number and position with external features. An equation representing back-calculated growth, based on external banding patterns of small unmarked specimens (19-60 mm) captured during summer 1978, was: $SL = 75.68-81.31\,(0.9056)^t$, where t is age in years. Length-frequency samples were available for the vicinity of the marking study from routine dredge surveys of clam resources during 1970-80. Growth rates inferred from progressions of length-frequency modes in 1970 and 1980 samples were similar to those computed from mark-recapture and age-length equations. Ocean quahogs are apparently among the slowest growing and longest lived of the continental shelf pelecypods; annual increases in shell length were 6.3% at age 10, 0.5% at age 50, and 0.2% at an estimated age of 100 years.

Research on the population dynamics of the ocean quahog, *Arctica islandica*, has become increasingly important in recent years. An intensive fishery for the species developed off New Jersey and the Delmarva Peninsula during the mid-1970's. The resulting increases in U.S. landings were dramatic: from 588 t of shucked meats in 1975 to a record 15,748 t by 1979. Estimates of the growth rate and longevity of ocean quahogs inhabiting the Middle Atlantic Bight are necessary to assess potential impacts of various harvesting strategies on the resources (Murawski and Serchuk[2]; Mid-Atlantic Fishery Management Council[3]).

Several early studies alluded to the age and growth rate of *Arctica islandica*, yet citations were largely anecdotal and generally did not reflect critical evaluations of the rate of growth or the validity of aging criteria. Turner (1949) reported an observation by G. Thorson that "European investigators who have studied the chemical composition of the shell found reason to believe that it took six years or more for mahogany (ocean) quahaugs (quahogs) to reach average size." Loosanoff (1953) stated that ocean quahogs he examined for reproductive studies "were adults, several years old, and averaged 3½ to 4 inches (89-102 mm) in length." Jaeckel (1952) noted *Cyprina* (=*Arctica islandica*) could perhaps attain ages up to 20 "Sie kann hohes Alter (Vielleicht bis zu 20 Jahven) erreichen." Skuladottir[4] did not elaborate on aging methodologies

but claimed "the oldest clams were up to 18 years and about 9 cm long. The bulk was in the 10-14 year group and 7-8.7 cm long."

The external color of large ocean quahogs (greater than about 60 mm shell length) is usually solid black; however, the periostracum of small individuals is variable in color, grading from pale yellow to deep brown (Lovén 1929; Hiltz[5]). Concentric dark bands appearing in the shell surface of small specimens have thus been interpreted as annuli by several authors. Although Lovén did not present age-size relationships explicitly, he did note the presence of external "annual rings" ("Jahresringe") and presented photographs of a size range of small ocean quahogs, illustrating the relationship between numbers of rings and shell lengths. Chandler[6] measured the maximum diameters of concentric rings and derived growth relationships based on eight specimens (96 total measurements, to millimeters). The largest number of such rings appearing on an individual ocean quahog was 21; the corresponding shell length was 58.5 mm. Caddy et al.[7] presented growth curves, based on external markings, for small ocean quahogs from the Northumberland Strait and Passamaquoddy Bay. Average length at age was consistently greater for the more southern area.

Unpublished manuscripts by Chéné[8] and Meagher and Medcof[9] document efforts to more precisely establish ocean quahog growth rates. Mark and recapture experiments were conducted in Brandy Cove, New Brunswick. Notched specimens ($n = 14$), averaging 57.4 mm (shell length) when recaptured, grew an average of 0.6 mm (shell height) between September 1970 and September 1971. Sequential observations of eight small ocean quahogs (mean length 20.16 mm) was undertaken to assess growth rates and seasonal changes in the color patterns of the periostracum. These individuals were held in cages and grew an average 17% in length from 4 June to 31 August 1971. Periostracum formed during the interval was brown, contrasting with yellow material formed before the study was begun. However, this banding pattern may not have been indicative of a normally occurring annual event since "the caged clams were sensitive to experimental treatments and produced disturbance rings each time they were air-exposed for observation" (Meagher and Medcof footnote 9).

Several recent studies have examined banding patterns present in shell cross sections and have attempted to validate the hypothesis of band formation as an annual event. Jones (1980) noted that marginal increments of shell deposition beyond the last band followed a seasonal progression; bands were formed once per year between September and February. The most rapid production of shell was from late spring to early summer; annulus formation overlapped the spawning period in mature individuals. Thompson et al. (1980) presented size-frequency data of small specimens from the Baltic Sea and interpreted external and cross-sectional banding in these specimens as supporting evidence for annual periodicity of band formation in larger (older) specimens from the Middle Atlantic Bight. Thompson et al. further stated that preliminary results from radiochemical analysis of shells corroborated age analysis based on shell banding patterns.

We initiated a project during summer 1978 to assess in situ growth rates of ocean quahogs at a deepwater site off Long Island, N.Y. Objectives of the study were to obtain growth increment data directly from mark-recapture, further evaluate the potential of banding patterns (both external and in shell cross section) as indicators of age, and correlate growth measurements with a 10-yr time-series of length frequencies collected in the vicinity of the marking site. Length-weight relationships have been established for the Middle Atlantic, based on a synoptic winter survey (Murawski and Serchuk 1979); however, no data have been published on seasonal variations. An additional objective of the project was to compare winter and summer length-weight relations at the marking site.

(Proceedings of the conference of Islandic Professional Engineers. Fish. Res. Board Can., Biol. Stn., St. Andrews, N.B., Trans. Bur., No. 1206.)

[5]Hiltz, L. M. 1977. The ocean clam (*Arctica islandica*). A literature review. Fish. Mar. Serv. Tech. Branch, Halifax, N.S., Tech. Rep. 720, 177 p.

[6]Chandler, R. A. 1965. Ocean quahaug resources of Southeastern Northumberland Strait. Fish. Res. Board. Can., Manuscr. Rep. (Biol.) 828, 9 p.

[7]Caddy, J. F., R. A. Chandler, and D. G. Wildler. 1974. Biology and commercial potential of several underexploited molluscs and crustacea on the Atlantic coast of Canada. Presented at Federal-Provincial committee meeting on Utilization of Atlantic Resources, Montreal, Feb. 5-7 1974. Prepared at Fisheries Research Board of Canada, St. Andrews Biological Station, N.B.

[8]Chéné, P. L. 1970. Growth, PSP accumulation and other features of ocean clams (*Arctica islandica*). Fish. Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1104, 34 p.

[9]Meagher, J. J., and J. C. Medcof. 1972. Shell rings and growth rate of ocean clams (*Arctica islandica*). Fish. Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1105, 26 p.

