A MARK-RECAPTURE TEST OF ANNUAL PERIODICITY OF INTERNAL GROWTH BAND DEPOSITION IN SHELLS OF HARD CLAMS, *MERCENARIA MERCENARIA*, FROM A POPULATION ALONG THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Individually marked and measured *Mercenaria mercenaria* were placed at natural depths in the sediments inside field enclosures of three types in an estuary near Cape Lookout, N.C., in June 1978. Subsets of hard clams were collected and sacrificed on October 1979, May 1980, October 1980, and October 1981. Sectioning one valve of each experimental clam along the axis of greatest growth revealed growth discontinuities (both in texture and coloration) in the middle and outer shell layers. These growth bands were deposited annually during the summer-early fall season. Enclosure type (microhabitat variation) did not alter the regular annual pattern of band deposition: 93% of the experimental clams in October collections (115 of 123) exhibited the predicted number of added growth bands in the increment of shell growth that had been deposited since initial marking. Examination of presumed daily lines on acetate peels and thin sections suggested that the annual band corresponds to a period of relatively slow growth. Only a few (≃6.7%) of the *M. mercenaria* recruits in spring samples failed to exhibit an identifiable growth band from their first summer-fall period. A comparison of the size-frequency distribution at first band on older clams to the size distributions of new recruits in September-October and in April-May revealed that the first growth band on a new *M. mercenaria* recruit is usually deposited soon after September-October during the clam's first fall. Thus, southeastern *M. mercenaria* near Cape Lookout can be aged by counting internal growth bands but, unlike northern populations, exhibit slow growth and annual band deposition during summer-early fall rather than in winter.

Application of the aging technique to a January-February 1980 collection of *M. mercenaria* from Core Sound, N.C., revealed a high proportion of older clams (up to 32 years of age) and a mean age of >9 years. Growth rates, inferred from the relationship between size and estimated age, were high; on average a legally harvestable size (4.46 cm in length) is reached by 1½ years. The age-frequency distribution from this collection revealed lower recruitment success of the 1977, 1978, and 1979 year classes than of previous year classes. This partial year-class failure corresponds with the period of fourfold increase in commercial harvest of *M. mercenaria* in North Carolina and suggests that further studies should test for a spawner-recruit relationship among hard clams.

The depositional regularity of macro- and microstructural features in bivalve mollusc shells has been exploited as a chronometer by scientists in several disciplines (reviewed succinctly by Jones 1980). Deposition patterns in bivalve shells have proved useful to 1) paleontologists and environmental biologists in reconstructing the local history of environmental change (Pannella and MacClintock 1968; Clark 1974; Rosenberg and Runcorn 1975; Pannella 1976; Rhoads and Lutz 1980), 2) archaeologists in dating the seasons of prehistoric site occupation (Coutts 1970; Koike 1973), and 3) population biologists and fisheries managers in constructing quantitative life history and growth schedules for the bivalves themselves (Rhoads and Pannella 1970; Kennish and Olsson 1975; Jones et al. 1978; Kennish 1980). Biologists and managers should probably make more use of the historical records preserved in bivalve shells to estimate survivorship curves by assessing age at death and growth curves by measuring growth increments between successive chronological markers because these integrative methods are more efficient than all rigorous alternative methods, which require measurements over at least a year's time. Concern over the paucity of controlled tests of the regular periodicity of repeating shell features (Clark 1974; Gould 1979; Jones 1981) may be partly responsible for the cautious use of shell information by invertebrate population biologists.

The hard clam, *Mercenaria mercenaria* (L.), has been used frequently by paleontologists, archaeologists, and population biologists as a subject for shell macro- and microstructural analysis (Barker 1964; Pannella and MacClintock 1968; Rhoads and

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Pannella 1970; Crenshaw 1972; Kennish and Olsson 1975; Gordon and Carriker 1978; Kennish 1980). Most published analyses of shell deposition patterns which are directed towards estimating life history parameters and growth rates in *M. mercenaria* have been conducted on northern populations (but see Clark 1979; Clark and Lutz 1982). Like many other marine bivalves (e.g., *Pecten maximus* in Mason 1957; *Scrobicularia plana* in Green 1957; and *Macoma baltica* in Segerstråle 1960), *M. mercenaria* from New Jersey (Kennish 1980) to Massachusetts (Pannella and MacClintock 1968) deposits a winter band of slow-growth increments that can serve as an annual marker. Because hard clams in southeastern populations show a pattern of nearly constant monthly growth year-round (Ansell 1968), we questioned whether *M. mercenaria* in the southeast would deposit a clear annual marker in its shell. Here we report on mark-recapture tests of whether *M. mercenaria* from the vicinity of Cape Lookout, N.C., deposits any regularly periodic feature in its shell that could be used to age the individual clams. A rigorous experimental test of the aging technique is of vital importance to the wide spectrum of scientists who would like to utilize internal shell markers to age *M. mercenaria* but cannot with confidence until test data displace the doubts justifiably expressed by Gould (1979) and Jones (1981). We also apply our results to a southeastern population of hard clams to demonstrate estimation of age-frequency distribution and to draw inferences about population dynamics and growth.

MATERIALS AND METHODS

Tests of Aging Methodology

1-Year Class and Older

A mark-recapture study was designed to test whether *Mercenaria mercenaria* in the vicinity of Cape Lookout deposits any distinct annual marker in its seasonal pattern of shell growth. On 21-22 June 1978, we placed 28 individually marked and measured *M. mercenaria* into each of six 1 m^2 field enclosures. This density is within the range occurring naturally in this area but about four times the average observed in a nearby Bogue Sound seagrass bed (Peterson 1982). We employed a wide range of initial sizes from 1.8 to 10.2 cm in length and kept size-frequency distribution similar in each enclosure. Marking was achieved by applying color-coded dots of Mark-Tex Corp.[2] paints to the external shell surface of each clam. Three perpendicular linear dimensions (length along the longest anteroposterior axis, height, and width) were measured to the nearest 0.1 mm on each clam using vernier calipers. On four subsequent occasions (17 October 1979; 22 May 1980; 8 October 1980; 9 October 1981), 5 to 11 (usually 7) clams were removed from each enclosure and killed by steaming in the laboratory to provide shells with varying, but known, histories of terminal (marginal) growth for macro- and microstructural analyses.

Field enclosures were located in muddy-sand sediments at a low-tide water depth of ≈0.5 m within a protected embayment inside Middle Marsh in Back Sound, N.C. (Fig. 1). Nelson (1979) and Homziak et al. (1982) have described this site. Water temperature in Back Sound is seasonally variable; monthly means at nearby Beaufort, N.C., vary from 4° to 29°C (Sutherland and Karlson 1977). Salinities remain high year-round, ordinarily above 32‰ but with lower values recorded after heavy rainstorms (unpublished data for nearby Bogue Sound, by H. J. Porter, University of North Carolina). All six enclosures were located in an unvegetated area within an eelgrass, *Zostera marina*, bed and were protected on the north, east, and west by emergent salt marshes (*Spartina alterniflora*) and on the south by a sandbar which was exposed on spring low tides.

