ANNUAL SHELL BANDING, AGE, AND GROWTH RATE OF HARD CLAMS (*MERCENARIA* SPP.) FROM FLORIDA

DOUGLAS S. JONES,[1] IRVY R. QUITMYER,[1]
WILLIAM S. ARNOLD[2] AND DAN C. MARELLI[2]

[1]*Florida Museum of Natural History*
University of Florida
Gainesville, FL 32611
[2]*Florida Marine Research Institute*
100 8th Avenue, S.E.
St. Petersburg, FL 33701-5095

ABSTRACT Year-round collection of hard clams (*Mercenaria mercenaria* and *M. campechiensis*) from three coastal sites in Florida permits documentation of the annual cycle of shell growth increment formation in these bivalve species in the southern portion of their range. This cycle consists of alternating, macroscopic light increments (opaque white to beige) and dark increments (translucent grey to blue to purple) that are visible in the inner, middle, and outer shell layers of radially sectioned valves. These increments form seasonally; the light increment, characteristic of rapid shell growth, forms primarily during the spring in *M. campechiensis* from the Gulf Coast and during the winter in *M. mercenaria* from the northeastern Atlantic Coast of Florida. Over the remainder of the year, and particularly during the late summer and fall, the dark, slow-growth increment is added.

The annual shell increments were used to determine age and growth rates in 10 clam populations from both the Atlantic and Gulf coasts of the State of Florida. Hard clam growth was then modeled using the von Bertalanffy growth function which facilitated the comparison of growth between the Florida sites as well as with other, more northerly populations. The greatest growth was observed in populations of *Mercenaria campechiensis* from Boca Ciega Bay, where the largest known specimens have been reported. The oldest specimens (28 years old) came from the Cedar Key area, which also yielded large clams. Gulf Coast populations of *M. campechiensis* did not always exhibit greater growth than Atlantic Coast *M. mercenaria*, and clear latitudinal gradients in shell growth were not evident on either coast. In fact, growth variations between populations from collection sites within a single estuary occasionally exceeded those among sites on separate coasts.

The growth rates measured for Florida hard clams are typically greater than those reported for clams from New England, the Middle Atlantic Bight, and the southeastern United States, although the life span of the Florida clams is apparently shorter. Our results provide an assessment of hard clam growth parameters in Florida where relatively little data were heretofore available for comparison and where commercial exploitation of the resource has increased dramatically in recent years.

KEY WORDS: *Mercenaria*, hard clam, growth, shell banding, Florida

INTRODUCTION

Possibly no other bivalve mollusk has been the focus of as much research into shell growth increment formation as *Mercenaria mercenaria* (Linné), the northern quahog or hard clam. Throughout the hard clam's geographic range in eastern North America, from the Gulf of Mexico to Cape Cod with isolated populations extending into Maine and Canada (Ansell 1968), its shell increments have been studied. Cyclical microgrowth patterns ranging in scale from subdaily tidal, through daily, fortnightly tidal, lunar monthly, and annual have been described in this species (e.g., Barker 1964; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Cunliffe 1974; Kennish and Olsson 1975; Thompson 1975; Gordon and Carriker 1978; Kennish 1980, 1984). In addition to these cyclical patterns, an entire spectrum of growth breaks, some periodic (e.g., annual spawning) and some stochastic (e.g., storms), is potentially interpretable from hard clam shell records (Kennish and Olsson 1975).

Among this plethora of shell increments and growth breaks, annual, incremental banding patterns have proven to be the most consistent and readily interpretable (Lutz and Rhoads 1980). Annual increments have received wide application in marine ecological contexts, particularly in determining age and growth rates. Annual increments have been identified in shells of *Mercenaria mercenaria* throughout most of its geographic range (e.g., New England—Rhoads and Pannella 1970; Jones et al. 1989; New York/New Jersey—Kennish and Olsson 1975; Ropes 1987; Grizzle and Lutz 1988; Maryland/Virginia—Fritz and Haven 1983; North Carolina—Peterson et al. 1983, 1985; Georgia—Clark 1979; Quitmyer et al. 1985).

The annual pattern of hard clam shell growth consists of macroscopic, alternating light and dark increments in the inner, middle, and outer shell layers, best viewed in radial sections of either valve (Fig. 1). Recent work on the seasonal timing of formation of these increments (e.g., Clark and Lutz 1982; Peterson et al. 1983; Grizzle and Lutz 1988) suggests there are geographic differences in annual shell growth patterns, reflective of seasonal differences in ambient water temperature fluctuations. Of particular importance are summer and winter extremes (Lutz and Rhoads 1980). In comparing hard clams from North Carolina and New Jersey, Clark and Lutz (1982) observed that,
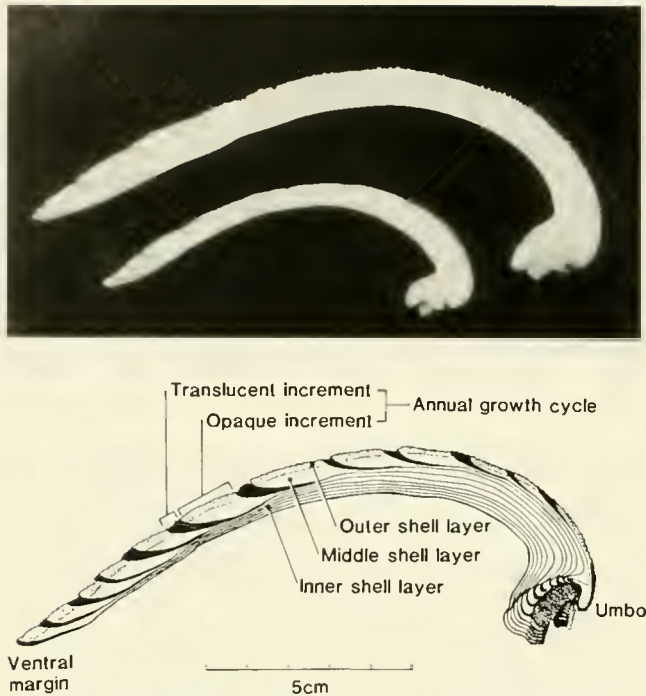
Figure 1. Reflected-light photograph of radial shell cross-sections of *M. campechiensis* (top), shell height = 104.66 mm, collected 10/14/88 at Cedar Key, Florida showing translucent (dark) growth increment forming at ventral margin and *M. mercenaria* (bottom), shell height = 67.38 mm, collected 5/23/82 at Kings Bay, Georgia showing opaque (light) growth increment forming at ventral margin. *M. campechiensis* specimen shows 10 annual shell growth increment cycles whereas *M. mercenaria* specimen shows 7 + years of growth. Lower schematic of radial shell section indicates annual growth cycle and structural elements of shell.