FIELD STUDIES

Intermittent surveys of offshore clam resources of the Middle Atlantic Bight have been conducted since 1965 by the National Marine Fisheries Service, and its predecessor the Bureau of Commercial Fisheries (Merrill and Ropes 1969; Murawski and Serchuk footnote 2; Serchuk et al.[10]). Cruises were designed to yield information on temporal and areal aspects of distribution, size composition, and relative abundance of both surf clam, *Spisula solidissima*, and ocean quahog. Stations were sampled in a grid array prior to 1978; surveys from 1978 to 1980 employed a stratified-random scheme. Commercial-type hydraulic clam dredges were modified to retain small individuals and used as survey gear; dredge specifications and vessels varied somewhat among cruises (Serchuk et al. footnote 10; Table 1).

We selected an area for intensive field study of ocean quahog growth, based on an evaluation of pre-1978 survey data and knowledge of commercial fleet activities. Specific criteria were: 1) sufficient clam densities for rapid capture of individuals used in the marking experiment, 2) abundant numbers of clams over a wide size range, 3) clam densities similar to sites frequented by fishing vessels, and 4) lack of previous exploitation and low probability of near-future use. These specifications were met at a site 48 km south-southeast of Shinnecock Inlet, Long Island, at lat. 40°25.1'N, long. 72°23.7'W.

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[10]Serchuk, F. M., S. A. Murawski, E. M. Henderson, and B. E. Brown. 1979. The population dynamics basis for management of offshore surf clam populations in the Middle Atlantic. Proceedings of the Northeast Clam Industries - Management for the Future, Coop. Ext. Serv. Univ. Mass.-MIT Sea Grant, p. 83-101.

Water depth was 53 m, and substrata consisted of coarse sand and shell, primarily ocean quahog and sea scallop, *Placopecten magellanicus*. Live invertebrates present in survey samples included *Lunatia heros*, *Echinarachnius parma*, *Venericardia borealis*, *Aphrodite aculeata*, and *Astarte* spp., in addition to ocean quahog and sea scallop.

Water depth at the study site precluded extended periods of bottom time using normal scuba methods, thus we elected to sample ocean quahogs with commercial and research dredging vessels. The probability of recapturing marked ocean quahogs at the site was considered to be relatively low because of water depth, width of sampling gear, difficulties in positioning the vessel at a precise location, and the accuracy of the loran-C navigation system. Hence it was decided to mark and redistribute large numbers.

Incremental increases in clam shell growth corresponding to known time durations can be measured if a point of reference is initially established at the margin of the growing shell. Growth is determined directly from recaptured specimens and shell length at marking can either be measured or back-calculated. Thus we needed only to indelibly etch the shell edge of live quahogs and return them to the sea bed, obviating the laborious and time-consuming process of measuring and number-coding individuals prior to release.

Notching techniques have been used successfully to study growth rate and to validate the periodicity of band formation in a number of bivalve species including soft shell clam, *Mya arenaria* (Mead and Barnes 1904); hard shell clam, *Mercenaria mercenaria* (Belding 1912); American oyster, *Crassostrea virginica* (Loosanoff and Nomejko 1949); sea scallop (Stevenson

TABLE 1.—Characteristics of survey gear and length-frequency statistics of ocean quahogs collected near lat. 40°25' N, long. 72°24' W, in the Middle Atlantic Bight, 1970-80.

Vessel	Dates	Hydraulic dredge blade width (cm)	Spacing between[1] bars or rings (mm)	Shell length (mm)			
				X̄	SD	Range	n
RV *Delaware II*	13 August 1970	122	30	[2]74.1	20.1	25-105	107
RV *Delaware II*	24 April 1976	122	30	74.1	16.6	40-115	271
RV *Delaware II*	27 February 1977	122	30	73.4	14.5	45-104	234
RV *Delaware II*	1 January-2 February 1978	122	30	74.5	14.3	34-113	211
FV *Diane Maria*[3]	26 July-5 August 1978	254	13	74.5	15.4	31-112	1,262
RV *Delaware II*	9 January 1979	152	25	71.4	14.5	33-116	1,317
RV *Delaware II*[4]	14-21 August 1979	152	25-51	76.5	15.2	38-111	811
RV *Delaware II*	8 February 1980	152	51	74.2	13.8	38-117	5,546
RV *Delaware II*[4]	9 September 1980	152	51	74.8	13.4	40-108	1,899

[1]Dimension in the portion of the dredge where catch is accumulated.
[2]Samples measured to the nearest 0.5 cm.
[3]Initiation of marking study.
[4]Recapture of marked individuals.

and Dickie 1954; Merrill et al. 1966); and surf clam (Ropes and Merrill 1970; Jones et al. 1978). Accordingly, we marked ocean quahogs by cutting shallow grooves from the ventral margin up the shell surface using thin carborundum discs mounted on an electric grinder (Ropes and Merrill 1970). Two parallel grooves 2 mm apart were cut into each shell to distinguish our marks from shells scratched by natural processes or during dredging (Fig. 1).

Marking operations were conducted from 26 July to 5 August 1978 (Table 1). A total of 41,816 ocean quahogs was notched by the previously described technique. Batches of 3,000-5,000 clams were dredged from within 9 km of the planting site, marked, and redistributed. The method of marking and planting clams was rapid; about 1,600 clams were marked per hour. A grid system based on loran-C coordinates, was used to indicate the location of each batch. Length-frequency samples were obtained during the marking phase (Table 1), and 134 small ocean quahogs (19-60 mm) were retained for maturity studies and analyses of exterior and cross-sectional banding.

An intensive effort to recapture marked individuals was undertaken, 1 calendar year after planting, during 14-21 August 1979 (Table 1). Forty-three hydraulic dredge tows, each of about 5-min duration, were completed at the site. A Northstar 6000[11] loran-C set and an Epsco loran-C plotter were used in the systematic search of a 20,000 m² area. A total of 14,043 ocean quahogs was examined; 74 (0.5%) had been marked. Recaptured specimens were photographed, measured, and frozen intact at sea. A random sample of 126 unmarked ocean quahogs was frozen for length-weight comparison with marked individuals.

Marked individuals were again recaptured, approximately 2 yr after planting, on 9 September 1980 (Table 1). Two dredge tows yielded 1,899 ocean quahogs; 249 individuals (13.1%) had been marked.

Length-frequency measurements were obtained from the site during routine assessment surveys in January 1979 and February 1980. Sampling within 10 km of the site was historically serendipitous; catch data were available from four surveys between 1970 and February 1978 (Table 1). Lengths of ocean quahogs taken

near the site exhibited a consistent bimodal frequency distribution throughout the time-series. Growth rate information from the mark-recapture and shell banding experiments was thus compared with that generated from modal progression in sequential length frequencies.