Enclosures were constructed from 4.2 m long by 13 cm high strips of 6 mm Dupont Vexar mesh, folded to form a 1 m^2 square, and forced vertically 10 cm into the sediments. To anchor the enclosures, 0.6 m long steel reinforcing rods were also pushed into the sediments and were attached with nylon cable ties to the Vexar mesh at each corner and at halfway points along each side. The belowground mesh inhibited *M. mercenaria* migration, while the aboveground mesh served to identify the boundaries of the plots and thereby aided recovery of the marked clams. To induce locally differing sets of environmental conditions, we added 1 m^2 tops made of 6 mm Vexar mesh to two enclosures and partial tops made of two parallel 0.25 m^2 Vexar strips to two other enclosures. All complete and partial tops were fastened to the enclosure walls with nylon cable ties at 5 cm intervals and supported above the sediment surface with wooden dowels implanted inside each enclosure. Thus, our complete design consisted of replicate clams inside two replicate enclosures of each of three different caging treatments.

Before introducing the experimental *M. mercenaria* into the field plots, we removed all large resident *M.*

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[2] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

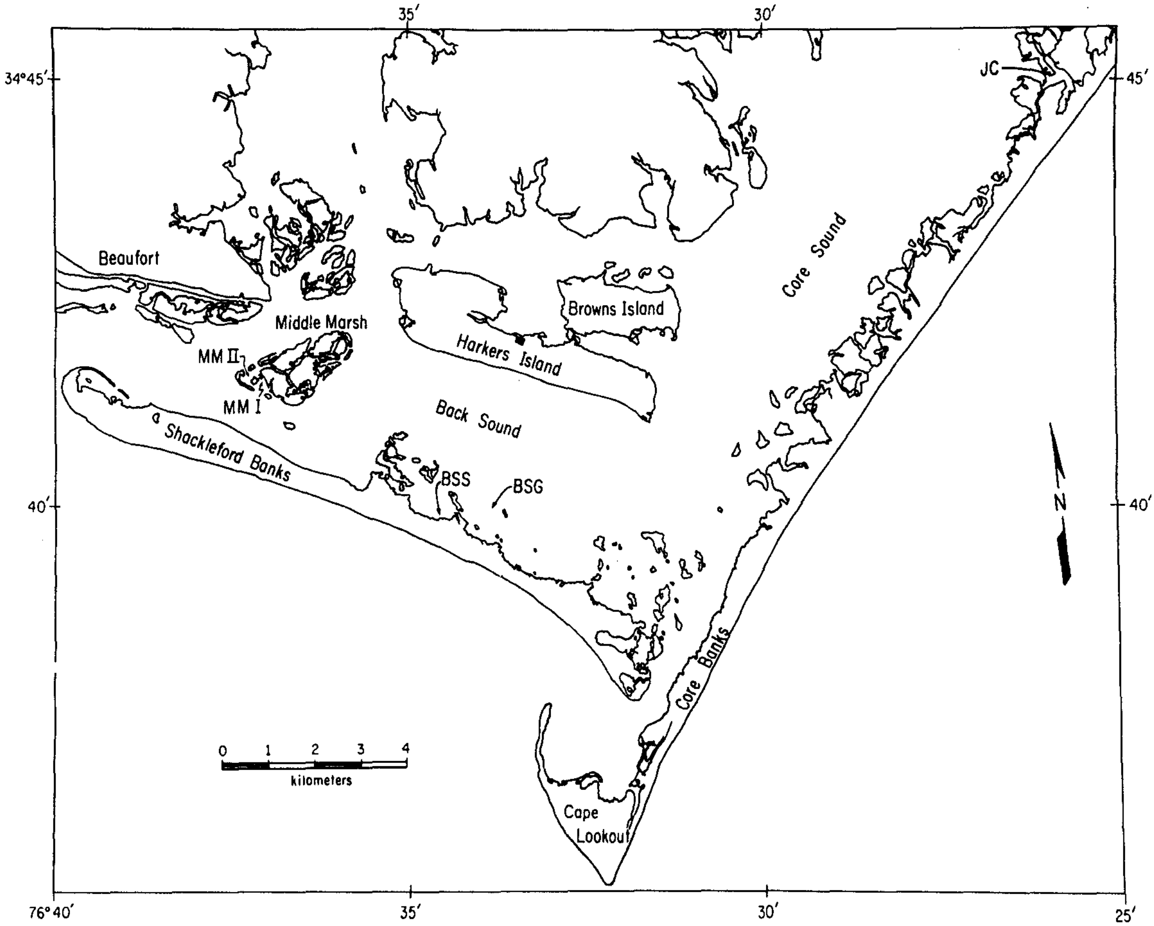

FIGURE 1.—Geographic relationships among study and collection sites in the Cape Lookout vicinity of North Carolina: MM I—the site of the mark-recapture experiment in a seagrass, *Zostera marina*, meadow at Middle Marsh and of the fixed 1 m^2 enclosures sieved seasonally for new recruits; MM II—the other site of fixed 1 m^2 enclosures sieved seasonally for new recruits on a muddy-sand flat near the west end of Middle Marsh; JC—the Johnson Creek collection site in Core Sound; BSS and BSG—the sand flat and the seagrass sites (respectively) in Back Sound from which 0-year class *Mercenaria mercenaria* were collected in February-April 1980 for estimation of the proportion without an annual band.

mercenaria by systematically plowing with fingers to a 10 cm depth followed by in situ sieving with 6 mm mesh to that same depth. This process permitted establishment of constant *M. mercenaria* density across all treatments and all replicates. The same procedure was also used to recover all marked clams from each plot on 20 September 1978 and on 21 April 1979. On those dates, each marked clam was remeasured and returned within 1 h to its assigned plot. On both those dates and on all four dates when clams were sacrificed for shell analyses, tops and partial tops were removed and replaced with new mesh to prevent extensive fouling. On the first two dates (17 October 1979 and 22 May 1980) when clams were sacrificed and returned to the laboratory for shell analyses, all clams were again excavated by this same sampling procedure and remeasured. Those not sacrificed were returned to their assigned plots within 1 h. On the two subsequent sampling occasions, no remeasuring occurred and a preset number of clams was removed from each field plot without excavating the others.

In the laboratory, we used calipers and a fine, felt-tipped pen to locate and mark on the outer shell surface of each clam its size at each measurement date (including size at introduction). A low-speed Buehler Isomet saw with a diamond blade was used to cut the marked valves from umbo to the ventral margin along the axis of greatest growth (Pannella and MacClintock 1968; Rhoads and Pannella 1970). This cut revealed the cross-sectional growth surface, which was then sanded with increasingly fine-grained grit and polished with alumina powder on a polishing wheel. We examined macroscopically the polished cross section of each clam to determine whether any repeating feature, like the winter growth bands of northern *M. mercenaria* (Pannella and MacClintock 1968; Kennish 1980), served as an annual chronometer. By comparing the inked lines marking size at introduction and size at known dates of measurement on the outer shell surface to the polished cross section, each of three independent observers recorded 1) an estimate of the number of growth bands deposited on each clam since introduction and 2) the season of band deposition. For a subset of experimental clams, acetate peels were prepared by the standard procedures (Rhoads and Lutz 1980) and examined under a Wild M11 microscope equipped with ocular micrometers 1) to ascertain if annual markers were more or less evident than in macroscopic view and 2) to utilize presumed daily growth lines to estimate the exact period of annual band deposition and to determine by measuring the daily increments whether the annual band represented a period of relatively slow or rapid growth

0-Year Class

Because our mark-recapture test of the aging technique did not include any clams in the 0-year class (which was unavailable in June) and because the first annual band might easily be overlooked, we designed an independent test of our ability to recognize the very first annual band in *M. mercenaria*. From February to April 1980, we collected all *M. mercenaria* from 432 samples that were taken by hydraulic suction dredge (described below) from 0.25 m^2 sampling frames to a depth of 15 cm and passed through a 3 mm mesh. This sampling process collected all clams >0.5 cm long with high efficiency and without size selectivity (see Appendix). Equal numbers of samples were taken from a shallow, subtidal eelgrass meadow and from nearby unvegetated sandy bottom at similar depths ($\simeq$1.0 m) along the Shackleford Bank edge of Back Sound, about 8 km northwest of Cape Lookout (Fig. 1). All *M. mercenaria* were brought to the laboratory, killed by steaming, measured with calipers, and sectioned to expose growth bands. Here we compared the total numbers of clams which lacked any growth band with the numbers with a single band. Recruits sampled in February-April lacked a growth band if 1) we failed to recognize the initial annual band or 2) the recruits settled too late in the season to be branded with that season's band. Under the assumption that the winter dredge sampling faithfully collected all surviving recruits from the previous year's recruitment season, the ratio of clams with zero bands to those with zero or one band represented an estimate of the frequency of clams in each year class whose age is underestimated by 1 yr.

