The presence of periodically repeating features in the preservable hard parts of various organisms allows scientists in several disciplines to make important inferences about the rates and timing of past events (Jones 1980; Rhoads and Lutz 1980). Analysis of growth lines deposited in shells of bivalve molluscs, for example, finds powerful application in the fields of paleontology (Rosenberg and Runcorn 1975), anthropology (Clark 1979), population ecology (Kennish 1980), and fisheries biology (Peterson et al. 1983). Possession of a reliable age marker in a bivalve shell enables fisheries biologists 1) to construct age-frequency distributions for various populations, which reflect the age-specific mortality rates and help permit estimates of sustainable yield, 2) to calculate individual growth rates and their variability among habitats, and 3) to understand age-specific reproductive schedules in exploited populations.

Unfortunately, the potential rewards in applying this aging technique have encouraged widespread use of growth line analysis prior to performing the necessary controls to test the annual periodicity of line deposition (Clark 1974; Gould 1979; Jones 1981). Because of the tremendous potential utility of this aging technique, we carried out mark-recapture tests of the annual nature of growth band deposition in shells of the commercially important hard clam, Mercenaria mercenaria, in a North Carolina sound (Peterson et al. 1983). Although these experiments provided convincing evidence that M. mercenaria deposits a reliable annual marker in the form of an internal growth band in its shell, this study was carried out in only a single locality in Back Sound, NC. Patterns of growth band deposition in bivalve molluscs may vary with environment on several scales: 1) over a broad geographic scale, M. mercenaria deposits summer bands in Back Sound, NC, and in Chesapeake Bay, but winter bands in all localities in northeastern states (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975; Clark 1979; Clark and Lutz 1982; Fritz and Haven 1983; Peterson et al. 1983); 2) among habitats within estuaries, Protobalanus staminea appears to deposit unambiguous annual bands in muddy sand but not in a clean-sand habitat in Mugu Lagoon, CA (Peterson and Ambrose 1985); and 3) among nearby individuals within a single habitat, both Chione fluctifraga and Protothaca staminea from within the same restricted sample at Mugu Lagoon exhibit radically different patterns of daily line deposition (Hughes and Clausen 1980).

We present here results of additional tests of the annual nature of internal growth band deposition in shells of M. mercenaria placed for 2 yr in several different field localities and estuarine habitats, in order to test whether our earlier (Peterson et al. 1983) demonstration of annual banding in North Carolina's M. mercenaria is robust to change in local habitat.

Materials and Methods

To extend the generality and power of our previous results, we designed a mark-recapture experiment to examine the frequency and clarity of band deposition in M. mercenaria at 5 additional sites (Fig. 1) within Carteret County, NC, near Cape Lookout. These sites were chosen to represent a wide geographic spread among several local water bodies, to permit contrasts between vegetated and unvegetated habitats, and to include more sandy (coarse) substrate than that in our original site. One site was selected on a fine sand flat in the North River about 12 km from our earlier Middle Marsh study site in Back Sound. Two sites were chosen about 38 km from Middle Marsh near the western end of Bogue Sound by the town of Cape Carteret: one on a fine sand flat and the other in a seagrass bed with mixed stands of Zostera marina and Halodule wrightii. The other two sites were situated in Core Sound about 6 km from Cedar Island Point and about 47 km from our initial Middle Marsh study site: one on a sand flat and the other in a Halodule wrightii meadow. All sites were on shallow subtidal bottom, accessible by wading and amenable to recovery of marked animals.

Table 1 summarizes the results of particle-size analyses done on duplicate surface (0-5 cm) sediment cores taken in August-September 1981 at each site to permit comparisons among the five new and one previous study sites. The five new sites are clearly characterized by having much coarser sediments than the previous study site but differ among themselves in sediment grade (Table 1). Contemporaneous
FIGURE 1.—Geographic locations of study sites (marked by dots near circled numbers) within North Carolina near Cape Lookout (marked by the arrow on the NC map): the previous site at Middle Marsh (1); new sites at North River (2); Bogue Sound sand (3) and seagrass (4); Core Sound sand (5) and seagrass (6).
TABLE 1.—Locations and sedimentary characteristics of the one previous (Middle Marsh) and five new study sites of Mercenaria mercenaria. Sedimentary data came from sieving and pipetting (Folk 1974) duplicate surface (0-5 cm) sediment cores taken in summer 1981 at each site. Percent silt-clay is percent of total sediment dry weight in fine (>44 µm) size classes.