A random sample of 278 ocean quahogs taken from the site during February 1980 was frozen whole for length-weight comparison with the August 1979 sample. Small ocean quahogs (≤60 mm) were also frozen intact for analysis of the timing of periodic band formation in the shells.

LABORATORY STUDIES

Mark-Recapture

Recaptured specimens were thawed but kept moist during all phases of analysis to prevent shell cracking and disintegration of the periostracum. A total of 67 of the 74 specimens recaptured in 1979 and 200 of 249 specimens recaptured in 1980 were suitable for growth analysis; the remaining samples were either shell fragments or from quahogs obviously dead when recovered. Shells were measured to the nearest 0.01 mm, using calipers or dissecting microscope equipped with an ocular micrometer. Periostracum obscured the shell edge of most specimens and was subsequently removed from the vicinity of the mark prior to measurement. Shell lengths were obtained by pressing the periostracum against the valves with calipers.

Growth increments of recaptured ocean quahogs were determined as the linear increase in shell dimension along an imaginary line passing through the umbo and equidistant between grooves that formed the mark (Fig. 1). The linear distance between the umbo and shell edge at the mark was designed as h'; shell length at marking was computed for each quahog by:

$$SL_t = SL_{t+1} - \left[\frac{SL_{t+1}}{h'_{t+1}} \cdot (h'_{t+1} - h'_t) \right] \quad (1)$$

where SL_t = shell length (longest linear dimension) at marking,
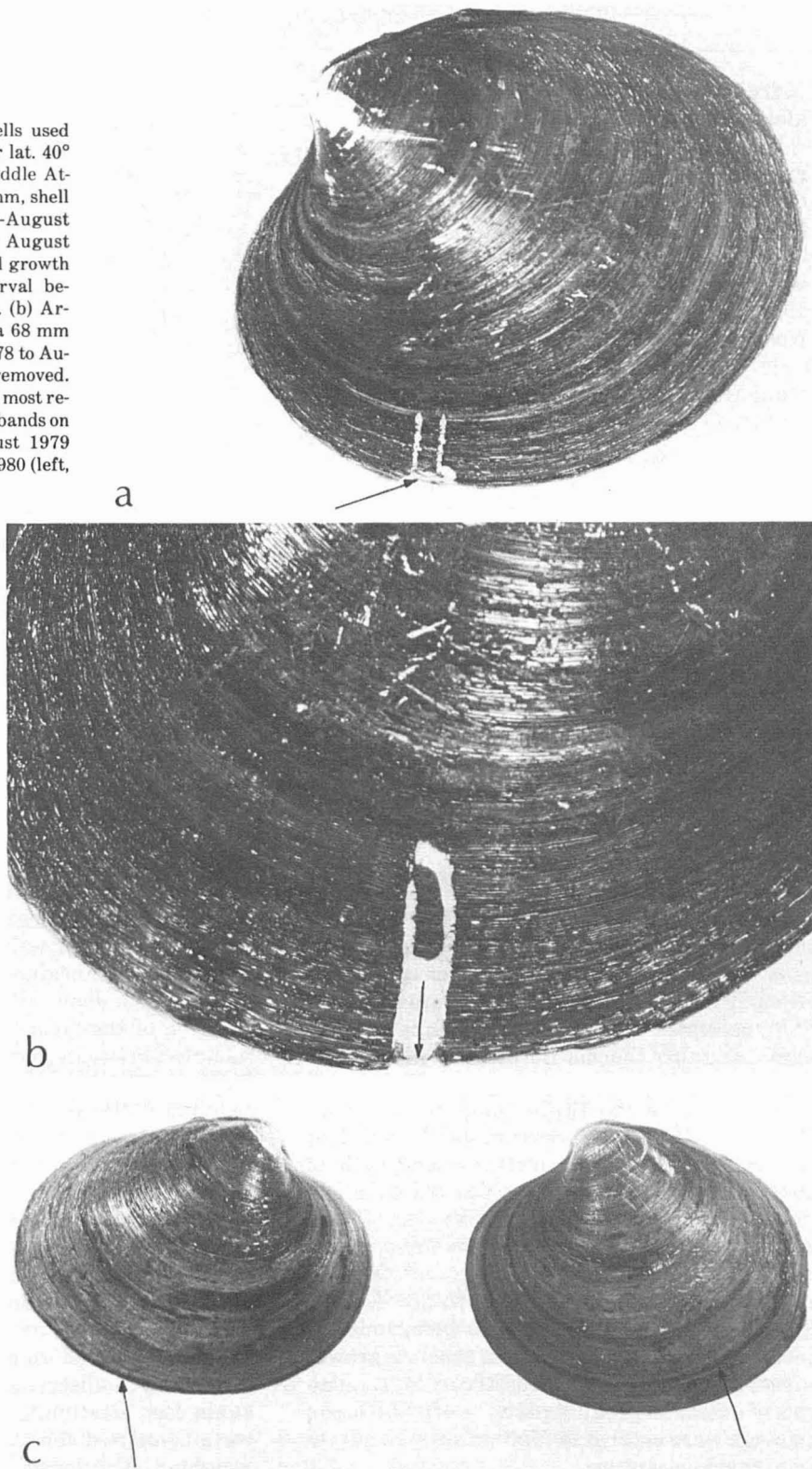
SL_{t+1} = shell length at recapture,

h'_t = linear measurement between umbo and edge of the shell equidistance between grooves, at marking,

h'_{t+1} = linear measurement between umbo and edge of the shell

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FIGURE 1.—Ocean quahog shells used for growth analyses taken near lat. 40° 25'N, long. 72°24'W, in the Middle Atlantic Bight. (a) Specimen 65 mm, shell length, marked during July-August 1978 and recaptured during August 1979. Arrow indicates external growth band formed during the interval between marking and recapture. (b) Arrow indicates shell growth of a 68 mm specimen from July-August 1978 to August 1979 with periostracum removed. (c) Arrows indicate positions of most recently formed external growth bands on small individuals from August 1979 (right, 43 mm) and February 1980 (left, 45 mm) samples.

equidistant between grooves, at recapture.

Marginal growth in shell length was thus equivalent to the bracketed term.