We devised one further test of the accuracy of identification of the initial annual band in *M. mercenaria* collected from the Cape Lookout vicinity of North Carolina and of the assumption that by late winter (February-April) *M. mercenaria* recruits had grown sufficiently to be efficiently collected in our hydraulic dredge sampling. In June 1978, we installed at Middle Marsh 36 1 m^2 field enclosures of the identical design described above and used in the topless treatment for the mark-recapture test of the aging methodology. All enclosures were located in shallow subtidal areas ($\simeq$0.5 m deep at low tide): 17 on a muddy-sand flat in a protected embayment at the western end of Middle Marsh and 19 in the *Zostera marina* meadow adjacent to the site used for the mark-recapture experiment (Fig. 1). After installation, all *M. mercenaria* >7 mm were removed from each plot by twice systematically sieving the top 10 cm through a 6 mm mesh. Marked *M. mercenaria* individuals were returned to these plots at densities varying from 0 to 28 per m^2 as a part of another experiment not reported here. The plots were resampled in September 1978, April 1979, October 1979, and May 1980. At each sampling, any unmarked *M. mercenaria* were collected by sieving, measured, and removed. Because most of these were new recruits, these data provided an indication of the size-frequency distributions of 0-year class *M. mercenaria* for both early fall and spring seasons in the Cape Lookout region of North Carolina. In April 1979, additional 1 m^2 enclosures were added at both sites, such that total areas sampled in October 1979 and May 1980 were 27 m^2 at the western Middle Marsh site and 29 m^2 at the *Z. marina* meadow site. We compared the seasonal size-frequency distributions of these new recruits with the distribution of size (length) at first band in a field collection of all age classes of clams (methods described below) made from nearby Johnson Creek in Core Sound, N.C. (Fig. 1). This comparison provides a further test of the accuracy of our recognition of the initial annual band of North Carolina *M. mercenaria*.

Application of Aging Technique to a Field Population

We collected *M. mercenaria* on two occasions from Johnson Creek to provide samples on which to apply our aging technique. Johnson Creek is a tidal creek on eastern Core Sound $\approx$18 km northeast of Cape Lookout (Fig. 1). Bottom type was soft, muddy sand.

The sampling site was in shallow subtidal waters just outside the area legally open to "clam kicking," a form of mechanical clam harvesting practiced by local commercial clammers. Our sampling site contained no bottom ruts or other disturbance features commonly left by mechanical clam harvesters.

On 16 January 1980, we collected 73 clams using a hydraulic suction dredge to sample haphazardly chosen locations within Johnson Creek. On 15 February 1980, another 51 clams were collected by excavating haphazardly located 0.25 m^2 sampling frames either using the hydraulic dredge (24 samples) or hand digging and sieving through 3 mm mesh (10 samples).

The hydraulic dredge consisted of a 3 hp gasoline engine attached to a pump which generated a water flow of ≈5 l/s through a 0.8 cm diameter metal tube. The tube penetrated at an angle into the side of a 12.7 cm diameter pipe. When water was forced into the pipe, suction was created at one end. To collect hard clams, the suction end of the pipe was swept slowly and systematically across the bottom such that it vacuumed up the top 15 cm of sediments and their living contents. All of this material was deposited into a 3 mm mesh nylon bag to permit sorting of clams from sediments and debris. This technique was nearly 100% efficient and was not size selective for *M. mercenaria* >5 mm long (tests given in Appendix).

All *M. mercenaria* collected from Johnson Creek were returned to the laboratory live, held overnight at 4°C, killed by steaming, and measured. One valve from each clam was then sectioned and aged by the techniques that we had tested earlier. From these measurements of length and estimates of age, we estimated the size (length)-frequency distribution, age-frequency distribution, and growth rate of *M. mercenaria* in the Johnson Creek area of Core Sound.

RESULTS

Tests of Aging Methodology

1-Year Class and Older

In total we recovered, sectioned, and analyzed marginal shell growth in 152 individual *M. mercenaria*, all initially planted on 21-22 June 1978. These clams were retrieved in approximately equal numbers on each of four dates from each of the three caging treatments (Fig 2). Macroscopic inspection of polished and sectioned shells revealed repeating features that could conceivably serve as annual markers. These features (analogous to those described by Jones (1980) for other species) appeared as bands in the outer and middle layers (following the terminology of Pannella and MacClintock 1968) that differed in appearance from the surrounding shell structure (Fig. 3). Bands near the umbo tended to be lighter in color and more translucent in appearance than the surrounding shell matrix, whereas bands toward the shell margin tended to be darker than the surrounding shell matrix and were usually purple in color. The first band deposited (nearest the umbo) differed consistently from all subsequent bands. It appeared more diffuse and was often united with the second band in the middle shell layer without an obvious termination at the shell surface. Although all bands extended to the external shell surface and were present in the outer layer, they did not always retain the coloration and textural distinctions outside of the middle shell layer. Attempts to relate surface growth breaks to the presence and absence of internal bands failed on most clams. The outer shell surface contained many more lines suggesting growth changes or interruptions, thus making an unambiguous matching with internal bands impossible.

Figure 2 presents the numbers of bands counted in the marginal growth increment of each hard clam retrieved from our field plots as a function of caging treatment and time of retrieval. For 91% of all clams, three independent observers counted an identical number of growth bands. In the rare cases of disagreement (listed by date on the legend to Figure 2), the majority vote was plotted. All 152 clams without exception showed a growth band having just begun at the time of initial planting (21-22 June 1978). For Figure 2 we chose to count that band and all successive ones. The numbers of bands added did not differ as a function of caging treatment on any of the four retrieval dates (Fig. 2). Thus, although our caging treatments may have altered the hydrodynamic regime and thereby the local growth environment for the test clams, the aging technique was consistent. This result extends the scope and generality of our test of whether growth bands are predictably repeating annual markers in a southeastern population of *M. mercenaria*.