gional as well as inter-regional comparisons with other hard clam populations are not presently possible; 2) appreciation of growth rates near the southern limit of *M. mercenaria* will further elucidate the often cited influence of temperature upon the growth of these animals (Ansell 1968); and 3) potential growth differences and similarities between *M. mercenaria* and *M. campechiensis* may be assessed. The recent and dramatic rise in shellfishing pressure upon these species in Florida, combined with the insufficient baseline growth data presently available and the burgeoning hard clam aquaculture industry in Florida, make these growth studies all the more important and timely.

MATERIALS AND METHODS

Hard clams were collected from nine sites located on both the Atlantic and Gulf coasts of Florida (Fig. 2). A tenth site in Boca Ciega Bay was analyzed from published data (Saloman and Taylor 1969). Hard clam collections (total N = 1,578) were assembled and analyzed by either the Gainesville authors (Kings Bay, N = 451; Matanzas River, N = 60; Bokeelia and Catfish Creek in Charlotte Harbor, N = 399; and Cedar Key, N = 259) or the St. Petersburg authors (Indian River Body C, N = 153; and Body F, N = 149; Tampa Bay, N = 50; and St. Joseph Bay, N = 57). Most specimens were located by treading in shallow water and were collected manually. However, those from the Indian River lagoon were hand-raked in August 1986, and those from St. Joseph Bay were mechanically harvested by Mr. Harry Lawder during March 1987. At three of these sites (Kings Bay, Charlotte Harbor, and Cedar Key), year-round hard clam collections were made at

". . . features characteristic of winter in one locality can occur in summer in the other." Recognizing that the variations may be considerable and that a latitudinal gradient in season of growth increment formation may exist, Grizzle and Lutz (1988) have emphasized the need for documentation and description of such patterns.

The purpose of this investigation was two-fold. First, we wanted to examine the seasonal cycle and verify the annual periodicity of macroscopic growth increment formation in hard clam populations from Florida, including both the northern quahog, *Mercenaria mercenaria*, and the southern quahog, *Mercenaria campechiensis* (Gmelin). Comparisons of these patterns with those described for populations to the north should verify the existence of latitudinal differences. Relative to *M. mercenaria*, much less is known about seasonal shell increment patterns, age, and growth rate in *M. campechiensis*, making the need for such information even more acute. Our second objective was to determine, using annual growth increments, the age and growth relationships for populations of both species from around the state. Such information is significant for several reasons: 1) growth rate and longevity estimates are generally lacking for both coasts of Florida; therefore, intra-re-
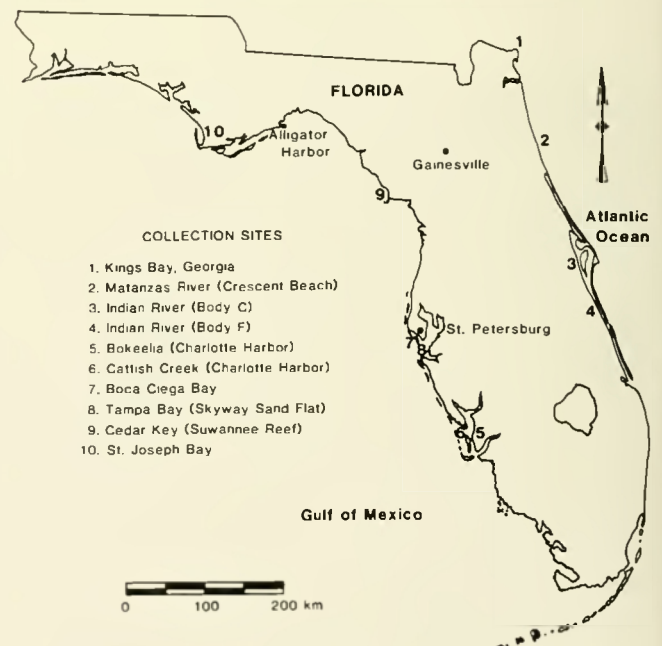

Figure 2. Map of Florida indicating hard clam collection localities. Site numbers are also identified in Table 1.

monthly intervals to investigate the annual cycle of growth increment formation. Specimens from the remaining sites were collected after one (Matanzas River—June 1988) or repeated visits to the site (Skyway Bridge—October 1986, June 1987; March 1988). Following transport back to the laboratory, each clam was eviscerated (usually with the aid of a microwave oven, which prevents shell damage), and the valves were washed, dried, numbered, and stored for later analysis.

All hard clams were prepared using similar techniques (see Rhoads and Lutz 1980). Each shell pair was disarticulated and one valve, usually the left, was appropriated. Clams from St. Joseph Bay, Tampa Bay, and the Indian River were embedded in Epon 815 epoxy resin prior to sectioning. When fully cured, the embedded valve was radially sectioned along the axis of maximum growth (maximum shell height, greatest distance from umbo to ventral margin) to reveal the growth increment record. This cut was made using a Highland Park Model 20SSP lapidary saw equipped with a diamond saw blade. The Gainesville group did not embed their shells. Sectioning was accomplished on a Lortone Model FS lapidary trim saw outfitted with an 8-inch diamond saw blade. In either case, the smooth cuts did not normally require further polishing or the preparation of acetate peels (Rhoads and Lutz 1980) in order to distinguish and measure the annual increments. In those cases where further polishing was required, 240-, 400-, and 600-grit emery papers were used in succession, followed by 1.0-micron alumina microgrit applied with a high-speed rotating lapidary wheel.