Implicit in Equation (1) is the assumption that ratios between the linear parameters SL and h' did not change between marking and recapture (isometric growth). The assumption is supported by comparisons of various standard shell dimensions (i.e., shell length, height, and width, Chandler footnote 6; Northeast Fisheries Center Woods Hole Laboratory unpubl. data), particularly considering the relatively small percent changes in shell size between marking and recapture (Table 2).
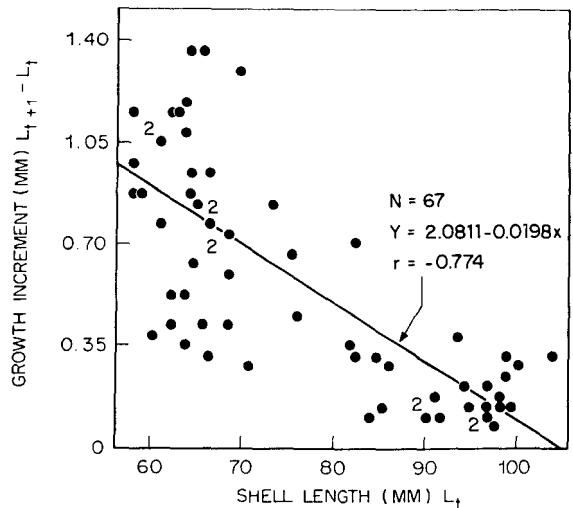

FIGURE 2.—Relation between calculated increment of growth in shell length (millimeters) and initial length for ocean quahogs marked during July-August 1978 and recaptured during August 1979 near lat. 40°25'N, long. 72°24'W, in the Middle Atlantic Bight.

TABLE 2.—Growth of ocean quahogs marked during August 1978, and recaptured during August 1979 ($n=67$), and September 1980 ($n=200$), at lat. 40°25' N, long. 72°24' W, in the Middle Atlantic Bight.

Parameter	Year	Mean (mm)	SD (mm)	Range (mm)
Shell length at recovery	1979	77.31	14.67	59.12-104.40
	1980	79.01	13.91	57.69-103.66
Calculated growth increment in shell length	1979	0.56	0.38	0.08-1.38
	1980	1.17	1.04	0.07-4.32
Calculated shell length at marking	1979	76.76	14.97	58.15-104.09
	1980	77.84	14.75	55.46-103.43

Three methods were used to fit growth equations to mark-recapture data. For ocean quahogs recovered 1 calendar year after marking, length at recapture was related to length at marking using Ford-Walford and linear annual increment plots described by Gulland (1969; Fig. 2). Additionally, a nonlinear exponential equation was fit to increment data and results compared with those assuming the von Bertalanffy model. The von Bertalanffy parameters L_∞ and K were also estimated using the BGC4 computer program (Abramson 1971). The program was designed for determining growth parameters when lengths of unaged individuals are known at two points in time, based on the algorithm of Fabens (1965).

Equations derived from mark-recapture data can be used to describe relative growth from an arbitrary point in time (i.e., SL_{t+1}, SL_{t+2}, ... SL_{t+n}), but without at least one independently derived age-length observation, absolute growth curves cannot be established. Accordingly, analyses of external banding patterns of small ocean quahogs were critical in "fixing" growth curves from mark-recapture.

Shell Banding

Small ocean quahogs retained from the July-August 1978 cruise were analyzed for external and internal shell banding patterns. Sequential growth of individual ocean quahogs was followed by measuring the maximum dimension (shell length) of exterior bands appearing on the periostracum, using calipers (Fig. 1). Maximum shell length beyond the last band was also recorded. The opposite valve was sectioned from the umbo to the ventral margin and polished (Saloman and Taylor 1969; Jones et al. 1978). An acetate impression of the polished surface was made and mounted between glass slides. Images were enlarged with a microprojector to reveal internal banding patterns.

Internal lines present in shell cross sections correlated in number and position with external bands when the latter were distinct. The periostracum on some shells was eroded near the umbo, obscuring external bands. In these cases "annuli" nearest the umbo were located on the peels, but measurements of shell size could not be made (Table 3). External marks present near the shell margins on some larger specimens also could not be discerned; internal banding was again used to estimate age. Shell length statistics were computed for each age/annulus subclass, weighted lengths at annuli for all ages and

TABLE 3.—Back-calculated growth (shell length, in millimeters) of small ocean quahogs. Samples taken from lat. 40°25′ N, long. 72°24′ W, 26-29 July 1978, in the Middle Atlantic Bight.

Number of annuli		Length at capture	1	2	3	4	5	6	7	8	9	10	11	12	13
2	$\bar{x}$	18.00	7.00	12.30											
	SD	0.00	0.00	0.00											
	n	1	1	1											
3	$\bar{x}$	23.36	4.59	10.59	18.01										
	SD	3.42	0.78	2.66	3.14										
	n	9	9	9	9										
4	$\bar{x}$	29.73	4.39	10.04	16.99	24.38									
	SD	2.00	0.73	2.13	2.38	1.96									
	n	14	14	14	14	14									
5	$\bar{x}$	34.58	4.43	8.80	14.45	21.72	29.72								
	SD	3.19	0.07	1.50	2.29	3.08	3.41								
	n	26	26	26	26	26	26								
6	$\bar{x}$	38.49	4.07	7.77	13.40	19.13	26.09	33.88							
	SD	2.73	0.59	1.57	2.49	2.58	2.73	2.92							
	n	27	[1]25	27	27	27	27	27							
7	$\bar{x}$	41.66	4.16	7.66	12.10	17.42	23.87	30.81	37.61						
	SD	2.00	1.10	1.34	1.72	1.57	1.87	1.98	2.05						
	n	29	[1]27	29	29	29	29	29	29						
8	$\bar{x}$	46.24	3.92	7.59	12.29	16.92	23.64	29.95	36.63	42.76					
	SD	1.78	0.98	1.44	2.39	2.77	2.38	2.52	2.22	1.99					
	n	10	10	10	10	10	10	10	10	10					
9	$\bar{x}$	47.60	3.10	7.50	11.00	15.90	21.30	27.40	33.50	39.20	44.90				
	SD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
	n	1	1	1	1	1	1	1	1	1	1				
10	$\bar{x}$	48.23	3.67	6.47	11.77	15.97	20.80	25.57	31.17	36.90	40.40	45.30			
	SD	0.59	0.29	0.50	1.19	2.48	2.31	2.35	1.89	2.07	0.36	0.30			
	n	3	3	3	3	3	3	3	3	3	3	3			
11	$\bar{x}$	54.35	3.90	5.70	9.35	13.80	20.30	27.60	34.20	40.20	44.45	48.50	51.95		
	SD	2.05	0.00	0.42	0.78	0.28	3.68	4.81	2.83	1.41	1.06	0.71	1.20		
	n	2	[1]1	2	2	2	2	2	2	2	2	2	2		
12	$\bar{x}$	53.87	3.73	7.23	10.07	12.97	19.13	27.00	31.60	35.67	39.50	43.50	44.75	49.55	
	SD	3.95	0.35	1.38	2.30	3.28	4.15	9.37	8.56	7.90	8.42	8.23	1.91	2.90	
	n	3	3	3	3	3	3	3	3	3	3	3	[2]2	2	
13	$\bar{x}$	53.90	—	5.20	9.70	12.80	17.50	22.20	28.00	34.70	38.30	43.70	46.40	50.00	52.00
	SD	0.00	—	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	n	1	[1]—	1	1	1	1	1	1	1	1	1	1	1	1
14[2]	$\bar{x}$	51.15	3.85	7.30	10.65	15.30	22.40	29.10	33.75	38.75	43.40	48.10			
	SD	5.16	0.50	2.26	2.19	0.42	0.57	1.56	1.34	0.07	1.98	0.00			
	n	2	2	2	2	2	2	2	2	2	2	1			
16[2]	$\bar{x}$	57.93	4.00	6.95	12.05	18.50	24.80	31.53	37.25	42.60	46.57	50.30	55.30		
	SD	2.90	0.00	1.11	2.24	2.49	3.95	3.75	2.91	2.60	1.59	1.84	0.00		
	n	4	[1]2	4	4	4	4	4	4	4	4	1			
18[2]	$\bar{x}$	57.10	3.60	7.55	10.95	16.40	24.60	29.85	40.10	43.40	46.80	49.00			
	SD	0.99	0.00	2.05	3.89	5.80	5.37	4.46	0.00	0.00	0.00	0.00			
	n	2	[1]1	2	2	2	2	2	1	1	1	1			
ALL	$\bar{x}$	38.94	4.21	8.27	13.59	19.17	25.44	31.13	36.28	40.40	42.82	46.52	49.18	49.70	52.00
	SD	8.65	0.85	1.95	3.03	3.69	3.95	3.75	3.47	4.01	4.41	4.32	4.58	2.07	0.00
	n	134	125	134	133	124	110	83	56	27	16	13	6	3	1
	Min	18.7	2.5	5.1	7.8	9.3	14.5	18.6	24.5	29.3	32.4	36.0	43.4	47.5	52.0
	Max	60.4	7.0	15.8	22.5	26.7	36.4	38.1	41.9	46.2	48.8	52.3	55.3	51.6	52.0