At each retrieval date, there was little variance among clams in the number of bands added since planting (Fig. 2). In the October 1979 collection, 38 of 39 clams had deposited exactly 2 additional bands; in the October 1980 collection, 35 of 38 clams had deposited 3 additional growth bands; and in the October 1981 collection, 42 of 46 clams had 4 additional growth bands. This represents a 93% level

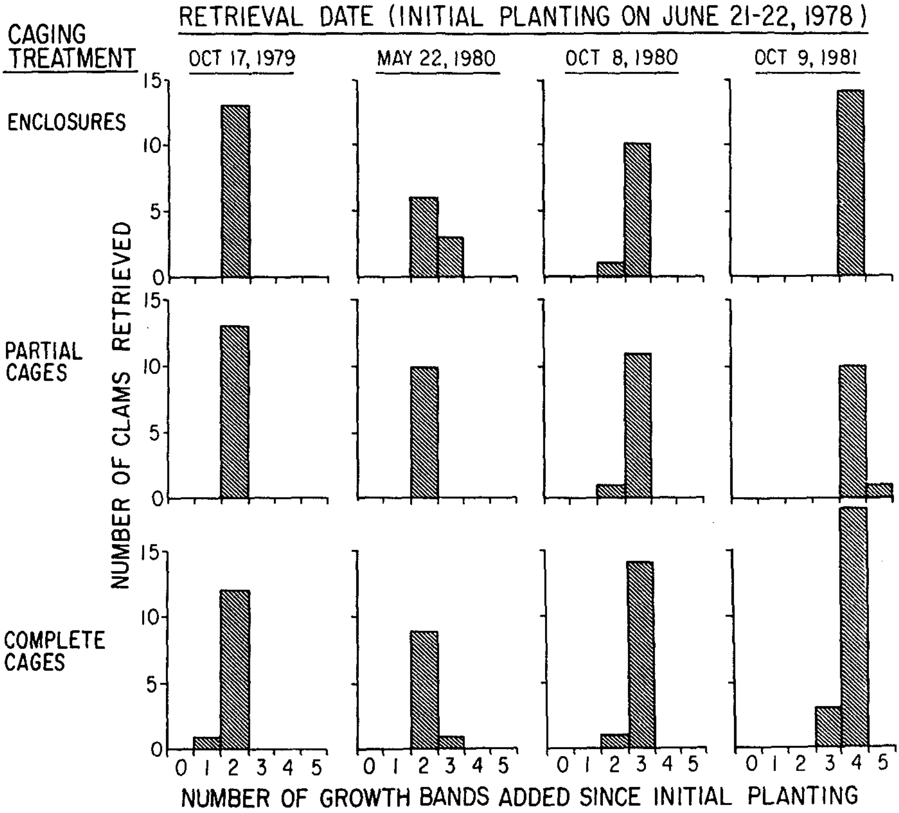

FIGURE 2.—The number of growth bands added per hard clam in the increments of marginal shell growth that occurred since planting in the field on 21-22 June 1978. Numbers of bands added were determined for each clam by majority vote of three independent observers, although disagreements in counts were rare (only 2 for October 1979, 4 for May 1980, 3 for October 1980, and 4 for October 1981). All counts include an annual growth band that had just begun to appear in all clams at the initiation of the experiment (21-22 June 1978). Each histogram represents the pooled results from duplicate 1 m^2 field plots for each caging treatment.

of agreement among clams collected on all October dates. In the May 1980 collection, 25 of 29 clams showed 2 additional growth bands. Although this represents a slightly higher level of disagreement among replicate clams, an examination of the seasonal pattern of line deposition helps explain this discrepancy. From the temporal data presented in Figure 2, the band appears to be laid down annually and predictably sometime during May to October. Each year's band was evident (although not necessarily completed) in virtually all clams collected on the three October dates. Furthermore, the initiation of the band was evident in June 1978 for all 152 clams. Thus, the somewhat higher variance in estimated numbers of growth bands added among replicate clams retrieved in May 1980 may be a consequence of variable dates of band initiation. All four clams that deviated from the mode of 2 in the May 1980 collection had a third band just beginning at the terminal margin of the shell, suggesting that late May was the approximate time of initiation of band deposition in 1980.

In June 1980, we counted annual bands to estimate the age of each of the 152 experimental clams at the time of their introduction into field enclosures. Figure 4 shows the initial age-frequency distribution 1) for all those clams that laid down an additional number of growth bands equal to that predicted by the number of additional summer seasons and 2) for all those clams for which additional age was either inaccurately or inconsistently estimated by the three age readers. Clams in this mark-recapture experiment ranged in initial age from 1 to 10. Because some clams planted as 10-yr-olds were not retrieved until October 1981, we actually examined line deposition in clams up to 13 yr of age. The two size-frequency distributions do not differ significantly ($P > 0.05$ in χ^2 tests of independence), implying that aging mistakes did not vary as a function of absolute age.

Microscopic examinations of acetate peels made

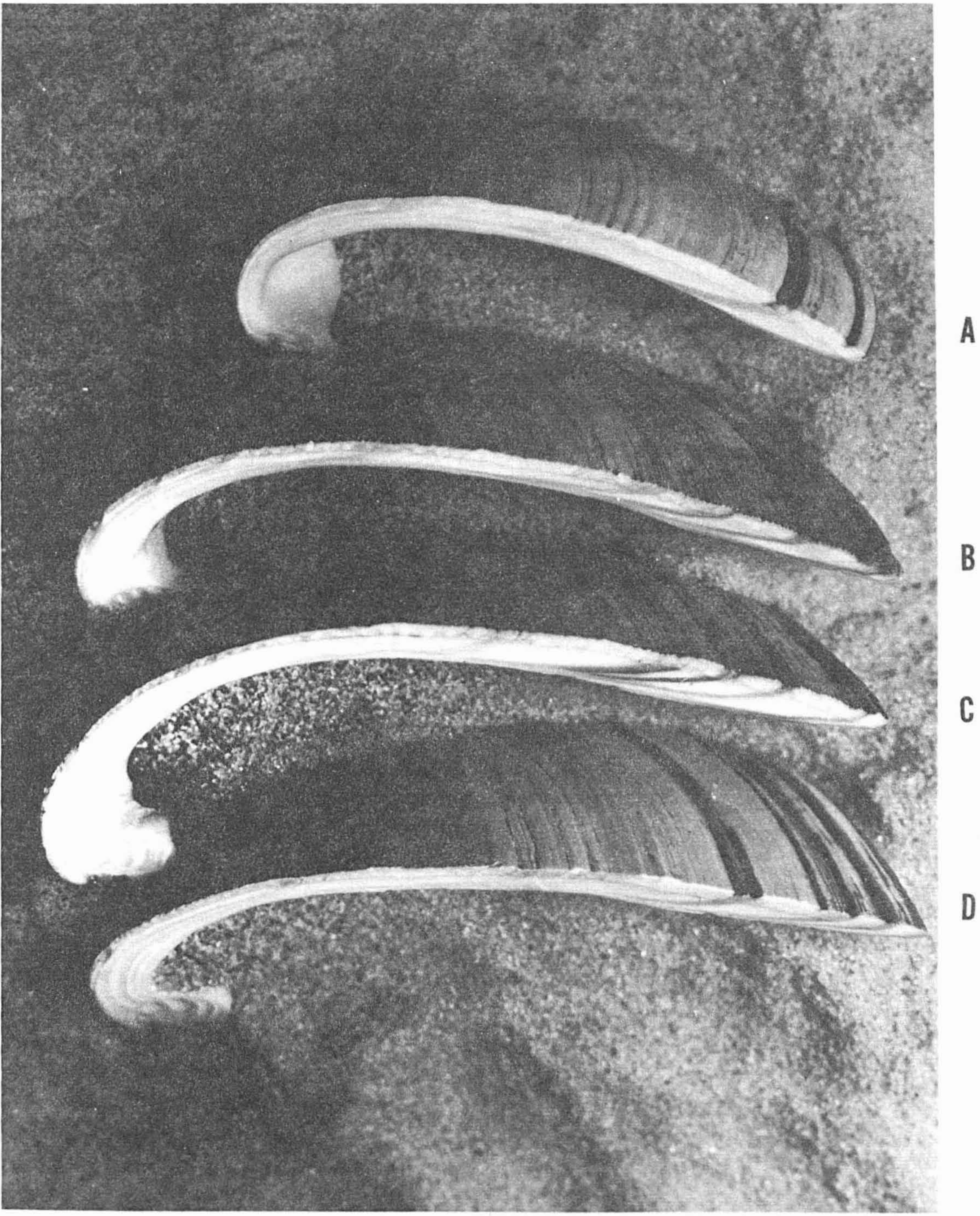

FIGURE 3.—A photographic illustration of a representative sectioned clam shell from each of the four collection dates (A-D: dates given in Figure 2 legend) in the mark-recapture test of whether *Mercenaria mercenaria* from Cape Lookout, N.C., deposits annual growth bands. Lines drawn on the outer surface of each clam shell represent the sizes at each measuring date: 21-22 June 1978; 20 September 1978; 21 April 1979; 17 October 1979; and 22 May 1980. Clam A lacks surface lines for the last two dates because it was collected on 17 October 1979, whereas clam B, collected on 22 May 1980, lacks the last surface line. The annual bands are visible as dark bands in the middle and outer layers in the cross-sectional cuts through each shell.

