

Sclerochronology and Growth of the Bivalve Mollusks *Chione (Chionista) fluctifraga* and *C. (Chionista) cortezi* in the Northern Gulf of California, Mexico

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Abstract. Sclerochronology and analysis of oxygen isotopes reveal the age, growth rate, and growth patterns of *Chione (Chionista) cortezi* and *Chione (Chionista) fluctifraga*. *Chione (C.) cortezi* grows more quickly than *Chione (C.) fluctifraga*, but has a shorter life span (8 years versus 16 years). Microgrowth increments form with tidal periodicity, and their width is mostly influenced by temperature. Microincrement patterns reveal that maximum growth occurs from April to June and again in October. Growth is reduced during the hottest part of the summer and the coldest part of the winter. Growth breaks often occur in December/January and August. Timing of shell growth and environmental conditions were verified by high-resolution oxygen isotope measurements.

INTRODUCTION

Bivalve mollusks of the genus *Chione* Megerle von Mühlfeld, 1811, inhabit many coastal areas around the world (Moore 1969:N686). Although they are often commercially exploited, little is known about their life span, overall growth patterns, and growth rates. The effect of temperature on the growth rate of *Chione* species is not well understood. Such information is important for the management of shellfish resources and mariculture.

Early attempts to determine the age and growth rate of mollusks used shell-weight or size-frequency analysis. The disadvantages of these methods have been reviewed by Berta (1976) namely: (1) the exact age of the youngest year class remains unknown; (2) year classes can be absent; and (3) size or weight ranges of specimens of different year classes can overlap due to differences in environmental conditions during their life. The major concentric rings on the external shell surfaces of mollusks have often been interpreted as annual growth patterns. However, they cannot always be distinguished unequivocally because rings may also be caused by non-seasonal disturbances. In addition, annual growth rings are crowded at the ventral margin in older specimens and make counting and interpretation difficult (see Zolotarev, 1980). Other researchers (e.g., Jones et al., 1978; MacDonald & Thomas, 1980) suggested that the most reliable method is to count the annual growth increments (first order increments or "1st-order layer" sensu Barker, 1964) preserved in radial cross-sections of the shells.

Since Wells's (1963) pioneering study, in which the microgrowth increments (higher order increments) of corals were used to infer the number of days in a Devonian year, many articles have dealt with the microgrowth increments of bivalve mollusks and other animals (for a review see Rhoads & Lutz, 1980 and references therein). This type of study has been termed "sclerochronology" (Buddemeier, 1975; Hudson et al., 1976).

Sclerochronology can be used to elucidate differences in growth rates and life histories of morphologically similar species. Sclerochronological methods can be applied to shells of fossil (Pannella 1976; Schöne, 1999) as well as living specimens. Organisms that produce accretionary hardparts serve as environmental recorders during their lives. Variation in growth rates and repeating growth structures have been interpreted to reflect endogenous rhythms, physiological periodicity, or environmental cycles. Varying widths of growth increments have also been attributed to random ecological fluctuations (e.g., Kennish & Olsson, 1975; Peterson, 1983). The stable isotope composition of growth layers is now being used in many paleobiological and paleoenvironmental studies (e.g., Turkian et al., 1982; Williams et al., 1982; Roux et al., 1990; Kirby et al., 1998; Jones & Gould, 1999); and a few studies address the chemical content of the growth increments (e.g., Mutvei et al., 1994).

Here we present the results of stable isotope and sclerochronological investigations on the bivalve mollusks *Chione (Chionista) fluctifraga* (Sowerby, 1853) and *Chione (Chionista) cortezi* (Carpenter, 1864, ex Sloat MS) from the intertidal zone of the northern Gulf of California, Mexico. We describe inter- and intra-annual growth patterns and growth rates and interpret them in order to