<table>
<thead>
<tr>
<th>Site</th>
<th>Location coordinates</th>
<th>Mean sediment parameters (±SD)</th>
<th>Graphic mean</th>
<th>Percent silt-clay</th>
<th>Sorting coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle Marsh</td>
<td>34°41'29&quot;N</td>
<td>5.07</td>
<td>47.22</td>
<td>3.00</td>
<td></td>
</tr>
<tr>
<td>in Back Sound</td>
<td>76°37'03&quot;W</td>
<td>(0.28)</td>
<td>(12.24)</td>
<td>(0.51)</td>
<td></td>
</tr>
<tr>
<td>North River</td>
<td>34°48'22&quot;N</td>
<td>2.35</td>
<td>2.97</td>
<td>0.61</td>
<td></td>
</tr>
<tr>
<td></td>
<td>76°36'48&quot;W</td>
<td>(0.02)</td>
<td>(1.72)</td>
<td>(0.01)</td>
<td></td>
</tr>
<tr>
<td>Bogue Sound</td>
<td>34°41'29&quot;N</td>
<td>2.83</td>
<td>2.15</td>
<td>0.47</td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>76°59'06&quot;W</td>
<td>(0.09)</td>
<td>(2.05)</td>
<td>(0.02)</td>
<td></td>
</tr>
<tr>
<td>Bogue Sound</td>
<td>34°41'36&quot;N</td>
<td>3.05</td>
<td>9.31</td>
<td>0.95</td>
<td></td>
</tr>
<tr>
<td>Seagrass</td>
<td>76°59'05&quot;W</td>
<td>(0.02)</td>
<td>(2.22)</td>
<td>(0.17)</td>
<td></td>
</tr>
<tr>
<td>Core Sound</td>
<td>34°57'03&quot;N</td>
<td>2.72</td>
<td>8.81</td>
<td>0.91</td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>76°12'44&quot;W</td>
<td>(0.07)</td>
<td>(2.03)</td>
<td>(0.16)</td>
<td></td>
</tr>
<tr>
<td>Core Sound</td>
<td>34°56'59&quot;N</td>
<td>2.40</td>
<td>3.10</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>Seagrass</td>
<td>76°12'43&quot;W</td>
<td>(0.00)</td>
<td>(1.33)</td>
<td>(0.06)</td>
<td></td>
</tr>
</tbody>
</table>

Water temperature and salinity data are not available for all sites, but records from a variety of sources (Brett 1963; Thayer 1971; Williams et al. 1978; Sutherland and Karlson 1977; H. J. Porter, University of North Carolina, Chapel Hill, unpubl. data; W. Kirby-Smith, Duke University, unpubl. data) suggest that 1) water temperature patterns probably do not differ greatly across sites, with monthly averages ranging from winter minima of 2°-4°C to summer maxima of 29°-30°C, and 2) that salinities are slightly more variable across sites. Localities close to Atlantic Ocean inlets (Bogue Sound sand and seagrass sites and the previous Back Sound site at Middle Marsh) experience uniformly high salinities (30-36‰), except after severe rainstorms (Brett 1963; H. J. Porter, unpubl. data). Salinities in the upper portion of North River are only slightly lower because there is little freshwater inflow into that system (Thayer 1971). The lowest (22-28‰) and probably most variable salinities on a week-to-week scale occur at the two Core Sound sites, where exchange with the ocean is reduced and where any persistent north winds bring intrusions of low-salinity waters from Pamlico Sound (Williams et al. 1973).

At each of the five new study sites, we placed groups of 80 Mercenaria mercenaria in 1 m² field plots in late summer 1980, excavated them by hand in late summer 1981 to estimate growth and mortality and to replace missing and dead clams, and then finally recovered all living clams present in late summer 1982 (Table 2). All M. mercenaria used in these experiments were individually marked on the external shell surface with color-coded dots of Mark-

TABLE 2.—Dates of experiment initiation and subsequent sampling of Mercenaria mercenaria for each of the five study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Measuring dates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1980 initiation</td>
</tr>
<tr>
<td>North River</td>
<td>6 August</td>
</tr>
<tr>
<td>Bogue Sound</td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>15 August</td>
</tr>
<tr>
<td>Seagrass</td>
<td>15 August</td>
</tr>
<tr>
<td>Core Sound Sand</td>
<td>3 September</td>
</tr>
<tr>
<td>Core Sound Seagrass</td>
<td>3 September</td>
</tr>
</tbody>
</table>

1Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Each site held 1 m⁻² enclosures of Mercenaria mercenaria at 80 m⁻²; one enclosure contained clams derived from a common Back Sound site (supplemented by 10-20 mm clams from other Back Sound origins), and at least one other enclosure contained only locally derived clams.
At each site, all *M. mercenaria* in these experiments >20 mm in initial length came from one of two different sources. One enclosure at each site held clams planted at the constant density of 80 m⁻² and collected initially from a single source, a seagrass bed along the southern shore of Back Sound (described in Peterson et al. 1984). One or two additional enclosures held clams collected locally at the specific study site, but again kept at the same 80 m⁻² density. Low availability of clams in the 10-20 mm size class from the Back Sound source forced us to add hatchery-reared clams (spawned from Back Sound individuals) and wild-caught clams from Middle Marsh also in Back Sound to represent the 10-20 mm sizes in the "common source" enclosure at each site. This smallest size class was available locally at each site to complete the "local-origin" enclosures. This design was chosen to enable us to test whether there were any effects of clam origin (the single Back Sound source vs. local clams) at each of the five study sites.

Upon termination of the experiment almost exactly 2 yr after initial planting of the marked clams (Table 2), subsets of those clams that had survived the complete 2-yr period were selected from each origin treatment at each study site in as wide a range of sizes as possible. These clams were returned to the laboratory and killed by steaming. One valve from each of these 2-yr survivors was then sectioned, using a diamond blade on a slow-speed Buehler ISOMET saw, from umbo to ventral margin along the axis of greatest growth. The shell sections were sanded and polished when necessary to enhance the clarity of natural banding patterns. Because the initial size in August-September 1980 and the intermediate size 1 yr later were known for each of the marked individuals and could be marked on the shell surface, and because the marking and measuring process itself almost invariably induces deposition of a disturbance check which serves as a very precise internal shell marker (Peterson et al. 1983), we were then able to count with the unaided eye the number of additional growth bands deposited in the internal shell matrix of each clam during its final 2 yr of life. We also observed where these bands were deposited relative to the known sizes at the initial, intermediate, and final measuring dates. These observations permit a test of whether the reliability of using summer growth bands to age North Carolina's *M. mercenaria* varies with site (habitat) or clam origin in the vicinity of Cape Lookout.

### Results

We sectioned shells from a total of 89 *M. mercenaria* collected alive in August-September 1982 and known by their paint codes to have been present in the field since the experiment's initiation 24 mo before (Table 2). Of these 89 individuals, 17 either exhibited insufficient growth to permit an accurate determination of the precise shell size at the experiment's initiation or else lacked a disturbance check to mark the precise size at initiation. Of the remaining 72 individuals, all but 2 deposited exactly 2 additional dark growth bands in the final 24 mo of life (Table 3). This pattern was consistent across all five study sites and did not change as a function of clam origin (Table 3). The appearance of the dark

<table>
<thead>
<tr>
<th>Clam origin</th>
<th>North River</th>
<th>Bogue Sound</th>
<th>Core Sound</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Back Sound</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North River</td>
<td>10</td>
<td>1</td>
<td>19-74</td>
<td>43-80</td>
</tr>
<tr>
<td>Bogue Sound</td>
<td>10</td>
<td>1</td>
<td>14-57</td>
<td>21-72</td>
</tr>
<tr>
<td>Seagrass</td>
<td>3</td>
<td>1</td>
<td>39-69</td>
<td>44-48</td>
</tr>
<tr>
<td>Sand</td>
<td>10</td>
<td>0</td>
<td>18-75</td>
<td>63-70</td>
</tr>
<tr>
<td>Core Sound</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>10</td>
<td>1</td>
<td>15-72</td>
<td>46-56</td>
</tr>
</tbody>
</table>

### Table 3

For each of five new study sites: 1) numbers of hard clams cut for growth analysis from each origin treatment, 2) numbers of those with insufficient growth to assess band deposition accurately, 3) range of initial clam lengths for those clams with sufficient growth, and 4) average number of bands deposited in the 2-yr experimental period.
band in cross-section was identical to that previously described and illustrated by photograph (Peterson et al. 1983) of clams harvested from the Middle Marsh locality.