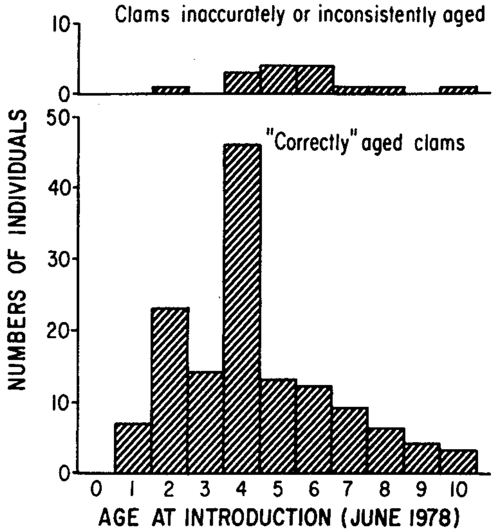

FIGURE 4.—The frequency distribution of age at introduction in June 1978 of all clams used in the mark-recapture test of whether growth bands are annual in *Mercenaria mercenaria* from Cape Lookout, N.C. Two age distributions are presented: The bottom distribution includes all 137 clams possessing marginal growth that was correctly aged without disagreement among three independent examiners and the top distribution includes all 15 clams with either incorrectly aged marginal growth or with disagreement among age readers. The two distributions do not differ significantly at $\alpha = 0.05$ in a χ^2 test of independence, pooling adjacent age classes where necessary to maintain expectations above unity.

from the sections of 20 of the October 1980 and October 1981 clams did not reveal any additional repeating patterns in the shell deposition of *M. mercenaria* that might be used as annual markers. Furthermore, the growth band that was so evident in macroscopic view of the polished section did not retain its coloration and textural distinctions on the acetate peels and was thus not as obvious. Numerous finer growth breaks found in acetate peels were not evident in macroscopic view. Some resembled disturbance checks (Kennish and Olsson 1975; Kennish 1980), occurring only in the outer layer and, in macroscopic view, appearing with slight brown discolorations incorporated into the shell matrix.

Many of these possible disturbance checks appeared to be associated with the excavation and measuring of the clams. To document this association, we examined closely the polished sections of 23 clams retrieved in October 1981 and drawn approximately equally from the three caging treatments. On the outer surface of each shell, we marked the position of the shell margin (the size) at each of the known measurement dates. Because each clam in this sample (except two that were missed during one sampling) was excavated and measured on five occasions, 113 (5 × 23 − 2) disturbance lines would be expected from sampling, if the sampling process suffices to produce disturbance checks in the shell matrix. Of these 113 positions on the shells, 96 contained clear disturbance checks in the outer shell layer. Only 35 additional disturbance checks were evident in these shells during the period June 1978 to October 1981, and 29 of those coincided with the initiation of deposition of the annual band. The six remaining disturbance checks were not associated with our handling or with annual band deposition, but their presence is not surprising given that natural disturbance breaks have been reported for *M. mercenaria* elsewhere (Kennish and Olsson 1975; Kennish 1980).

Disturbance checks deposited at most times of measuring provided several specific chronological markers. We used these markers together with presumed daily growth lines to estimate the exact period of annual band deposition and relative growth rates within and outside of the period of annual band deposition. Because we had no good test of the daily nature of the presumed daily lines, we chose to carry out these estimates only for shell growth increments where we had an approximately year-long period of growth bracketed by measurement growth checks and containing the expected number (±20) of "daily" lines.

We examined six growth periods, one on each of four clams and two on a fifth individual, which met our criteria (Table 1). These clams exhibited great variability in date of annual band initiation (June-October) and termination (September-January). However, the period of annual band deposition consistently included summer or fall. Average daily growth rate during the period of annual band deposi-

TABLE 1.—The period of Annual band deposition and the average daily growth[1] of hard clams during and outside the period of annual band deposition, as estimated by using daily growth lines on acetate peels or on thin sections. The six intervals examined (all but the first two on separate clams) were bracketed by disturbance checks in the outer shell layer that served as known chronological markers and contained a number of daily lines equal to the number of days (±20) between the known dates.

Time interval examined	Period of annual band deposition	Average daily growth during band deposition (μ)	Average daily growth outside period of band deposition (μ)
6/21/78-4/10/79	6/21/78-1/4/79	4.6	4.8
4/10/79-5/22/80	10/17/79-11/10/79	2.4	3.8
10/17/79-10/8/80	8/5/80-10/8/80[2]	1.8	2.9
6/21/78-4/10/79	6/21/78-9/28/78	2.3	2.4
9/25/78-10/17/79	7/3/79-10/17/79	1.7	3.3
9/25/78-10/17/79	7/12/79-10/17/79	1.1	2.4

[1] Growth was measured by calibrated ocular micrometer in the center of the shell cross section along the axis of growth but converted geometrically to corresponding lengths.

[2] The annual band was still being deposited on 10/8/80, whereas for all other intervals examined these dates mark actual initiation and termination dates for band deposition.

tion was consistently lower than when the band was not being deposited. The magnitude of the ratio of these two different growth rates varied considerably from 1.01 to 3.27. The major reason for this variability was probably the logarithmic nature of growth in *M. mercenaria*. All clams chosen for this analysis of daily lines were young (1-3 yr old at introduction in June 1978) and within a size range (3-6 cm long) where the rate of decline in absolute growth rate with increasing size is substantial. Consequently, in those clams where the annual band fell at the end of the time period that was analyzed, the inherent logarithmic growth pattern enhanced the apparent difference in growth rate in- and outside of the period of annual band deposition. Conversely, when the annual band fell at the beginning of the time period analyzed, the relative difference in growth rate was masked by the inherent general pattern of slowing of growth with increased size. Despite this dependence on the band's position within the growth interval analyzed, it is clear that the period of annual band deposition represents a time of relatively slow growth.