There was little difficulty identifying the first 5 to 10 annual shell increments in most specimens. Thereafter, crowding together of increments as ontogenetic shell growth rates declined occasionally resulted in the inability to uniquely distinguish between successive years, particularly in older specimens. If polishing and preparation of acetate peels could not resolve the situation, the shell was not used. Approximately 5% of the sectioned specimens were discarded.

To determine the season of increment formation, a total of 451 hard clams were analyzed from Kings Bay, Georgia, near the northeasternmost corner of Florida. These clams were collected at monthly intervals (approximately 20 per month) for two year-long periods, from August 1981 to July 1982 and again from November 1983 to November 1984. The results of the 1981–1982 study have been published as a modern comparative data set for an archaeological investigation of aboriginal seasonal clam harvesting in this region (Quitmyer et al. 1985). The second year of collection was undertaken to gauge interannual variability.

Two analogous collections were recently completed on the Gulf Coast of Florida in areas were large coastal shell middens and seasonal aboriginal habitation are of archaeological interest. Monthly collections were made at two localities within Charlotte Harbor (near Bokeelia and at the mouth of Catfish Creek) from March 1986 to February 1987. Bokeelia and Catfish Creek samples were pooled for analysis (N = 399). Similarly, monthly collections were made at Cedar Key (Suwannee Reef) from December 1987 to November 1988 (N = 259). In contrast to the Kings Bay study, southern quahogs, *Mercenaria campechiensis*, were recovered from these sites.

Specimens were collected during ebb tide and generally were from subtidal habitats, except for a few individuals from exposed sand bars at Bokeelia and Kings Bay. The substrates at each site were variable. Typically, muddy sand was dominant with shell hash present at all sites and seagrass beds common in Charlotte Harbor and at Cedar Key. Temperature and salinity were recorded concurrently with the monthly clam collections at all three sites.

The ventral shell margins of specimens collected monthly at the three sites involved in the seasonal banding study (Kings Bay, Charlotte Harbor, and Cedar Key) were examined in detail. In order to assess the annual pattern of growth increment formation, each sectioned shell was assigned to one of two categories, T or O. This assignment depended on whether the translucent (dark) or opaque (white) increment (as viewed in reflected light on the shell cross-section) was forming at the edge when the clam was captured (Fig. 1). By noting the percentages of clams in both of these categories on a monthly basis throughout the year, an annual pattern was described.

For the growth comparison study, a random subsample of 50 clams was selected from each population for analysis. This procedure served to standardize the sample sizes of all populations. To the nine stations actually visited in this study, a tenth was added based upon age and growth-rate data for 93 large specimens of *Mercenaria campechiensis* from Boca Ciega Bay reported by Saloman and Taylor (1969). These authors also interpreted age by counting the internal shell growth increments, considered to form annually.

With the naked eye or occasionally with the aid of a low-power binocular microscope, the ventral (distal) edge of each annual growth increment was marked with a sharp pencil at the point where it intersected the outer shell surface. Counting the total number of annual increments (pairs of light and dark bands) yielded the age of each specimen. The shell height at each age within a given shell was determined by measuring from the umbo to each successive pencil mark, so that a complete shell height versus age record (growth curve) was produced for every specimen. For consistency, we assumed that the first dark band in each shell represented an age of one year, and constructed our age profiles accordingly. In actuality, the time represented by the first dark band is almost always less than one year; it can vary from place to place as well as from year to year and depends upon the season in which the clams were spawned.

Measurements were performed with electronic, digital

calipers (MAX-CAL, Fred V. Fowler Co., Newton, Massachusetts) that read to 0.01 mm and were configured to an IBM-PC microcomputer. INCAL, a general purpose data entry and digital caliper drive program for the IBM-PC, was used to create and store data files which were later transferred to LOTUS 1-2-3 for analysis.

To facilitate comparison between regions, hard clam growth was modeled by fitting a von Bertalanffy growth function to the shell height-age data. This function is described by the following equation:

$$SH_t = SH_\infty[1 - e^{-k(t-t_0)}]$$

where t = time (or age in years), SH_t = shell height at t, SH_∞ = maximum asymptotic shell height, k = growth constant, and t_0 = time when SH_t = 0. The von Bertalanffy function was fit to the data using the NLIN procedure of SAS (1985). This iterative curve-fitting procedure employs nonlinear least-squares regression (multivariate secant method) and yields parameter values, estimates of their asymptotic standard errors, and an asymptotic correlation matrix of the parameters.

The von Bertalanffy growth function has traditionally received wide application in the analysis of bivalve growth (e.g., Brousseau 1979; Gallucci and Quinn 1979; Appledoorn 1983; Schick et al. 1988; Tanabe 1988; Jones et al. 1989). However, it is not the only function used to describe molluscan growth (e.g., Peterson and Black 1987). In fact, Kennish and Loveland (1980) reported that ontogenetic growth in *Mercenaria mercenaria* from Barnegat Bay, New Jersey, was best described by the Gompertz equation. In coastal Georgia, Walker and colleagues have used the power function to describe hard clam growth (Walker 1984; Walker and Humphrey 1984; Walker and Tenore 1984). To insure that the von Bertalanffy growth curve was the most appropriate for our study, four other commonly used functions (see Kaufmann 1981), including the Gompertz, logistic, exponential, and power curve (with and without intercept), were also fit to the data. As in an analogous study of hard clam growth in Rhode Island (Jones et al. 1989), the von Bertalanffy curve provided the best fit (highest R^2 values) and was used throughout the remainder of the investigation.

The single growth parameter, ω (= $k \times SH_\infty$), along with its variance, was calculated from the von Bertalanffy parameter estimates for each sample site according to the methods of Gallucci and Quinn (1979). Since ω is more robust than either k or SH_∞, this parameter offers a powerful and straightforward way of comparing organism growth curves between regions (Gallucci and Quinn 1979; Appledoorn 1980, 1983). The t_0 variable is basically a position parameter. It does not affect the growth rate comparisons and is not considered here. The ω parameter corresponds to the growth rate near t_0 and is suitable for comparisons of the compound null hypothesis $H_0:k_1 = k_2 = \ldots$

$= k_n$ and $SH_{\infty 1} = SH_{\infty 2} = \ldots = SH_{\infty n}$ for n regions. A ω value and its 95% confidence interval were calculated according to the method of Appledoorn (1980) for each sample site. It was then possible to rank the ω values and ascertain which of the sample sites were statistically different ($P \leq 0.05$) from one another by noting whether or not their confidence intervals overlapped. This procedure is straightforward, easily interpretable, and conservative.

