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A LONG-TERM MARK-RECAPTURE STUDY DOCUMENTING ANNUAL GROWTH BANDS WITHIN THE SHELLS OF NORTHERN QUAHOGS (= HARD CLAMS) *MERCENARIA MERCENARIA*

RICHARD A. LUTZ*

Department of Marine and Coastal Sciences, School of Environmental and Biological Sciences, Rutgers University, 71 Dudley Rd, New Brunswick, NJ 08901

ABSTRACT In the late 1940s and early 1950s Thurlow C. Nelson and Harold H. Haskin conducted a series of mark-recapture experiments to assess the growth of hard clams (*Mercenaria mercenaria*) on Delaware Bay mud flats adjacent to the Rutgers University Oyster Research Laboratory in Cape May County, NJ. Two specimens from these experiments were recovered alive on September 7, 1980. The growing shell margin of one of these clams (Specimen #1) had been notched with a hack saw between March and December 1947. The growing shell margin of the second clam (Specimen #2) had been notched with a small triangular file between March 1948 and December 1951. Examination of polished shell sections (cut along the axis of maximum growth) of specimens #1 and #2 revealed, respectively, 33 and 30 dark (translucent) bands within the postnotch regions of the outer and middle shell layer of each specimen. The presence of light (opaque) shell material in the outer and middle shell layers at the growing margin of each of these specimens is consistent with the observations of other workers that indicate the formation of dark (translucent) bands in this species during the winter months in certain coastal environments from the MidAtlantic region northward along the east coast of North America. The present study provides convincing evidence that alternating light (opaque) and dark (translucent) bands within the outer and middle shell layers of *Mercenaria mercenaria* from Delaware Bay, NJ mud flats reflect annual cycles of growth and can be used for estimating the age of hard clams from this region. It is believed that the present study represents the longest mark-recapture study of growth patterns within the shells on any bivalve mollusc.

KEY WORDS: *Mercenaria mercenaria*, hard clam, annual growth bands

INTRODUCTION

For over half a century, growth patterns within the shell of the northern quahog (= hard clam) *Mercenaria mercenaria* (Linnaeus, 1758) have been a focus of research efforts in a myriad of ecological, paleontological, and archaeological studies (Pannella & MacClintock 1968; Pannella et al., 1968; Rhoads & Pannella 1970; Kennish & Olsson 1975; Lutz & Rhoads 1977; Gordon & Carriker 1978; Clark 1979; Kennish 1980, 1984; Kennish & Loveland 1980; Lutz & Rhoads 1980; Fritz & Haven 1983; Peterson et al. 1983, 1985a, 1985b; Quitmyer et al. 1985, 1997; Ropes 1987; Arnold et al. 1991, 1998; Grizzle & Lutz 1988; Jones et al. 1990; Slattery et al. 1991; Jones & Quitmyer 1996; Richardson 2001; Surge et al. 2008; Brown et al. 2010; Ridgway et al. 2011; Palmer et al. 2021). In many of these studies, various authors have provided evidence that alternating light (opaque) and dark (translucent) bands (when viewed by the naked eye or under a microscope with reflected light) in polished, radial shell sections within the outer and middle shell layers of *M. mercenaria* reflect annual cycles of growth, facilitating age estimates of individual specimens (e.g., Clark 1979; Peterson et al. 1983; Jones et al. 1990; Jones & Quitmyer 1996; Quitmyer et al. 1997; Arnold et al. 1998; Fritz 2001). In polished thin sections (when viewed under a microscope with transmitted light), the opaque bands appear dark and the translucent bands appear light (Clark 1979, 1980). Similarly, when viewing acetate peels of polished and etched shell sections under a microscope with transmitted light, dark (translucent) regions seen in polished shell sections appear light in the peels and light (opaque) regions seen in polished shell sections appear dark (Kennish et al. 1980; Fritz & Haven 1983; Richardson & Walker 1991; Fritz 2001; Richardson 2001). Throughout the geographical range of *M. mercenaria* along the east coast of North America, translucent bands are formed during periods of slow growth, whereas opaque bands are formed during periods of relatively rapid growth (Clark & Lutz 1982; Grizzle & Lutz 1988; Surge et al. 2008). As a result, translucent bands in *M. mercenaria* shells collected north of New Jersey to Maine are generally formed during the winter when water temperatures are at a minimum and growth is slow (Rhoads & Pannella 1970; Jones et al. 1989; Quitmyer et al. 1997). In contrast, dark (translucent) bands in the shells of specimens collected along the Atlantic coast from Virginia to Florida are generally formed during the summer when high water temperatures inhibit growth (Clark 1979; Fritz & Haven 1983; Peterson et al. 1983, 1985a, 1985b; Jones et al. 1990; Arnold et al. 1991, 1998). As articulated by Jones and Quitmyer (1996, p. 340), a "transition zone occurs in the MidAtlantic region where aspects of both patterns are observed. Water temperature extremes (high or low) appear to be the primary factor controlling the timing of dark (translucent) increment formation." The results reported in the present paper from a 30+ year mark-recapture experiment provide additional evidence for the annual nature of alternating light and dark bands in the outer and middle shell layers of *M. mercenaria* in Delaware Bay, NJ.