0-Year Class

In the 432 0.25 m^2 samples taken in February-April 1980 from Back Sound, we collected 546 *M. mercenaria*. Only 9 individuals (all $<$1.25 cm long) lacked evidence of a growth band, whereas 126 contained a single annual band. (The other 411 clams contained more than one band.) Assuming that virtually all clams in the 0-year class had grown sufficiently by winter (February-April) to be efficiently captured in our sampling process (this assumption is tested below), then the fraction 9/135 (6.7%) estimates the frequency of error made in assuming that all clams in the 0-year class are branded with their first identifiable growth band in their first fall season. This result implies that we underestimate the age of a relatively

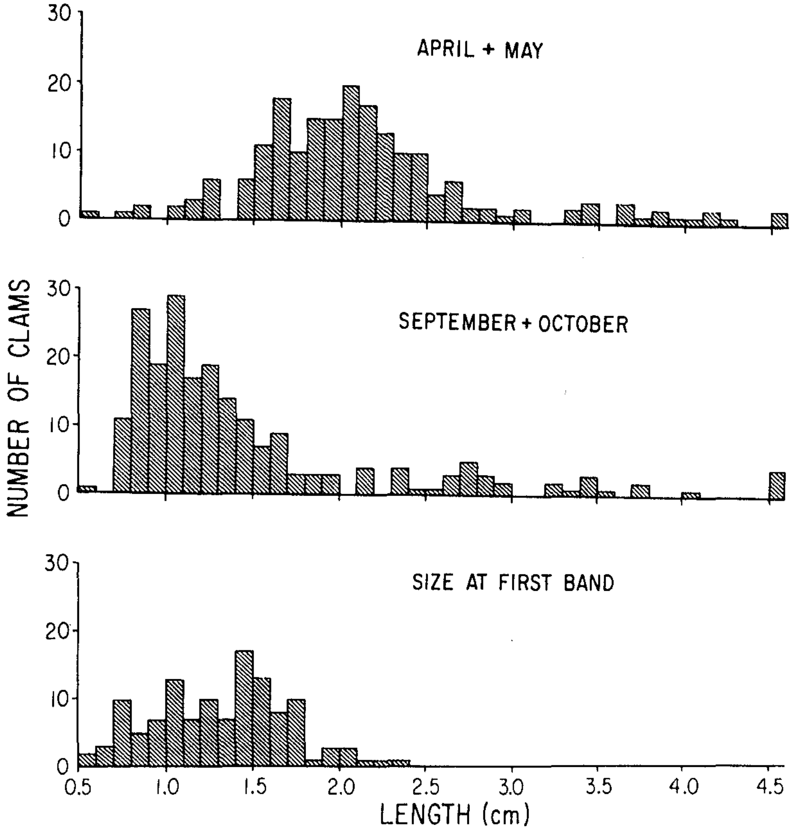

FIGURE 5.—The size (length)-frequency distributions of all unmarked *Mercenaria mercenaria* recruits collected and removed at two seasons (fall and spring) from fixed 1 m^2 enclosures in Middle Marsh, as compared with the distribution of size (length) at first band for all clams collected in January-February 1980 from Johnson Creek, Core Sound, N.C. See text for details on methods.

small percentage of *M. mercenaria* in the Cape Lookout region by using the technique of counting internal growth bands.

Figure 5 presents the size-frequency distributions of all unmarked *M. mercenaria* collected from the fixed 1 m^2 plots in Middle Marsh in both falls (pooled) and both springs (pooled) along with the size (length)-frequency distribution at first band for all *M. mercenaria* collected in our samples from nearby Johnson Creek. Because *M. mercenaria* >0.7 cm long could not easily invade our fixed 6 mm mesh enclosures, virtually all unmarked clams collected in the sampling enclosures are recruits. Recruitment occurs during the summer months in North Carolina (Chestnut 1952; Ansell 1968). Consequently, the fall size-frequency distribution (Fig. 5) represents the fall sizes of the 0-year class, truncated at 0.7 cm because smaller clams are not efficiently retained on our 6 mm sampling mesh and extended to larger size classes by inclusion of some recruits from previous year classes that were missing during sampling. The spring size-frequency distribution (Fig. 5) contains those 0-year class recruits that were missed and, therefore, not removed during the previous fall's sampling or that settled late (after September-October) plus some larger recruits from other year classes that were missed in previous years' sampling.

The spring size-frequency distribution given in Figure 5 is biased towards smaller size classes, relative to the natural spring distribution of 0-year class *M. mercenaria* near Cape Lookout, because the previous fall's sampling already removed the larger sizes preferentially. Despite this bias, the sizes at which the first annual band was deposited in the Johnson Creek clams resemble the fall size-frequency distribution of 0-year class recruits much more closely than the spring size-frequency distribution (Fig. 5). This helps confirm the accuracy of our recognition of the initial growth band in *M. mercenaria* from Cape Lookout. A comparison of the fall size-frequency distribution of 0-year class clams and the distribution of size at first band (Fig. 5) also suggests that the first annual band may be deposited somewhat later in the season (perhaps October-November) than the subsequent bands (June-October in our earlier mark-recapture data).

The size-frequency distribution of unmarked clams in spring (Fig. 5) demonstrates that virtually all new recruits in this system have grown sufficiently large to have been efficiently sampled in our late winter dredge sampling of Back Sound. Dredge sampling efficiently captures clams down to 0.5 cm long (see Appendix), and Figure 5 demonstrates that even in this spring size-frequency distribution, which is biased towards the smaller size classes, a very small proportion of the 0-year class in the Cape Lookout region is ±1.0 cm long.

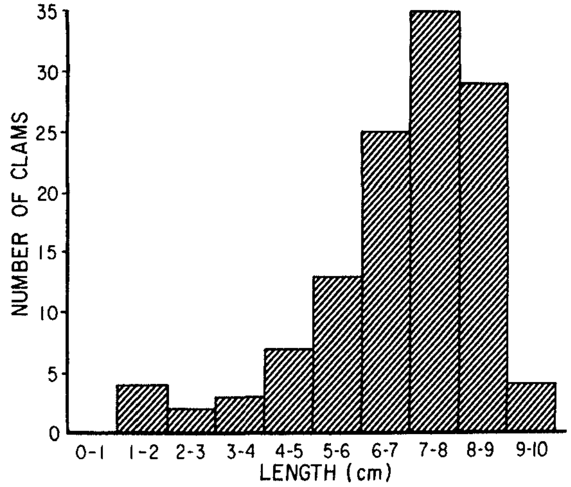

FIGURE 6.—Size (length)-frequency distribution for all 124 *Mercenaria mercenaria* collected during 2 d (16 January and 15 February 1980) of sampling from Johnson Creek in Core Sound, N.C.

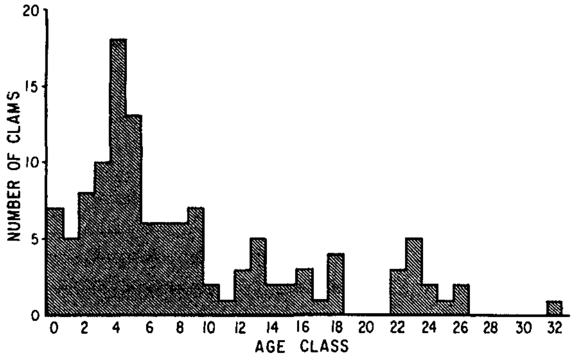

FIGURE 7.—The distribution of 124 clams collected in January-February 1980 at Johnson Creek, Core Sound, N.C., into age classes. Age class was estimated for each clam by counting the number of annual growth bands and subtracting one (assuming that each new recruit laid down its first annual band in its first fall). Average age class is 8.59 and, assuming that settlement occurred in July-August, average age is 9.09 yr.