[1]External mark eroded but mark present in shell cross section.
[2]Number of annuli exceeds the number of lengths at annulus because marks could be distinguished in shell cross sections that were too closely spaced to discern on shell surfaces.

lengths at capture were also determined (Table 3).

Specimens recaptured in 1979 ranged in shell length from 59 to 104 mm, most had a deep brown or black periostracum. Several specimens did, however, exhibit the characteristic external banding pattern (Fig. 1), and were useful in validating the presumed annual periodicity of marks.

Marginal shell growth beyond the last external mark was strikingly different among small ocean quahogs from August 1979 and February 1980 samples. Mean lengths at capture for individual age classes from summer 1978 (particularly ages 1-9) were substantially greater than lengths at the last annulus, and were nearly equivalent to mean lengths at the last annulus for the next age class (Table 3). Ocean quahogs from winter 1980 invariably had formed or were forming an annulus at the shell margin (Fig. 1). A similar pattern was noted in shell cross sections.

Modified exponential and logistic growth equations were fitted to mean back-calculated lengths at age, from the July 1978 samples (Table 3), using the asymptotic regression and nonlinear least squares computer programs BMDO6R and BMDO7R, respectively (Dixon 1977; Fig.. 3). Few aged shells were as large as those recaptured (Tables 2, 3). Growth functions generated from aging data were thus extrapolated to the size range of recaptured specimens and results compared with annual growth increments predicted from mark-recapture (Figs. 2, 3). An age-size point necessary to initiate the mark-recapture growth function was computed from growth equations fitted to age-length data generated in shell banding experiments; the mark-recapture equation was then iterated to encompass most shell lengths present at the marking site (Figs. 4, 5).
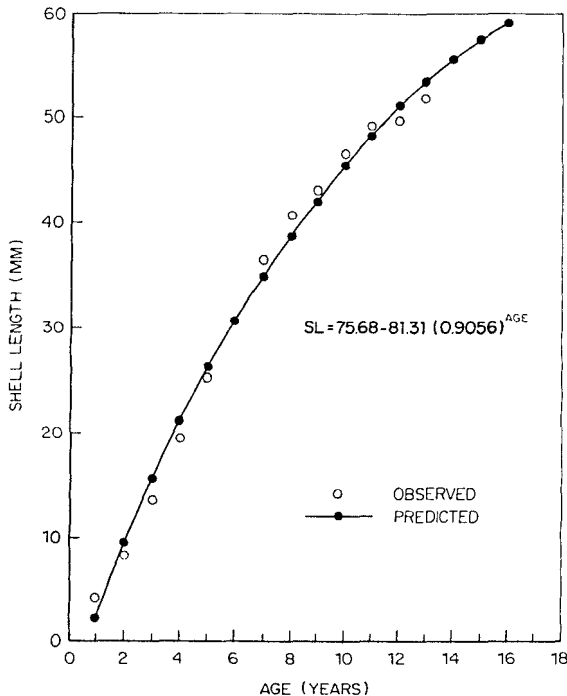

FIGURE 3.—Observed and predicted shell lengths at age for small ocean quahogs sampled during July 1978 near lat. 40°25′ N, long. 72°24′W, in the Middle Atlantic Bight.

Length-Weight

Shell length-drained meat weight relationships were computed for samples taken during August 1979 and February 1980. Laboratory
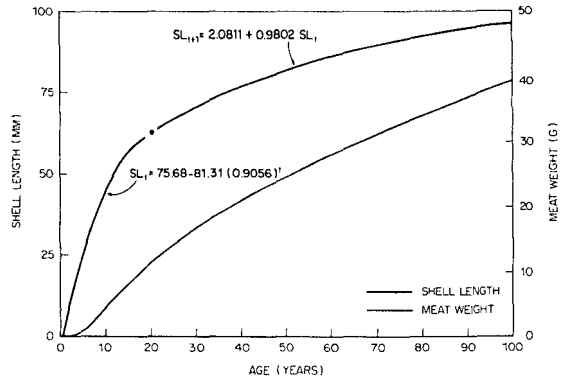

FIGURE 4.—Predicted shell lengths (millimeters) and drained meat weights (grams) at age for ocean quahogs at lat. 40°25′ N, long. 72°24′W, in the Middle Atlantic Bight. Growth in length is described by an equation derived from studies of external banding patterns of small individuals (left of dot), and the Ford-Walford equation from mark-recapture data (right of dot). Weights at age are derived by applying the overall length-weight equation presented in Table 5 to calculated mean lengths at age.

and statistical methods are given in Murawski and Serchuk (1979). Equations for recaptured and unmarked specimens from August 1979 were compared by covariance analysis to assess effects of marking (Table 4). Presumably, if physiological processes of the animal were significantly disrupted by the marking procedures, the adjusted mean of the length-weight equation might be statistically lower than that of controls. Seasonal variability in length-weight was investigated by comparing summer and winter equations (Table 5).