MATERIALS AND METHODS

Between March and December 1947, the growing margin of shells of numerous hard clams (*Mercenaria mercenaria*) were notched with a hack saw and transplanted in Delaware Bay mud flats adjacent to Rutgers University's Cape Shore Laboratory (Cape May County, NJ) as part of an experiment conducted

*Corresponding author. E-mail: rlutz@marine.rutgers.edu
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by Thurlow C. Nelson and Harold H. Haskin to assess growth rates of this species in the region. Between March 1948 and December 1951, the growing margin of the shells of additional specimens of *M. mercenaria* were notched with a small triangular file and transplanted in these same mud flats in another experiment to obtain additional growth rate data for clams living in the area (Lutz & Haskin 1985). Two specimens from these experiments were recovered alive on September 7, 1980.

The soft tissues from both specimens were removed, and the shells were embedded in an epoxy resin and subsequently sectioned using a diamond saw along the axis of maximum growth as figured in Rhoads and Pannella (1970). As articulated by Jones et al. (1990), the axis of maximum growth is also the maximum shell height (i.e., the greatest distance from the umbo to the ventral margin). The resulting cross sections were polished using 240-, 400-, and 600-grit emery papers in succession followed by 1.0-micron alumina microgrit using a high-speed, rotating lapidary wheel as outlined by Jones et al. (1990). High-resolution photographs were taken of the polished sections, which were enlarged to view and document growth patterns within the outer and middle shell layers of the specimens.

RESULTS

Of the two clams recovered on September 7, 1980, one of these specimens (Specimen #1) had a shell length at the time of recovery of 87 mm) and a conspicuous hack saw notch on the surface of the shell which indicated that the shell length of the specimen at the time of notching (sometime between March and December of 1947) was 49 mm (Fig. 1). The second specimen (Specimen #2) had a shell length at the time of recovery of 99 mm and had a conspicuous V-shaped notch which indicated that the shell length of the specimen at the time of notching with a triangular file (sometime between March 1948 and December 1951) was 58 mm.

A cross section of the polished, embedded shell of Specimen #1 is depicted in Figure 2, revealing alternating light (opaque) and dark (translucent) bands within the outer and middle shell layers, with 33 dark (translucent) bands between the hack saw notch (N) (made between March and December, 1947) and the ventral margin of the cross section. The presence of a light (opaque) band in the outer and middle shell layers at the ventral margin (forming when the shell was sampled on September 7, 1980) is consistent with the formation of light (opaque) bands during the warmer months and dark (translucent) bands during the winter months in this region of the Delaware Bay.

A cross section of the polished shell of Specimen #2 is depicted in Figure 3, revealing alternating light (opaque) and dark (translucent) bands within the outer and middle shell layers, with 30 dark (translucent) bands between the triangular file notch (N) (made between March and December, 1951) and the ventral margin of the cross section. The presence of a light (opaque) band in the outer and middle shell layers at the ventral margin (forming when the shell was sampled on September 7, 1980) is once again consistent with the formation of light (opaque) bands during the warmer months and dark (translucent) bands during the winter months in this region of the Delaware Bay.