RESULTS

The seasonal cycle of annual shell growth increment formation in *Mercenaria mercenaria* from Kings Bay, Georgia, and in *M. campechiensis* from Charlotte Harbor and Cedar Key, Florida, shows the same general pattern at all three sites, with some apparent differences in timing (Fig. 3). Monthly examinations of growing shell margins indicate that at Kings Bay, the episode of most rapid shell growth occurs throughout the winter, when the opaque (light) growth increment is added. At any give time within this period (December–March), 70–80% of the population is forming an opaque increment. A transition occurs during April/May when the percentages are reversed and a greater proportion of the hard clam population is characterized by having the translucent (dark) increment at the shell margin. Following this transition, from June through October, virtually 100% of the specimens were forming translucent increments. The annual shell growth pattern then comes full cycle in November/December when another transition occurs and clams with opaque marginal increments predominate.

The analysis of *Mercenaria campechiensis* from Gulf Coast localities indicates a similar pattern with a temporal shift. In Charlotte Harbor the opaque increment is added primarily during the spring; this period of rapid shell growth is centered around the month of April and is apparently briefer here than it is at Kings Bay. During the remainder of the year, and particularly from July through December, nearly 100% of the clam population is forming the translucent increment.

At Cedar Key the pattern is very similar, but the distinctions between periods of opaque and translucent increment formation are not as sharp. As illustrated in Figure 3, the episode of opaque growth increment formation is of longer duration but is still principally a spring phenomenon. It appears to begin slightly earlier (November/December) and extend slightly longer (into July). As the proportion of specimens with opaque marginal increments declines in the early summer, the percentage of clams forming translucent increments increases. This percentage reaches a maximum during the months of August, September, and October, when nearly 100% of the specimens collected were characterized by having the translucent marginal increment. During the succeeding months, from November through February, approximately 60–75% of the population was
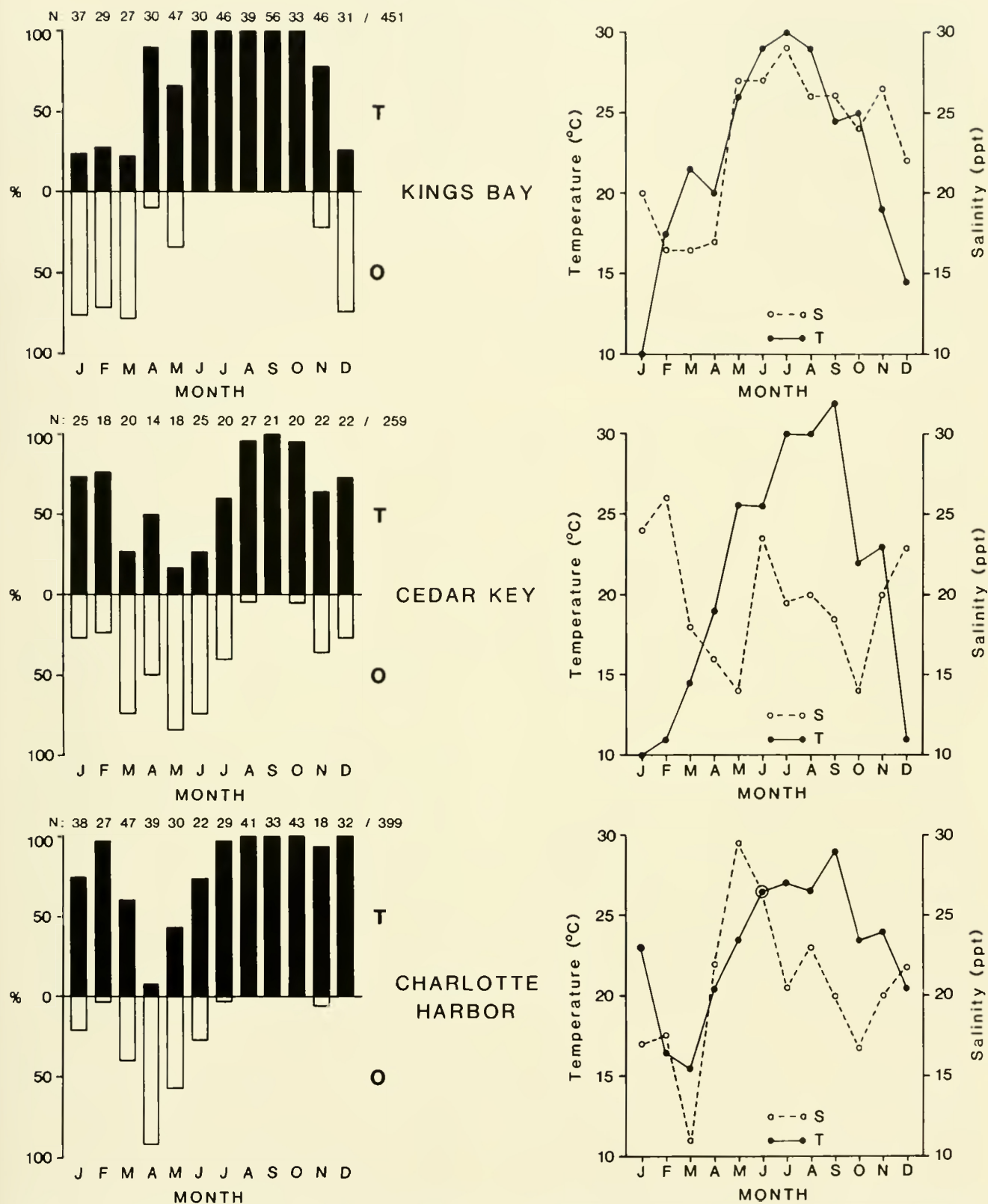
Figure 3. Annual cycle of growth increment formation in populations of *M. campechiensis* from Charlotte Harbor and Cedar Key, Florida and *M. mercenaria* from Kings Bay, Georgia, based on monthly collections of specimens. Vertical bars represent the percentage of the monthly sample forming either the translucent (T, dark) or opaque (O, light) growth increment. Accompanying temperature and salinity values were measured concurrently with hard clam collections.

still forming the translucent increment, whereas the re-mainder, mostly in the smaller, faster-growing size classes, had begun to form the opaque increment.