RESULTS AND DISCUSSION

New shell growth of recaptured individuals was clearly discernible in small specimens (<70 mm) not only at the mark, but all along the

TABLE 4.—Ocean quahog shell length-meat weight regression equations, and analysis of covariance for marked and unmarked individuals sampled at lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight, during August 1979.

| Sample | Linear regression parameters | | | |
	Intercept (a)	Slope (b)	r	n
Marked	−9.8373	2.9530	0.975	55
Unmarked	−9.0170	2.7637	0.953	126

| Sample | Test of adjusted mean | | | Test of slope | |
	Adjusted mean	df	F	df	F
Marked	2.8702				
Unmarked	2.8714	1,178	0.001 n.s.	1,177	2.13 n.s.

n.s. = P>0.05.

FIGURE 5.—Length-frequency distributions (1 mm intervals) of ocean quahogs sampled near lat. 40°25′N, long. 72°24′W, in the Middle Atlantic Bight, April 1976-February 1980.
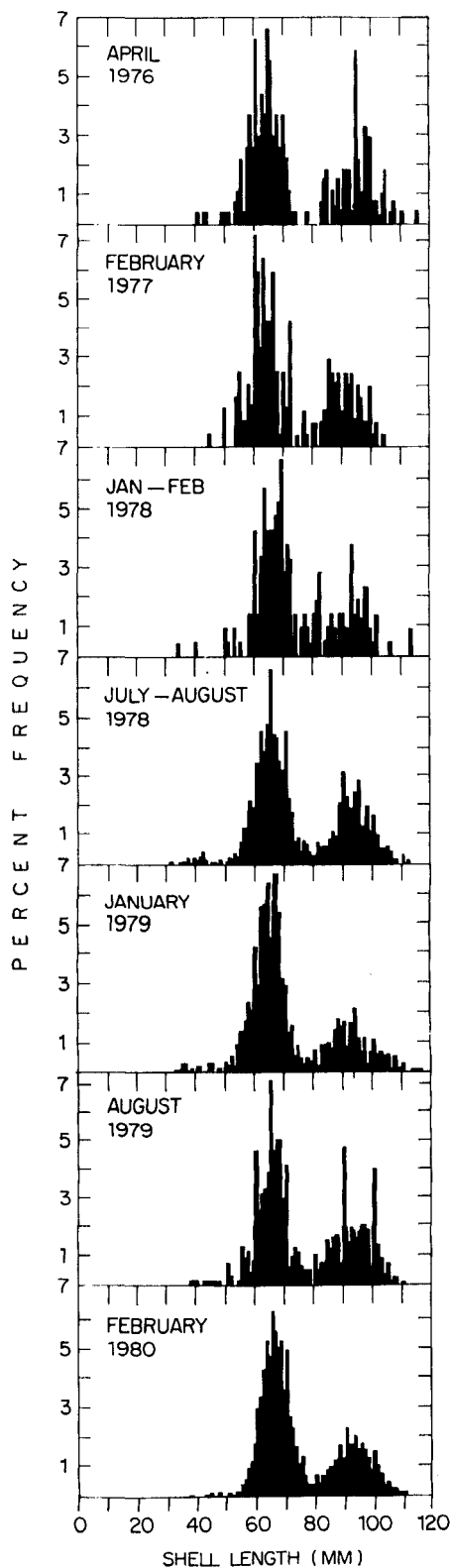
TABLE 5.—Ocean quahog shell length-meat weight regression equations, and analysis of covariance for August 1979 and February 1980 samples taken near lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight.

Sample	Linear regression parameters			
	Intercept (a)	Slope (b)	r	n
August 1979	−9.2901	2.8274	0.961	181
February 1980	−8.6865	2.7086	0.976	278
All data	−9.0627	2.7871	0.967	459

Sample	Test of adjusted mean			Test of slope	
	Adjusted mean	df	F	df	F
February 1980	3.0302				
August 1979	2.9398	1,456	58.86**	1,455	3.22 n.s.

**$P \leq 0.01$; n.s. = $P > 0.05$.

ventral margin when the periostracum was removed (Fig. 1). A growth interruption was produced at the previous shell edge of small specimens; new material was formed slightly below the earlier shell margin and was shinglelike in appearance (Fig. 1). Growth in larger ocean quahogs was less distinct and thus more difficult to measure. Where clear growth interruptions were not present, a faint yellowish band contrasting with white shell material was interpreted as a marking-induced check and growth was measured from that point. Shell growth was assessed midway between grooves that formed the mark since, in the case of larger specimens, the depth of the grooves was actually greater than the amount of new shell deposited (Figs. 1, 2).

A total of 11,658 ocean quahogs was measured directly from dredge catches at the marking site during 1970-80 (Table 1; Figs. 5, 6). Although minimum spacing of bars or rings in the rear portion of dredges varied somewhat (Table 1), size selectivity was apparently not significantly altered. Repeated tows were made at the marking site during August 1979 with 25 × 25 mm and later 51 × 51 mm wire mesh in the after portion of the dredge. Size distributions of ocean quahogs were nearly identical before and after the alteration. A possible explanation for the lack of differential selectivity is that shell, sand, and live invertebrates may have clogged the dredge at the beginning of tows, negating further filtering ability.

Two discrete length-frequency modes were exhibited in all sets of samples (Figs. 5, 6). Few small ocean quahogs (<50 mm) were encoun-
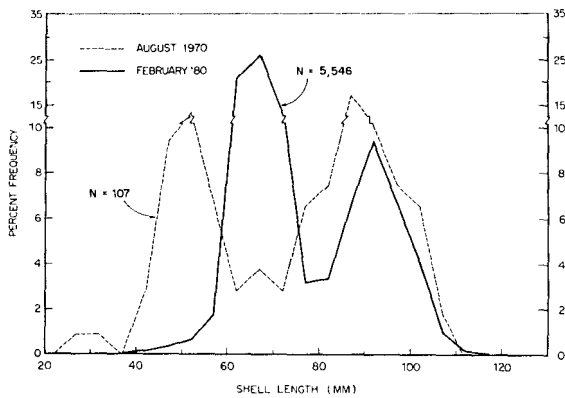
FIGURE 6.—Length-frequency distributions (5 mm intervals) of ocean quahogs sampled near lat. 40°25'N, long. 72°24'W, in the Middle Atlantic Bight, August 1970 and February 1980.

tered from 1976 to 1980 (Fig. 5) and, considering uniformity of modes over time, recruitment was probably equally poor during 1971-76. Thus, corresponding modes in the 1970 and 1980 samples were probably composed of the same year classes (Fig. 6). Average size of the small mode increased about 13 mm during the 9½-yr interval between August 1970 and February 1980, while the large group shifted about 3 mm (Figs. 5, 6; Table 1). Size progression of modes was minimal during 1976-80; intersample variation may be primarily related to differential sample sizes (Table 1). The effects of a sevenfold increase in sampling intensity can be seen by comparing August 1979 and February 1980 frequencies. Modes are smoothed in the latter sample, yet respective peaks are at precisely the same 1 mm intervals in both (65 and 90 mm). Average shell sizes ranged from 71 to 77 mm; however, trends in shell length among samples were not apparent (Table 1).