DISCUSSION

As articulated by Ridgway et al. (2011, p. 35), the "annual periodicity of increment formation in the shell of *Mercenaria mercenaria* has been demonstrated by mark-and-recapture experiments (Peterson et al. 1983), stable isotope profiles (Jones et al. 1990; Jones & Quitmyer 1996; Surge et al. 2008), and sequential sampling (Clark 1979; Peterson et al. 1985a, 1985b; Jones et al. 1990; Arnold et al. 1991; Arnold et al. 1998)." Perhaps the most conclusive of these studies was a mark-recapture study conducted by Peterson et al. (1983) over the period of several years to document the annual periodicity of growth banding patterns

Figure 1. Right shell valve of a hard clam (*Mercenaria mercenaria*) (Specimen #1) that was sampled on September 7, 1980 from the Delaware Bay mud flats adjacent to Rutgers University's Cape Shore laboratory in Cape May County, NJ. The notch (N) was formed using a hacksaw between March and December 1947 when the hard clam had a shell length of 49 mm.

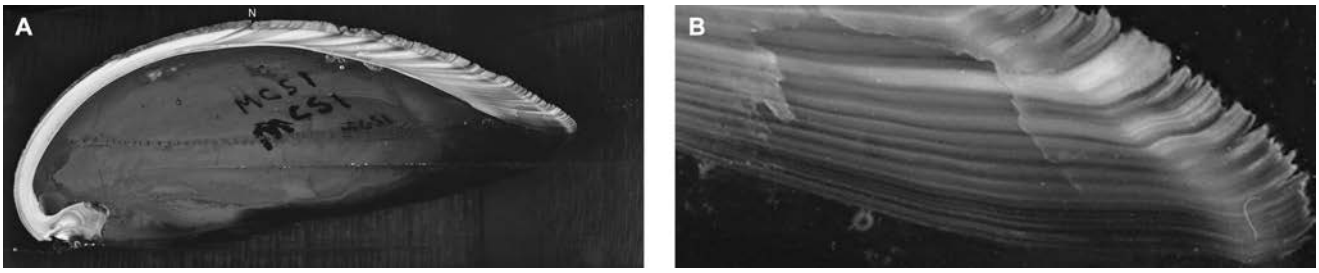

Figure 2. (A) A cross section of the polished left shell valve of the hard clam (Specimen # 1) depicted in Figure 1, revealing alternating light (opaque) and dark (translucent) bands within the outer and middle shell layers, with 33 dark (translucent) bands between the hack saw notch (N) (made between March and December 1947) and the ventral margin of the cross section. (B) An enlargement of the ventral portion of the cross section seen in (A) that facilitates the counting of growth bands in this region of the shell and reveals the presence of a light (opaque) band at the ventral margin (forming when the shell was sampled on September 7, 1980), which is consistent with the formation of light (opaque) bands during the warmer months and dark (translucent) bands during the winter months in this region of the Delaware Bay.

in the shells of *M. mercenaria* in North Carolina populations. In this study, individually marked and measured specimens of *M. mercenaria* were placed in sediments inside field enclosures near Cape Lookout, NC in June 1978. Subsets of these hard clams were collected and sacrificed in October 1979, May 1980, October 1980, and October 1981. One shell valve of each collected specimen was sectioned and revealed that dark (translucent) bands were formed in the outer and middle shell layers during periods of slow growth in the summer and early fall. This was in marked contrast to results reported by other workers studying *M. mercenaria* from more northern populations, which indicated that dark (translucent) bands were formed during the winter months (Rhoads & Pannella 1970; Clark & Lutz 1982; Jones et al. 1989). Other sequential sampling studies conducted along the North Atlantic coastline in waters south of North Carolina provided additional evidence that dark (translucent) bands in the outer and middle shell layers of *M. mercenaria* shells were formed during the warmer months of the year and not during the winter months in these more southern regions of the east coast of North America (Clark 1979; Jones et al. 1990; Arnold et al. 1991, 1998; Quitmyer et al. 1997).

In a study of growth patterns within the shells of *Mercenaria mercenaria* collected from a coastal lagoon in southern New Jersey, Grizzle and Lutz (1988) collected specimens during various seasons to photographically document when various banding patterns were formed during the year. These studies indicated a "seasonal pattern consisting of: (1) a wide light-colored spring band; (2) a wide dark summer band; (3) a wide light fall band; (4) a thin dark slow-growth band, or "break," deposited in winter" (Grizzle & Lutz 1988, p. 367). This pattern was similar to that described by Peterson et al. (1983) in shells of *M. mercenaria* from North Carolina and quite different from the pattern described in the present study. This is in line with the statement by Grizzle and Lutz (1988) that "the pattern reported herein for *M. mercenaria* from southern New Jersey may not be the only one possible for New Jersey specimens." Indeed, in contrast to the results presented by Grizzle and Lutz (1988), shell growth patterns in the outer and middle shell layers of the two sectioned hard clam shells depicted in the present paper indicate that dark (translucent) bands reflect slow growth during the winter months, with no wide, dark summer bands.