Comparison of the yearly shell cycle at any of these three sites where the temperature data were collected simul-taneously (Fig. 3) reveals that the translucent increments are added during the warmest portion of the year, whereas the opaque increment is more characteristically formed during cooler conditions. This pattern is particularly evi-dent in the Kings Bay and Charlotte Harbor data but is somewhat less clear-cut in the Cedar Key data. At none of the sites is the relationship so precise as to suggest that the changeover occurs at a particular temperature. Comparison of the shell cycle with the salinity data does not indicate a direct relationship, except possibly in the case of Kings Bay, where the temperature and salinity profiles are posi-tively correlated.

The results indicate that annual growth increment pat-terns are present in these two species in Florida and that they are valid age indicators in hard clams living in this portion of their range. Using these increments, the shell height for each year of growth was determined for 50 hard clams for each sample site. A von Bertalanffy growth curve was then fit to the data for each site according to the proce-dures outlined earlier. A curve was also fit to mean shell height versus age data for 93 hard clams reported by Sal-oman and Taylor (1969). These curves are shown in Fig. 4 for all ten sample sites, including both the Atlantic (*Mercenaria mercenaria*) and Gulf (*Mercenaria campe-chiensis*) coasts. The von Bertalanffy parameter estimates and their asymptotic standard errors for each site are listed in Table 1.

Also listed in Table 1 are the ranked values of ω for each sample site and a 95% confidence interval about each ω. These ω values and confidence intervals are graphically displayed (Fig. 5) to enhance appreciation of variability. Inspection of the ω values (Table 1, Fig. 5), as well as the growth curves shown in Figure 4, indicates that the null hypothesis of identical growth properties for hard clams at each sample station should be rejected. The greatest ω value was associated with the hard clams from Boca Ciega Bay reported by Saloman and Taylor (1969). This site has produced the largest recorded specimens of *Mercenaria campechiensis* (Sims 1964). The growth curve for this site plots well above all the others, indicating gigantic final sizes ($SH_∞$) produced by rapid initial growth rates that re-main high throughout the first decade or so of life. After Boca Ciega Bay, the next highest ω values were from Cat-fish Creek in Charlotte Harbor and Tampa Bay, respec-tively. The k value or growth constant determined for the former site was the largest encountered in this study, whereas both the k and $SH_∞$ parameters at the latter site were relatively large. A 95% confidence interval could not be calculated about the ω value for Boca Ciega Bay be-cause of the nature of the data reported by Saloman and Taylor (1969); however, this highest ω value falls within the 95% confidence interval for Catfish Creek, indicating statistically inseparable (P ≤ 0.05) ω values.

In order of descending rank, the next four ω values are associated with populations of *Mercenaria mercenaria* from the Atlantic Coast of Florida: Matanzas River, Indian River Body C and Body F, and Kings Bay. The ω values of the Matanzas River population and both populations from the Indian River are not statistically different at the 0.05 level. The ω value for the Kings Bay population, while separable at the 0.05 level, is nevertheless quite similar to the other east coast stations. Clearly, there is a greater de-gree of homogeneity among the von Bertalanffy growth pa-rameters associated with these hard clam populations than there is between the populations on the west coast of Florida (Fig. 5).

The lowest three ω values were determined for *Merce-naria campechiensis* populations at Bokeelia, situated at the northern end of Pine Island in Charlotte Harbor; for St. Joseph Bay on the Florida Panhandle; and for Suwannee Reef, located just north of Cedar Key. As indicated in Table 1, hard clams for Bokeelia achieve final sizes that are similar to those attained by clams from Catfish Creek, also located within Charlotte Harbor. The difference in the ω values between these two sites results from the higher k at the latter site. This difference within one estuary exceeds that observed between clams from either Bokeelia or Cat-fish Creek and clams on the Atlantic Coast (Table 1). The $SH_∞$ determined for the St. Joseph Bay clams was the lowest for any of the Gulf Coast *M. campechiensis* popula-tions and is largely responsible for the low ω. In fact, the growth curve for this area (Fig. 4) illustrates that the size versus age relationship for these clams was much more similar to that of Atlantic Coast *M. mercenaria* than to their Gulf Coast counterparts. Finally, the lowest ω was ob-tained for the Cedar Key population. Though this locality produced large clams (second only to Boca Ciega Bay), the growth constant k was clearly the lowest encountered in this study. Because k is largely responsible for the curva-ture of the von Bertalanffy function (Gallucci and Quinn 1979), the Cedar Key growth curve (Fig. 4) appears much straighter than the other nine curves.

Whereas their growth rates were the lowest, the oldest measurable clams in this study (28 years) came from the Cedar Key locality, followed by St. Joseph Bay (23 years), Boca Ciega Bay (22 years), and Bokeelia, Tampa Bay and Indian River Body F (20 years). The oldest specimens at the remaining stations were 13 years old at capture (Figure 4). For several reasons discussed in the following section, these age determinations necessarily represent minimum estimates of maximum age and should be carefully inter-preted in the context of longevity.