Application of Aging Technique to a Field Population

Because the size (length)-frequency distributions of *M. mercenaria* collected on the two sampling dates did not differ significantly ($0.10 < P < 0.20$ in a χ^2 contingency test), we pooled all samples to form estimates of the size- and age-frequency distributions of *M. mercenaria* at Johnson Creek in January-February 1980. Average clam density from the 34 quantitative samples was 1.59 ± 1.28 (SE) per 0.25 m^2. The size-frequency distribution of all 124 clams collected (Fig. 6) was dominated by relatively large clams in the 6-9 cm range. Figure 7 presents the distribution of these same 124 clams among age classes. This figure was constructed by counting the number of annual growth bands on each clam and subtracting one, under the assumption (tested earlier) that new recruits lay down their first annual growth band during their first fall. Because the January-February sample occurred about ½ yr after settlement (assuming an average settlement time of July), the ages of clams in years are estimated by their year class plus one-half. Average age of the clams collected at Johnson Creek was 8.59 + 0.50 or just over 9 yr old. The oldest clam in the sample was estimated to be 32 yr old (Fig. 7). This age distribution (Fig. 7) reveals that each of the three most recent year classes (1977-78-79) at Johnson Creek contributed less to the total sample than each of the three previous year classes (1974-75-76).

In Figure 8, the shell length of each clam collected is plotted against its total number of annual bands (= age + ½). This graph illustrates the generally logarithmic form of growth and provides an estimate of age-specific growth of *M. mercenaria* in the Johnson Creek area of Core Sound. The best fitted logarithmic growth curve through all points is

$$\text{length (in cm)} = 3.176 + 1.819 \ln (\text{no. of annual bands})$$
$$r^2 = 0.673, P < 0.001.$$

On the graph, we plot the minimum length at which hard clams can be legally harvested in North Carolina. This size was calculated by converting the minimum legal width of 25.4 mm to length by the regression equation

$$\text{length (in mm)} = -1.73 + 1.83 \text{ width (in mm)}$$

derived from fitting all 124 Johnson Creek clams ($r^2 = 0.97$; $P < 0.001$). Figure 8 implies that most clams at Johnson Creek reach legal size by age 1½, sometime during their second winter. This graph also reveals how extremely variable a clam's size is for any given age older than about 4½ yr. For instance, a clam 75 mm long can be anywhere from age 4½ to at least age 25½. For clams older than 4½ yr of age, size is a very poor predictor of age ($r^2 = 0.07, n = 75, 0.02 < P < 0.05$ in a linear regression).

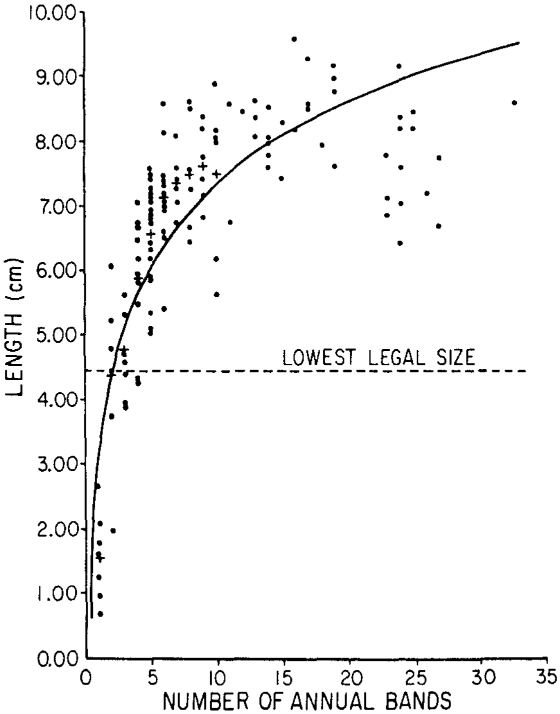

FIGURE 8.—The relationship between number of annual bands (= age in years + one-half for clams collected in January-February) and length for all 124 clams collected in January-February 1980 from the Johnson Creek site in Core Sound, N.C. Also indicated on the graph is the minimum legal size for harvest in North Carolina. + indicates mean sizes in each age class up to the 10th. The growth line drawn in is the best fitted ($r^2 = 0.673$; $P < 0.001$) logarithmic curve [length (cm) = 3.176 + 1.819 ln (no. of annual bands)].

DISCUSSION

The results of mark-recapture (Fig. 2) demonstrate that the individuals of at least one population of hard clams along the southeastern coast of the United States can be accurately aged by counting macroscopic annual growth bands in sectioned shells. The population that we examined exhibited little ambiguity in what constituted an annual band and little variation among individual clams. These results held true across a wide range of clam ages (1-13 yr) and the aging errors made were not a function of clam age (Fig. 4). Attempts to alter local environment by adding mesh cages of two differing structures also failed to alter the clear pattern of annual band deposition. Nevertheless, because growth rate declines with age (Fig. 8), annual bands came at closer intervals in older clams and were somewhat difficult to resolve in *M. mercenaria* older than about 19 yr of age. An examination of all small *M. mercenaria* collected in February-April 1980 from a location in Back Sound revealed that only a small percentage (6.7%) of the 0-year class lacked an annual band. Since settlement had almost certainly occurred before the onset of winter (Chestnut 1952; see also data in Figure 5), this implies that for a small percentage of *M. mercenaria* age was underestimated by 1 yr. This is not a large bias in view of *M. mercenaria*'s life span (Fig. 7), but may cause misinterpretation in studies where distinguishing small differences is important.

Prior to our mark-recapture results and recent observations by Clark and Lutz (1982), most scientists suspected that this aging technique, so successful for northern populations of *M. mercenaria* (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975), could not be used for hard clams in the southeastern United States because *M. mercenaria* there lacked the winter period of slow, almost negligible, growth that is associated with annual band deposition in northern populations (Ansell 1968). Our analysis of presumed daily growth increments along with sectioning evidence in Clark and Lutz (1982) implies that southeastern *M. mercenaria* also deposit the annual band during a period of slow growth, but that this period usually occurs from about June to October. The results of our mark-recapture study confirm that annual band deposition in 1-year class and older clams occurs sometime in that same period (Fig. 2). This season of annual band deposition corresponds both with maximum seasonal water temperature (Sutherland and Karlson 1977) and with the spawning season for *M. mercenaria* in the Cape Lookout region of North Carolina (Porter 1964). Because water temperature serves as the usual proximate cause of spawning in marine bivalves, separation of these two factors is difficult. The deposition of an initial band in clams only a few months old (Fig. 5) does not permit rejection of the spawning hypothesis because this initial band differed in appearance from all subsequent annual bands and seemed to occur later in the fall season (Fig. 5), implying that this first band is of a different nature from all subsequent ones. Jones (1980) also demonstrated that both *Spisula solidissima* and *Artica islandica* deposit annual bands at times of spawning, analogous to our results for *M. mercenaria*. Regardless of the mechanism, results of our mark-recapture experiments dispel the justifiable doubts expressed by several scientists concerning the interpretation of shell growth lines (Clark 1974; Gould 1979; Jones 1981) and permit paleontologists, archaeologists, and environmental biologists to interpret banding patterns in shells of *M. mercenaria* from the southeastern coast of North America and to apply this biological chronometer to a wide spectrum of problems.

Application of this aging technique to a population of *M. mercenaria* in Johnson Creek off Core Sound revealed a surprisingly large frequency of older clams and a high average age (>9 yr old). In comparison, Kennish (1980) demonstrated almost 100% mortality of *M. mercenaria* in Barnegat Bay, N.J., by age 9. A relatively low rate of commercial fishing mortality in North Carolina prior to 1977 may contribute to this difference in population parameters. Figure 9 presents clam landing data illustrating the recent increase in hard clam harvest in North Carolina. This recent intense harvest is perhaps made possible by the sudden utilization of the accumulation of several years' reproduction, whereas northern populations of *M. mercenaria* may have been subjected to continuous high fishing intensity for a long period and therefore exhibit age-frequency distributions that are shifted towards the younger age classes. Alternatively, the differences in age distributions between areas could be the consequence of natural differences in factors affecting hard clam life histories.