The average lengths of recaptured ocean quahogs (Table 2) were slightly greater than concurrent length-frequency samples (Table 1), although length extremes of the marked individuals were not as great. Recaptured ocean quahogs also exhibited the bimodal length-frequency distribution (Fig. 2), indicating recaptured specimens represented a relatively unbiased sample of marked individuals and the ocean quahog population in the immediate vicinity of the study area. Calculated increments of shell growth from ocean quahogs recaptured in 1979 ranged from 0.08 to 1.38 mm, and averaged 0.56 mm (Table 2). Those recaptured in 1980

grew an average of 1.17 mm (range 0.07-4.32 mm). Thus, incremental growth approximately doubled between summer 1979 and summer 1980, implying growth rates were similar during the 2 yr of the experiment and that marking procedures probably did not significantly disrupt growth patterns. Growth increments of ocean quahogs at liberty 1 yr generally declined with increasing shell length, although there was substantial variation about a linear fit (Fig. 2). The linear equation for predicting annual increment of growth from initial length is given in Figure 2; the Ford-Walford equation is: $SL_{t+1} = 2.0811 + 0.9802\ SL_t$, where SL is shell length (in millimeters) at age t. An exponential equation fitted to data in Figure 2 ($Y = 14.1216$ (exp $(-0.0459X)$)) explained about 8% more of the residual variance about the predicted line than did the linear equation. However, growth rates implied from length-frequency analyses were substantially greater than those from the exponential fit, and were similar to rates computed from the linear (von Bertalanffy) model. Thus, the latter model was considered more valid. Estimates of the asymptotic length (L_∞) and growth coefficient (K) from two fitting methods are:

	BGC4	Annual increment
L_∞ (mm)	107.06	104.95
K	0.0195	0.0200

Values of L_∞ from the two methods are >99.5% (BGC4) and 98.5% (annual increment) of the cumulative 1980 length-frequency distribution at the study site. Estimates of K are relatively low and characteristic of slow-growing, long-lived species (Beverton and Holt 1959).

Analyses of shell banding features present in small specimens indicate both external and internal marks are produced once during the biological year in these sizes. Several of the small recaptured ocean quahogs exhibited concentric external rings, and these specimens formed one such band during the interval between marking and recapture (Fig. 1a). Studies of small unmarked individuals retained from summer and winter sampling demonstrate that external and internal marks generally correspond in number and position. Internal marks were particularly useful in age determination when external marks were eroded near the umbo or closely spaced at the shell margin. Small ocean quahogs captured during the summer exhibited wide

marginal increments of shell growth from the last external and internal marks to the shell edge, whereas winter samples had recently formed annuli (Fig. 1c; Table 3). Thus, mark formation probably occurs during the last half of the calendar year. These observations are consistent with data presented by Jones (1980). In a study of the seasonality of incremental shell growth, he noted that internal growth bands in shell cross sections were formed from September to February. The formation of growth bands apparently overlaps the spawning period (Jones 1980); however, both events may be related to other physiological or environmental stimuli since specimens that were reproductively immature formed bands concurrently with mature ocean quahogs.

Back-calculated mean lengths at age varied considerably depending on the subset of data analyzed in Table 3. Mean lengths at age for all year classes (bottom rows in Table 3) were generally smaller than mean lengths at the last complete annulus (rightmost diagonal vector), and growth of recent age groups (2-8) appeared more rapid than for older ocean quahogs (Lee's phenomenon; see Ricker 1969). However, conclusions regarding the growth of older age groups (9-18) are tenuous due to the relatively small numbers of these ages sampled (87% of the samples were ≤8-yr-old).

Age analyses were limited to ocean quahogs that exhibited suitable contrast on the shell surface to discern external concentric rings. Thus, the oldest aged ocean quahogs (particularly ages 14-18) may represent the smallest, slowest growing individuals of their year classes; faster growing individuals may have reached sizes associated with color changes of the periostracum. Nevertheless, back-calculated mean lengths at age for 14- to 18-yr-old ocean quahogs did not tend to be progressively smaller than means for ages 9-13, perhaps indicating that size selectivity of older individuals was not a significant bias (Table 3).

The objectives of fitting statistical models to age-length data were to describe growth during the juvenile and early adult phases of life, and more importantly, to predict ages associated with the lengths of the smallest recaptured specimens (59-65 mm) thereby linking the age-length data and mark-recapture results into a continuous growth function. Recognizing the disparate nature of data subsets in Table 3, a series of exponential and logistic growth equations were fitted to: 1) weighted mean back-calculated lengths at age for all quahogs, 2) weighted mean lengths at age for ages 2-8, and 3) mean lengths at the last completed annuli (rightmost diagonal vector) for ages 2-10 and 2-13. For our purposes, the applicability of a particular model fit was judged not only by the total amount of variance between length and age explained by the equation, but by predicted annual growth increments in the 59-65 mm range. An appropriate model would fit as much of the age-sample data as possible and yield calculated annual growth increments consistent with those observed from recaptured specimens.

Exponential equations utilizing weighted mean back-calculated lengths for ages 2-8, and lengths at the last complete annulus for ages 2-13 yielded unacceptable fits by our criteria. The former equation was calculated with information from the linear portion of the growth curve, predicted lengths beyond age 8 were unrealistically high. The latter equation incorporated one negative growth increment (between ages 11 and 12) and thus the calculated asymptote was only 62.8 mm; predicted annual growth near the asymptote was considerably less than observed increments for that size (Fig. 2).