DISCUSSION

Annual shell growth increment patterns have been re-ported in *Mercenaria* from New England to the south-
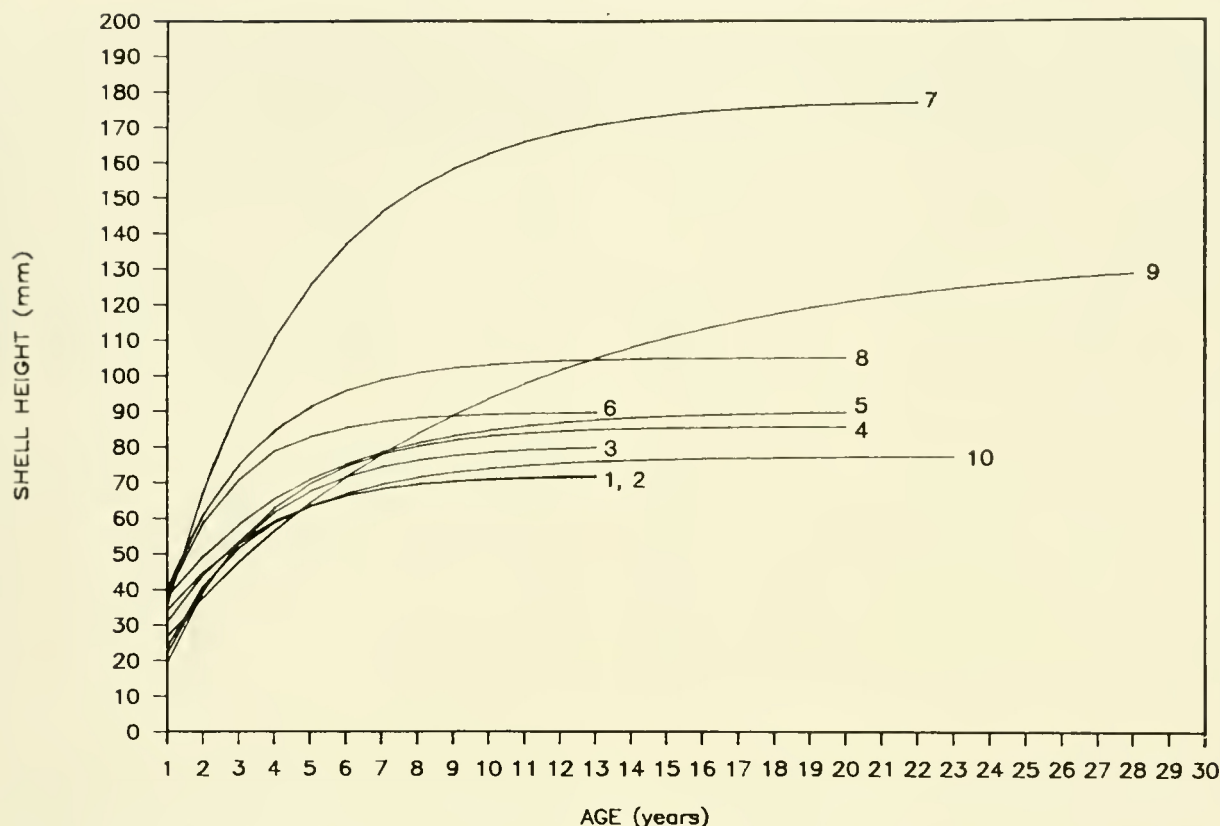
Figure 4. Best fit von Bertalanffy growth curves relating shell height and age for each of the 10 sites investigated in this study. Site numbers are identified in Fig. 2 and Table 1, as are the von Bertalanffy parameter estimates. Both *M. mercenaria* (1–4) and *M. campechiensis* (5–10) are represented here.

eastern United States. The "classic" interpretation of the dark increments as winter, slow-growth phenomena arose from studies of northern populations (e.g., Kerswill 1941; Pannella and MacClintock 1968; Rhoads and Pannella 1970). However, Kennish and Olsson (1975) showed that high as well as low temperatures can cause growth-rate inhibition and induce shell increment formation. Recent studies have emphasized geographic differences in this basic pattern that appear to have a latitudinal component. Therefore, it is important to compare the shell increment patterns described herein for Florida hard clams with those described elsewhere for other localities.

Clark and Lutz (1982) described incremental growth patterns for *Mercenaria mercenaria* from sites extending from Maine to Georgia. These authors stated that features characteristic of winter in one locality can occur in summer in the other. Clark (1979) reported that hard clams from coastal Georgia formed the translucent increment during times of warm water temperatures; growth slowed during the summer and fall and was fastest during winter and spring. He also observed that the summer growth halt, ". . . fits the data reported by Ansell (1968), who shows that *Mercenaria mercenaria* has a winter growth halt in waters from Virginia to Canada, and a summer growth halt from North Carolina to Florida." Peterson et al. (1983)

suggested the dark increment formed between May and October, whereas the light increment formed from November to April. This pattern is very similar to that observed here for the Florida hard clams (Fig. 3), except that in Florida the interval of translucent increment formation is extended by a month or two. This may be a real difference or it may reflect the particular year in which sampling occurred. In the present study, temporal trends in annual shell increment formation were assessed for one-year intervals (except for Kings Bay, where two years' data were combined) so that the average natural cycle might be shifted to the extent that the particular year of observation was atypical.

A similar pattern was reported by Fritz and Haven (1983) for clams from Chesapeake Bay, Virginia, and more recently by Grizzle and Lutz (1988) for those in New Jersey, except that in both of these cases, a second dark increment often formed in the winter. Thus, dark increments have been reported from northern specimens as occurring both in summer and winter. The summer dark increment is apparently wider and bounded in spring and fall by white increments reflecting rapid growth phases. The winter dark increment, when present, is apparently much narrower and is perhaps better described as a dark 'break' (Grizzle and Lutz 1988). No such winter breaks were re-

TABLE 1.

Best fit von Bertalanffy growth curve parameter estimates and asymptotic standard errors (parentheses) for each sample location. Sample site numbers refer to Fig. 2. Ranked values of ω ($= SH_\infty \times k$, see Gallucci and Quinn, 1979) with 95% confidence intervals indicate spectrum of growth variation and possible statistical differences ($p \leq 0.05$) between sites.