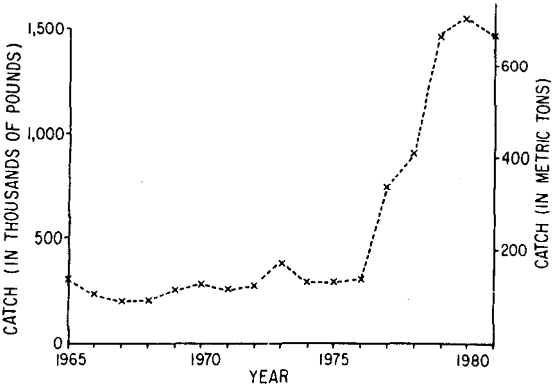

FIGURE 9.—Annual hard clam, *Mercenaria mercenaria*, catch by commercial clammers in North Carolina from 1965 to 1981, as estimated by the North Carolina Division of Marine Fisheries.

The growth rate exhibited by *M. mercenaria* from Johnson Creek (Fig. 8) is higher than that demonstrated by Chestnut (1952) for a sand-bottom area of Bogue Sound, and higher than many (but not all) of the growth rates recorded from other areas (Ansell 1968). In particular, our age-size plot (Fig. 8) implies that the average *M. mercenaria* in Johnson Creek reaches the legal minimum size for harvest (4.46 cm long) by age 1½, whereas Chestnut's (1952) data implied that it usually required 3 yr for North Carolina hard clams to enter the catchable population. Clearly there is a large degree of individual variation in growth rate and size at any given age (Fig. 8). Nevertheless, this new estimate of average time to marketable size at Johnson Creek is quite important to managers of the commercially harvested and valuable *M. mercenaria* resource in North Carolina. For instance, although gametes produced by a 1-yr-old clam, even of this size, may be viable (Porter 1964; pers. commun.[3]), the mass of gametes produced is almost negligible when compared with larger individuals (Peterson 1983).

Although the general shape of the estimated *M. mercenaria* growth curve (Fig. 8) is logarithmic, as expected, the variance in the relationship is substantial. Among all clams older than 4½ yr of age collected from Johnson Creek, age explained only 7% of the variance in size. Consequently, aging of Johnson Creek *M. mercenaria* by inference from size-class frequency would fail. Only in a population dominated by young clams in the fast growing sizes could North Carolina *M. mercenaria* be adequately aged by size information. Thus, the utilization of growth band analysis is an important key to inference on population parameters in North Carolina *M. mercenaria*. Unfortunately, the annual bands are not unambiguously evident on the outer shell surface, where disturbance checks and other growth breaks appear (as reported for other species such as *S. solidissima* (Jones et al. 1978)), so that shell sectioning is necessary for accurate aging.

If recruitment success (reproductive effort times subsequent larval and early postlarval survivorship) were to remain constant across years, frequencies of age classes would decline progressively with age at a rate corresponding to the age-specific mortality function. Yet, the age-frequency distribution for Johnson Creek *M. mercenaria* in January-February 1980 (Fig. 7) is characterized by lower numbers in each of the three most recent year classes (1977-78-79) than in the three previous year classes (1974-75-76). Tests of sampling efficiency (Appendix) and data on the seasonal progression in the size distributions of 0-year class recruits (Fig. 5) demonstrate that the "gap" in *M. mercenaria*'s age distribution (Fig. 7) is not caused by a sampling artifact. The relatively low numbers in the 1977-78-79 year classes are a consequence of reduced reproductive success, relative to at least the three previous years, either because of reduced reproductive effort or increased mortality of larvae and early postlarvae. Although we have no unequivocal way of distinguishing between these two explanations, the close match between the increase in North Carolina's commercial harvest of *M. mercenaria* (Fig. 9) and the 3-yr decline in recruitment success suggests that future studies should investigate the possibility that a recent reduction in the spawning population of *M. mercenaria* in North Carolina through increased harvest (mostly from Core Sound) has had an impact on reproductive effort and recruitment success. The persistent uncertainty among invertebrate population biologists about the strength and nature of spawner-recruit relationships remains the single biggest barrier to effective management of invertebrate fisheries.

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APPENDIX

Two tests were performed to estimate the efficiency and size selectivity of our hydraulic dredge sampling. First, two sets of quantitative samples were taken at Johnson Creek by placing a circular 0.25 m^2 sampling frame at haphazard locations and then excavating it to a depth of 15 cm. For one set of 24 samples, we used the hydraulic dredge, while we excavated the other set of 10 samples by hand. In each case, the contents of the top 15 cm were passed through a 3 mm mesh sieve. By comparing the average hard clam densities and size-frequency distributions in these two sets of samples, we have one test of whether the efficiency and size selectivity of samples from the hydraulic dredge differ significantly from analogous hand-collected samples, all collected in the actual field site.

As a second test of the size selectivity and as a quantitative estimate of sampling efficiency, 22 marked *Mercenaria mercenaria* were placed at natural living depths within an otherwise undisturbed bottom inside our 0.25 m^2 sampling frame. The lengths of these clams ranged from 0.89 to 9.53 cm, with 5 in the 0-2 cm range, 3 in the 2-4 cm range, 3 in the 4-6 cm range, 7 in the 6-8 cm range, and 4 in the 8-10 cm range. We then used the hydraulic dredge to sample this 0.25 m^2 area within the frame in the usual fashion to a 15 cm depth. This trial was repeated five times, moving the frame to a new location each time and recording the numbers and sizes of all clams recovered.

Average density of hard clams did not differ significantly (at $\alpha = 0.05$ in a Student's t-test) between the dredged and hand-collected samples from Johnson Creek (Appendix Table 1). Furthermore, the size-frequency distributions (Appendix Table 1) were nearly identical and did not differ significantly (at $\alpha = 0.05$ in a χ^2 contingency test). These results imply that the two techniques did not differ in efficiency or size selectivity. *Mercenaria mercenaria* as small as 0.5 cm long were collected by both techniques. In the five trials to estimate the numerical efficiency of the dredging technique, only one clam was missed (5.84 cm long). Thus, the capture efficiency exceeded 99% and did not vary significantly with clam size within the range of clams used (0.89-9.53 cm). This result implies that we did not collect a biased size (or age) distribution of hard clams in our field sampling.

APPENDIX TABLE 1.—A comparison of the relative efficiency and size selectivity of hydraulic dredge and hand sampling of hard clams in Johnson Creek, Core Sound, N.C. Also given are results of quantitative estimates of capture efficiency as a function of clam size for the hydraulic dredge technique.

a) Johnson Creek sampling results

	Sampling technique	
Statistics	Hand excavation	Hydraulic dredge
Number of samples (0.25 m^2)	10	24
Average hard clam density (±1 SD)[1]	1.70 (±1.70)	1.54 (±1.02)
Size frequency distribution[2]		
0.5-2 cm	12%	16%
2-4 cm	6%	5%
4-6 cm	24%	19%
6-8 cm	41%	32%
8-10 cm	18%	27%

b) Results of five trials to estimate capture efficiency

Size class (cm)	Numbers present	Numbers collected by dredge	Sampling efficiency (%)
0.5-2	25	25	100
2-4	15	15	100
4-6	15	14	93
6-8	35	35	100
8-10	20	20	100
Total	110	109	>99

[1] Difference not significant at $\alpha = 0.05$ in t-test.

[2] Difference not significant at $\alpha = 0.05$ in χ^2 test.