The pattern of band deposition relative to times of initial planting, first measurement (12 mo), and collection (24 mo) was also extremely consistent across all data sets. Initial planting in 1980 occurred during the period of annual band deposition for 70 of the 72 clams. (In one clam, the 1980 annual band was just completed and in another the 1980 annual band was just about to begin at the time of initial planting.) The disturbance check caused by the 12-mo measurement fell near the end of the growth band for 70 clams and just after the band for the two others. The time of collection in 1982 fell during or just immediately after the deposition of the 1982 annual band for all clams except those from local origin at North River. Of the 16 cut clams in that data set with sufficient growth for band resolution, 12 were just beginning to deposit their 1982 band at the time of collection (2 August, 3-4 wk earlier than the other sites—Table 2). Two of the 16 lacked the terminal band, whereas the remaining two had already deposited a substantial amount of the 1982 band. This North River local data set was the only one that contained any clams (only three) which had bands sufficiently faint to cause any doubt about recording them.

By counting all presumptive annual bands over the complete growth record of each clam, we also estimated the age of each of the 89 M. mercenaria used in this experiment. The estimated age at the experiment's initiation for the 17 clams excluded from our 2-yr tests ranged from 6 to 29 yr and averaged 15.5 yr (±1.7 SE). For the 72 clams that grew sufficiently and included a sufficient shell marker at initiation to be used in our 2-yr tests, age at experimental initiation ranged from 0 to 17 yr and averaged 3.9 yr (±0.3 SE). Thus, the average age of the clams that could not be used for our tests was significantly \( P < 0.01 \) in a \( t \)-test) higher than that of the 72 clams that were used. Most (16 of 17) of the excluded clams lacked both sufficient growth and an obvious disturbance check at initiation. Only one clam was excluded with sufficient growth but without an adequate disturbance check. Although 16 clams lacked sufficient growth to determine accurately the shell size at the initiation of the experiment and were therefore excluded from our tests, all of these clams possessed discrete bands in their shells that could be counted separately. They were, however, close together at the terminal margin of the shell where separating them was not always possible and caused some uncertainty in their age estimates.

**Discussion**

Our banding data from recovery of marked and measured M. mercenaria after virtually 24 mo of terminal growth provide a compelling case for the reliability across different habitats of using major growth bands in sectioned shells to age hard clams in the Cape Lookout region of North Carolina. Our previous test of the annual periodicity of banding in North Carolina's M. mercenaria (Peterson et al. 1983) was carried out in only single locality, a Back Sound seagrass bed, characterized by almost equal proportions by weight of sands and muds in its surface sediments (Table 1). Through this study, we extend our tests of the reliability of annual band deposition in M. mercenaria to several additional sites, located in different bodies of water and characterized by much sandier sediments (Table 1). Of the six sites that we used for these tests, three were vegetated by seagrasses and three lacked macrophytic cover (Table 1). (Although our initial experiment in Middle Marsh was situated inside a seagrass bed, seagrasses were removed from the experimental plots during each sampling.) Despite these differences in local geographic location (and probably salinity), sediment grade, and seagrass presence, banding patterns were consistent and bands were deposited annually.

By using relatively high densities of 80 m\(^{-2}\) (over 10 times the average natural density found in a Bogue Sound seagrass bed by Peterson 1982, in North River, Bogue, Back, and Core Sounds by Beal 1983, and in Back Sound seagrass beds and sand flats by Peterson et al. 1984), we ran the risk of causing inhibition of growth. In fact, we were unable to analyze growth band deposition in 17 of our 89 clams largely because of insufficient growth in the terminal 2-yr increment. This problem may have been induced by our choice of relatively high density in these experiments, but it does have a natural analog. In areas with relatively slow growth and in older age classes where growth rate slows, aging North Carolina's M. mercenaria by counting annual bands in shell cross-section may be more difficult and lead to greater error than the consistency of banding results on our other 72 clams implies (Table 3). Nevertheless, banding even in these generally older clams that were excluded from our analyses was discrete and sufficient to permit us to estimate their ages. Aging does not appear to imply cessation of annual band deposition but only an increased dif-
difficulty in distinguishing one band from another. Observations on the timing of annual band deposition in this study agree well with our previous results (Peterson et al. 1983). The 6 August-3 September period in 1980 consistently fell within the season of annual band deposition and near the end of the band at all five new study sites. Furthermore, the annual band was still being formed or had just been completed in all clams collected 24 August-3 September 1982. The banding of *M. mercenaria* in North Carolina appears to be a summertime event in contrast to the winter banding in northeastern populations (Barker 1964; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Clark and Lutz 1982).