Sample Site #	Sample Location	n	t_0	k	SH_∞	ω	Rank ω	95% CI
Mercenaria mercenaria								
1	Kings Bay (Southern Georgia)	50	− 0.45 (0.16)	0.38 (0.04)	72.38 (1.75)	27.50	7	26.85−28.15
2	Matanzas River (Crescent Beach)	50	0.07 (0.09)	0.43 (0.03)	71.83 (1.42)	30.89	4	30.21−31.57
3	Indian River (Body C)	50	0.15 (0.09)	0.38 (0.04)	80.51 (3.08)	30.59	5	29.99−31.19
4	Indian River (Body F)	50	0.28 (0.07)	0.35 (0.03)	85.86 (1.92)	30.05	6	29.48−30.62
Total/Mean		200	0.05	0.39	77.65	29.76		
Mercenaria campechiensis								
5	Bokeelia (Charlotte Harbor)	50	− 1.15 (0.21)	0.25 (0.02)	90.19 (1.96)	22.55	8	22.16−22.94
6	Catfish Creek (Charlotte Harbor)	50	− 0.13 (0.11)	0.49 (0.05)	89.77 (1.74)	43.99	2	42.93−45.05
7*	Boca Ciega Bay (near Tampa Bay)	93	0.09 (0.08)	0.25 (0.01)	177.80 (1.03)	44.45	1	—
8	Tampa Bay (Skyway Sand Flat)	50	− 0.23 (0.07)	0.39 (0.02)	105.19 (0.69)	41.02	3	40.49−41.55
9	Cedar Key (Suwannee Reef)	50	− 1.05 (0.13)	0.11 (0.01)	134.98 (2.44)	14.85	10	14.55−15.15
10	St. Joseph Bay (Panhandle)	50	− 1.04 (0.14)	0.28 (0.02)	77.36 (0.70)	21.66	9	21.27−22.05
Total/Mean		343	− 0.59	0.30	112.55	31.42		

* Curve fit to mean size-age data from Saloman and Taylor (1969), confidence intervals not calculable.

ported for North Carolina clams by Peterson et al. (1983), nor were they encountered in the Florida samples.

The seasonality of shell growth observed in this study matches that determined by R. W. Menzel (1963, 1964;

Figure 5. Plot of ω values and 95% confidence intervals (vertical bars) for *M. mercenaria* (M) and *M. campechiensis* (C) from each collection site in this study, contrasting intermediate and tightly-clustered values for Atlantic Coast *M. mercenaria* with highly variable ω values for *M. campechiensis* from the Gulf Coast. Site numbers are identified in Table 1 and Fig. 2.

Menzel and Sims 1964) nearly 25 years ago for hard clams from Alligator Harbor, Florida (Fig. 2). In the late 1950s and early 1960s, growth of transplanted *Mercenaria mercenaria* and local *M. campechiensis*, as well as their hybrids, was investigated by experimental plantings and periodic measurement of clams at this Gulf Coast site. Apart from the growth curve presented by Saloman and Taylor (1969) for the unusually large clams from Boca Ciega Bay, these early studies represent the only previously published data on hard clam growth in Florida. The results suggest that *M. mercenaria* grew fastest in spring and late fall, less in winter, and slowest in summer. *M. campechiensis* exhibited a similar pattern but apparently grew slowest in winter. Menzel (1963) felt that *Mercenaria* spp. from Florida exhibited greater annual growth than at other sites from Maine to the southeastern U.S. because of continued growth throughout winter. He also speculated that *M. campechiensis* might be more vigorous with a faster innate growth rate.

The data of Ansell (1968) and others (e.g., Loosanoff 1939; Pratt and Campbell 1956; Hamwi 1969; Walne 1972) argue forcibly for the role of temperature as a major influence on growth and physiological activity of *Mercenaria*. This idea has found recent support in an investigation of long-term hard clam growth in Narragansett Bay (Jones et al. 1989). Ansell (1968) reported an optimum growth temperature for *M. mercenaria* of 20°C. Growth declined symmetrically above and below this value and ceased below 9°C and above 31°C. No evidence of a geographical trend was reported.

Within temperature limits, other factors such as food availability and substrate character may often determine the actual rate of growth of hard clams (Ansell 1968; Pratt
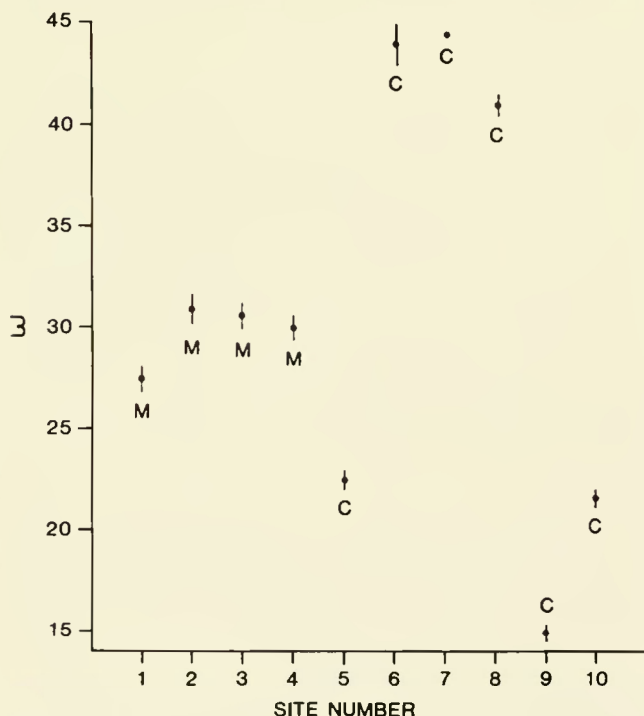
1953; Pratt and Campbell 1956; Eversole 1987). Recent data by Peterson and Fegley (1986) suggest that juvenile and adult hard clams may grow at different size-adjusted rates throughout portions of the year. Anomalously low adult relative to juvenile growth rates during the winter may not result solely from cold temperatures, but from differences in resource partitioning related to adult gametogenic activity in spring. Clearly, temperature is not the only factor involved. Nevertheless, given these caveats, it is interesting to note (Fig. 3) that the lowest temperature measured during our year-round monitoring study was 10°C (January, Kings Bay and Cedar Key), whereas the highest was 32°C (September, Cedar Key). The bulk of our temperature data and a perusal of unpublished, longer-term water temperature variations for Florida indicate that the temperature limits for growth in *Mercenaria mercenaria* cited by Ansell (1968) are seldom and only briefly exceeded. Thus, the generally high growth potential for these populations at the southern extreme of their range is not totally unexpected.