The counting of growth bands within the shells of *Mercenaria mercenaria* has been used in a wide variety of studies to estimate the age of individual clams (Peterson 1983, 1986; Ropes 1987; Jones et al. 1989, 1990; Ridgway et al. 2011). Based on growth band counts in the outer and middle shell layers of *M. mercenaria*, Jones et al. (1990) reported the presence of hard clams from Cedar Key, FL as old 28 y, whereas Peterson (1986) reported

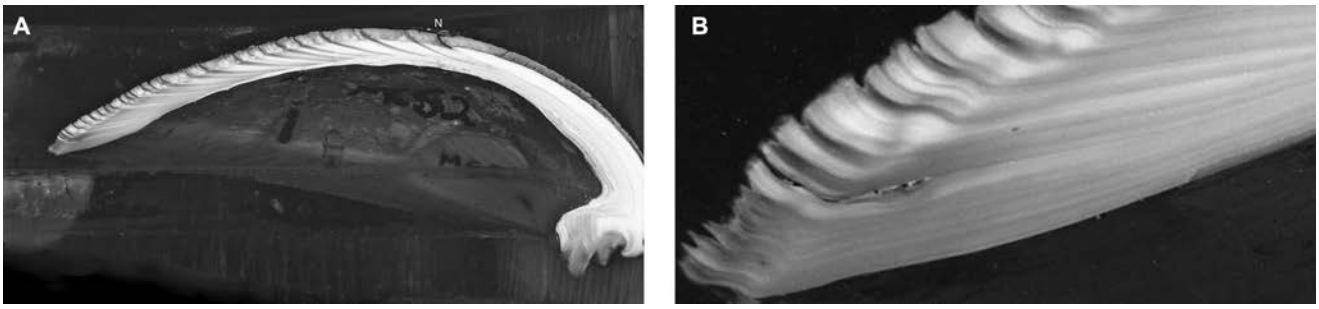

Figure 3. (A) A cross section of the polished shell valve of a hard clam (*Mercenaria mercenaria*) (Specimen #2) that was sampled on September 7, 1980 from the Delaware Bay mud flats adjacent to Rutgers University's Cape Shore laboratory in Cape May County, NJ. The shell of this specimen was notched with a triangular file sometime between March 1948 and December 1951 when the hard clam had a shell length of 58 mm. The cross section reveals alternating light (opaque) and dark (translucent) bands within the outer and middle shell layers, with 30 dark (translucent) bands between the triangular file notch (N) (made between March 1948 and December 1951) and the ventral margin of the cross section. (B) An enlargement of the ventral portion of the cross section seen in (A) that facilitates the counting of growth bands in this region of the shell and reveals the presence of a light (opaque) band at the ventral margin (forming when the shell was sampled on September 7, 1980), which is consistent with the formation of light (opaque) bands during the warmer months and dark (translucent) bands during the winter months in this region of the Delaware Bay.

specimens living up to 46 y in North Carolina populations. Based on the counting of banding patterns in the hinge region of the shells of 22 specimens of *M. mercenaria* from Buzzards Bay, MA, Ridgway et al. (2011) estimated the age of the oldest to be 106 y. As mentioned earlier, a number of studies have provided convincing evidence for the annual nature of these bands from certain locations but, as emphasized by Grizzle and Lutz (1988, p. 367), "caution has been urged with regard to using shell growth patterns for ecological and other studies until particular patterns for the species being studied have been well assessed …. Only if a specific pattern is adequately documented (i.e., determined by adequate tests that the pattern is repeating and periodic) and described, can it be useful in such studies." To this end, the present study has provided convincing evidence that alternating light (opaque) and dark (translucent) bands within the outer and middle shell layers of *M. mercenaria* from Delaware Bay, NJ mud flats reflect annual cycles of growth and can be used for estimating the age of hard clams from this region. It also provides evidence that the hard clams in this region are capable of living in excess of 33 y. It is believed that the present study represents the longest mark-recapture study of growth patterns within the shells of any bivalve mollusc.

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