The only clams that failed to deposit two additional annual bands in the 24 mo of this study were taken from the North River locals. This is also the only group that deviated in the timing of final band deposition relative to the 1982 collection date. Most of these clams had just initiated their 1982 bands at the time of collection in contrast to those from all other sites where 1982 band deposition was either far advanced or even terminated. This difference between sites is probably a consequence of the 3-4 wk earlier date of collection at North River (Table 2). Despite an identical, early collection date, the Back Sound clams transplanted to North River exhibited a pattern of band deposition in 1982 that more closely resembled the other four sites than did the North River local clams. This difference provides our only suggestion of an effect of clam origin, but we have no explanation for the possible effect and do not consider it a serious cause to doubt the consistency of annual band deposition in North Carolina’s *M. mercenaria*.

The tests of consistency of annual band deposition across habitats in a local estuarine system provide an additional source of confidence in the accuracy of using internal banding patterns to age *M. mercenaria* in the Cape Lookout region of North Carolina. Concern over the lack of such controlled tests had earlier prompted Clark (1974), Gould (1979), and Jones (1981) to question the widespread assumption of regular periodicity in repeating shell features. Our demonstration of consistency in annual banding across local habitats should remove any doubts about the general applicability of using annual bands to age *M. mercenaria* in the Cape Lookout region of North Carolina. The variation in line deposition patterns which has been shown across habitats for *Protostaca staminea* (Peterson and Ambrose 1985) and among individuals within habitat for *P. staminea* and *Chione fluctuifraga* (Hughes and Clausen 1980) does not exist for *M. mercenaria* near Cape Lookout. Our results will not only enable invertebrate fisheries biologists to use growth bands with confidence to age North Carolina’s *M. mercenaria* but also should stimulate further research on understanding the environmental causes of variation in bivalve shell deposition patterns.

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THAYER, G. W.

CHARLES H. PETERSON

P. BRUCE DUNCAN

HENRY C. SUMMERSON

BRIAN P. BEAL

Institute of Marine Sciences
University of North Carolina at Chapel Hill
Morehead City, NC 28557

STANDING STOCK OF JUVENILE BROWN SHRIMP, Penaeus AzteCUS, IN TEXAS COASTAL PONDS

The increased demand for timely information concerning management of shrimp stocks has renewed interest in developing reliable methods of predicting brown shrimp, Penaeus aztecus, crop size for the offshore Gulf of Mexico fishery. Advance information regarding shrimp abundance would also enable elements of the shrimp industry to prepare for a potentially good or poor harvest. Studies exploring the feasibility of predicting the annual abundance of brown shrimp off the Texas coast, initiated in 1960 (Baxter 1963), are based on the premise that postlarval and juvenile shrimp abundances are proportionally related to the subsequent commercial harvest (Berry and Baxter 1969).

A "good" predictor is one that is precise, timely, and cost effective. The abundance of postlarval shrimp as they move from the Gulf of Mexico into coastal bays is determined from semiweekly collections made by the National Marine Fisheries Service, Galveston, at the entrance to Galveston Bay between late February and early May (Baxter 1963). The postlarval shrimp index gives the earliest but least reliable indication of potential harvest. A more accurate but less timely prediction is derived from landings of the bait shrimp fishery. Statistics for bait shrimp landings since 1960 provide the basis for a predictive model developed by K. N. Baxter (Klima et al. 1982) defining the relationship between the bait abundance index and subsequent offshore catch. However, this prediction is not available until mid-June, just prior to the seasonal opening, because recruitment of brown shrimp into the bait fishery does not begin until May (Chin 1960). A third possible indicator is the standing stock size of juvenile shrimp in estuarine nursery areas measured before shrimp emigrate and become vulnerable to the bait fishery. This would provide an estimate earlier in the season than the bait index and may be a more accurate predictor than the postlarval abundance. Predictive capability increases with each successive life stage because of the decreased time span between the estimate and subsequent commercial harvest.

To examine the relationship between juvenile brown shrimp standing stock and offshore harvest, and to determine the suitability of juvenile brown shrimp abundance as a predictor, we conducted a mark-recapture study in Galveston Bay, TX, during the first week of June 1983.