Ansell (1968) used Menzel's Florida data in his geographic survey of hard clam growth. Ansell concluded, however, that there were no regional trends in the values of shell growth parameters and that the growth/age curves for sites within the continuous range from the Gulf Coast of Florida to Massachusetts were similar. A standardized, four centimeter clam, whether from Florida or New England, had approximately the same maximum annual growth increment. In Figure 5 of Ansell (1968), length versus age relationships are plotted for *Mercenaria mercenaria* from many localities. The curve for Florida indicates that most rapid size increase with age although it is not appreciably higher than the curves for other sites. To better compare this growth relationship of Ansell (1968) with the ones determined here for the ten Florida sites, we converted the shell length data from Ansell's Figure 5 to shell height based upon the average height:length ratio (0.91) for our samples and then fit a von Bertalanffy curve to the data. The resulting parameters, $k = 0.34$ and $SH_\infty = 82.94$, yielded a $\omega = 28.41$. This value is almost identical to the ω values reported for the Atlantic Coast *Mercenaria mercenaria* populations from Kings Bay, Matanzas River, and *Mercenaria* spp. from the Indian River (Body C and Body F) and is intermediate with respect to the ω values for the *M. campechiensis* stations (Table 1; Fig. 5).

Despite living for two or three decades, most of the significant size increase in the Florida hard clams occurs during the initial several years of life (Fig. 4). Thereafter, the rate of increase declines progressively with age. This relationship, modeled here and in Rhode Island (Jones et al., in press) by the von Bertalanffy growth function and elsewhere by the Gompertz equation (Kennish and Loveland 1980) or a power function (e.g., Walker 1984), has been observed in hard clams throughout their distribution. When the growth curves for *Mercenaria mercenaria* shown in Figure 4 are compared to those assembled by Ansell

(1968, Fig. 5) for his "best growth" North American sites (and shell lengths are converted to heights), the Florida sites all plot above the others. This suggests that growth of Florida hard clams is indeed more rapid, as Menzel (1963) hypothesized.

It would facilitate inter-regional comparison of growth curves if modeled growth parameters were available for each region. In a recent study of hard clam growth in Narragansett Bay, Rhode Island, the ω parameter of Gallucci and Quinn (1979) was used to expedite growth comparisons around the Bay (Jones et al. 1989). The ω values determined for Narragansett Bay ranged between 11.33 and 21.87, with a mean of 15.40. The hard clam growth in Narragansett Bay was judged comparable to that recently reported by Ropes (1987) for northern New Jersey. Both of these sites, as the ω values indicate, fall near the bottom of the spectrum of growth determined for the Florida clams (Table 1; Fig. 5). A great deal of variability surrounds growth estimates in Florida as well as in Rhode Island, but the idea that real geographic differences in growth of *Mercenaria mercenaria* exist and that growth in Florida is among the highest appears well supported. The growth of *M. campechiensis* can exceed that of *M. mercenaria* but it apparently does not in all cases (Fig. 5).

The maximum age encountered in the Florida hard clam samples is significantly less than that reported elsewhere. For example, Jones et al. (1989) reported two specimens from Narragansett Bay that were 40 years old at the time of capture. Lutz and Haskin (1985) described two marked-and-recaptured specimens from New Jersey that were 36 and 33 years old. Peterson (1983, 1986) reported old individuals, living up to 46 years, from North Carolina and Hopkins (1941) as well as Ropes (personal communication) felt that a 75-year longevity may be attained in hard clams. In contrast, the oldest specimen measured in this study came from Cedar Key and was 28 years old when captured. The next oldest specimen also came from Cedar Key and was 25 years old. Overall, less than 1% of all clams in this study attained an age of 25, only 4% lived to age 20, and 12% had survived to age 15 when captured. Longevity determinations for the Florida clams should be considered minimum estimates for two reasons: 1) the animals were still alive at the time of capture; and 2) the ±5% of the clams that were discarded from analysis because of difficulty uniquely interpreting their shell records were invariably old individuals with growth increments crowded at their margins and were potentially the oldest specimens. Nevertheless, none appeared to approach the ages of the oldest specimens reported from northern poopulations.

CONCLUSIONS

Both *Mercenaria mercenaria* and *M. campechiensis* from coastal Florida form annual shell increments which can be utilized in age and growth rate determinations. The yearly incremental growth pattern consists of macroscopic, alternating dark (translucent) and light (opaque) increments

best viewed in radial shell cross-sections. In *M. mercenaria* from Florida's Atlantic coast, the light increment, representing episodes of rapid shell growth, forms primarily during the winter. In *M. campechiensis* from the Florida Gulf Coast, the light increment is added principally during the spring. The translucent or dark, slow-growth increment forms over the remainder of the year, especially the late summer and fall. No winter dark increments were observed in the Florida specimens and the annual shell cycle is similar to that described for hard clams from North Carolina and Georgia.

Using annual shell increments as age markers, shell height versus age relationships were investigated for ten sites around Florida, including both coasts. Measured shell growth was modeled with the von Bertalanffy equation and the ω parameter of Gallucci and Quinn (1979). Growth was found to be highly variable both within and between localities. The greatest growth was observed in populations of *Mercenaria campechiensis* from Boca Ciega Bay where the largest known living specimens of hard clams occur. Enhanced growth also was encountered at Catfish Creek in Charlotte Harbor on the Gulf Coast. Intermediate growth characterized populations of *M. mercenaria* from the Atlantic Coast whereas lower ω values were associated with *M. campechiensis* from Bokeelia (Charlotte Harbor), St. Joseph Bay, and Cedar Kay. While a wide spectrum of hard clam growth was observed, comparison with growth data for populations from New England and the Middle Atlantic Bight confirmed earlier suggestions of overall higher annual growth rates in Florida. This may be related to favorable temperature regimes which permit growth throughout the winter months.

The use of annual shell growth increment patterns in age determination has generally had the effect of increasing estimates of hard clam longevity. The oldest specimen encountered in this investigation was 28 years old at the time of capture, far younger than the oldest reported elsewhere. Only 4% of the Florida specimens had attained the age of 20, even though they were often of considerable size. It appears that both species of *Mercenaria* from Florida grow faster than their counterparts to the north but do not seem to live as long.

ACKNOWLEDGMENTS

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