The logistic growth equation fitted to weighted mean lengths at age for all ocean quahogs ($SL = 52.09/1 + \exp(2.4722 - 0.4702(t))$) was superior to the respective exponential fit considering the residual sums of squares criterion. The reverse was true for the logistic equation describing mean lengths at the last annulus for ages 2-10 ($SL = 43.12/1 + \exp(2.9361 - 0.8069(t))$). However, asymptotic lengths were, for both logistic equations, well below the range of shell lengths considered in the mark-recapture experiments. Thus, extrapolation of logistic age-length relationships, necessary for initializing the Ford-Walford equation, was not feasible. On the contrary, the two exponential equations yielded reasonable asymptotic lengths and adequately described ocean quahog growth relative to that inferred from modal progressions in 1970 and 1980 length-frequency distributions (Fig. 6) and observed growth increments (Fig. 2).

Exponential growth equations computed from weighted mean lengths at age for all ocean quahogs and mean lengths at the last annulus for ages 2-10 were: $SL = 75.68-81.31 (0.9056)^{t}$ and $SL = 72.70-75.22 (0.8935)^{t}$, respectively. Mean lengths at age predicted from the two equations generally reflect differences among data sets

over the range of shell sizes used to fit the functions; however, estimated lengths at age converge near the sizes of the smallest recaptured specimens. Estimated lengths at age 20 were 64.49 and 64.29 mm, respectively. Corresponding growth increments from age 20-21 were 1.06 and 0.84 mm, well within the range of observed growth for those sizes (Fig. 2). If calculated lengths at age 20 are assumed to be the starting points for the Ford-Walford equation ($SL_{t+1} = 2.0811 + 0.9802 SL_t$), the two acceptable exponential equations yield virtually identical growth curves when the Ford-Walford relationship is iterated. Additional growth analyses were conducted using the regression equation fitted to weighted mean back-calculated lengths for all ages because the maximum amount of information was used and the equation's behavior in the vicinity of marking data was consistent with empirical observations. However, further research on the growth patterns of small ocean quahogs is indicated in order to resolve differences between various data subsets in Table 3 and thus to define a more appropriate growth model for these sizes.

A composite growth curve incorporating the aged samples and mark-recapture data is given in Figure 4. The Ford-Walford equation was iterated to age 100 and a predicted shell length of 96.91 mm. Although ocean quahogs reach a size of at least 117 mm in the vicinity of the marking site (Table 1), ages substantially in excess of 100 are not necessarily implied because of the statistical variability in the marking data used to fit the predictor (Fig. 2). Annual growth in shell length is rapid during the first 20 yr of life, but declines significantly thereafter. Average yearly shell growth is 6.3% at age 10, 0.5% at age 50, and 0.2% at age 100.

Estimates of the von Bertalanffy parameter t_0 (age at zero length) were computed as -27.29 yr and -27.62 yr for the BGC4 and annual increment equations respectively, with $SL_{20} = 64.49$ mm (Gulland 1969, equation 3.5). Although predicted lengths at ages >20 are similar to those in Figure 4, a relatively poor fit to younger ages results from both von Bertalanffy equations.

The validity of using the age-length functions given in Figure 4 to describe ocean quahog growth at the marking site can be assessed by comparing predicted growth to that from modal progressions in length-frequency samples. Frequency distributions from 1976 to 1980 exhibit inter-sample variability in the position of major

modes but no progressive shifts are discernible (Fig. 5). However, expected growth during the 5-yr period (Fig. 4) was smaller than could probably be identified, given the precision of length-frequency sampling (Table 1; Fig. 5). Length modes can be used to compute growth at the site between August 1970 and February 1980 (Fig. 6). Average growth of the smaller mode (52 mm in 1970) was about 13 mm, and the larger mode (87 mm in 1970) added about 3 mm shell length during the 9½-yr interval (Figs. 5, 6). Ocean quahogs 52 mm in length are about 12-yr-old and average 21-yr-old at 65 mm; the estimated age of 87 mm individuals is 60 yr and 90 mm quahogs average 70-yr-old (Figs. 3, 4). Thus, predicted growth during the period 1970-80 is strikingly similar to that inferred from length mode progressions, implying that age analyses and mark-recapture data adequately describe historical ocean quahog growth at the site.

The age-length relationships presented herein have been computed for shell sizes in excess of 95 mm and ages up to 100 yr. However, computed relationships for large sizes (>65 mm) are based on average growth rates from mark-recapture results and not from aging of individual specimens. It is likely, based on these analyses, that ocean quahogs do reach 100 yr in age; however, direct age determination of large individuals is contingent upon development and validation of suitable methodologies. Internal banding patterns present in shell cross sections were useful in aging small specimens since formation of the bands apparently occurs once annually. Seasonal shell formation patterns (Jones 1980) and age analyses of large individuals based on internal banding (Thompson et al. 1980; Jones 1980) are generally consistent with our data. Analysis of shell cross sections of large recaptured specimens may be useful in determining the periodicity of internal banding and the validity of the aging technique for large ocean quahogs; study of this material continues.

The regressions of shell length vs. drained meat weight for marked and unmarked ocean quahogs taken during August 1979 were not significantly different in slope or adjusted mean (Table 4). If in fact soft-tissue robustness is a valid index of relative condition, then marked individuals apparently suffered no lasting effects from the stress of dredging and handling. This observation is supported by the conclusions that incremental shell growth of marked specimens was similar to that computed from progressive

length frequencies of the population as a whole, and growth rates of marked individuals were nearly equal between 1978-79 and 1979-80.

Length-weight equations from February 1980 and August 1979 were parallel (Table 5); winter samples were apparently heavier in drained meat weight at a given shell length than summer samples. However, the magnitude of predicted differences in weight at length was small (4-11% for 65-115 mm ocean quahogs). Differences may be related to weight changes associated with sexual development, or merely a statistical artifact. Samples from winter and summer were combined to predict average weight for a given length during the year (Table 5). The resulting length-weight equation was applied to computed lengths at age to derive an age-weight relationship (Fig. 4). Initial weight gains are proportionally greater than concomitant length increases, but growth rates are nearly identical at the oldest predicted ages. Average annual increases in drained meat weight are 18.1% at age 10, 1.6% at age 50, and 0.2% at age 100 (Fig. 4).

Growth rates determined from the examination of concentric external banding patterns indicate small ocean quahogs may grow faster off Long Island than in the Northumberland Strait and in Passamaquoddy Bay (Caddy et al. footnote 7). However, data are insufficient to conclude that a latitudinal cline in ocean quahog growth exists. Factors influencing growth rates in a particular area are speculative; however, density dependence must be considered. Murawski and Serchuk (footnote 2) noted relative population stability and poor recruitment for ocean quahogs in the Middle Atlantic during 1965-77. Stable population size, poor recruitment, and slow growth are characteristic of populations under density dependent regulation. Investigation of ocean quahog growth rates at various densities may help to elucidate their interrelationship and indicate the population consequences of cropping high density areas.

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