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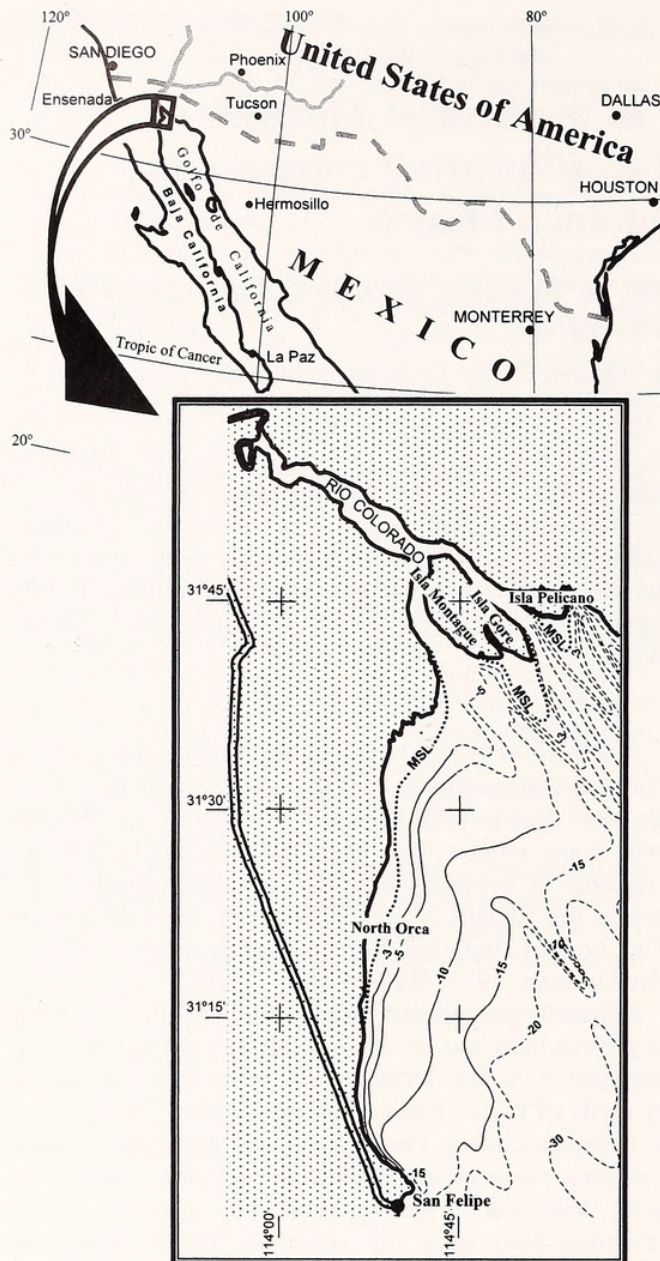


Figure 1. Sample localities in the Northern Gulf of California region. Samples were taken in mid-intertidal at low tide from North Orca (31°20.087'N, 114°52.957'W) Isla Montague (31°40.3'N, 114°41.4'W) and Isla Pelicano (31°45.7'N, 114°38.9'W).

elucidate the life cycles and ages of the species. Intra-annual oxygen-isotope profiles provide further insight into temperature conditions during growth.

MATERIALS AND METHODS

More than 300 specimens of *C. (C.) cortezi* and *C. (C.) fluctifraga* were collected alive at low tide from the mid intertidal zone at three different localities in the northern Gulf of California, Mexico: North Orca, Isla Montague, and Isla Pelicano (Figure 1). Collecting was done in late

February 1997 and 1998, late May, early August, early November and early December of 1999. The tidal regime of the northern Gulf of California is semidiurnal with a mean tidal range of about 5 m. Average salinity of open Gulf water is $38\text{‰} \pm 2\text{‰}$ in this area. Monthly average sea surface temperatures (SST) provided by satellite measurements (NOAA; <http://www.cdc.noaa.gov/>; WebWinds Java application, a software package to read the *.netcdf files, was obtained from <http://webwinds.jpl.nasa.gov>) vary between 15 and 30°C. Local temperatures may be 10 to 15°C higher or lower than those indicated by satellite measurements (personal observation).

Discrimination of the two species is often difficult. According to Villearreal-Chávez et al. (1999), *C. (C.) cortezi* is geographically restricted to the uppermost part of the Gulf of California, i.e., 31°30'N, whereas *C. (C.) fluctifraga* is more widely distributed. Both species are recorded as present in the study area. According to Keen (1971), *C. (C.) cortezi* is larger and has a more trigonal form than *C. (C.) fluctifraga*. Smooth and polished concentric ribs characterize *C. (C.) fluctifraga*.

Fifty live specimens of *C. (C.) cortezi* were collected at North Orca (Figure 1) in early December 1999. Specimens were collected during four successive low tides in order to determine the time needed to produce the smallest shell growth increments. In addition, notching and staining experiments were conducted at the same location. Two-hundred specimens (120 *C. (C.) cortezi* and 80 *C. (C.) fluctifraga*) were held in buckets (also containing sediment from the collection site) in a tetracycline (1000 mg/L) or Alizarine Red solution (ambient seawater) in order to stain newly formed growth increments of the shells. Salinity ranged from 39 to 43‰ during the experiment. Forty specimens were sacrificed every 6 hours.

The flesh was removed from all shells immediately after collection to prevent further shell deposition. After coating with epoxy resin, valves were cut along the axis of maximum growth using a low speed (Buehler Isomet) saw, ground on glass plates (600, 800, and 1000 grit powder) and polished on laps (9, 6 and 0.3 microns) in order to enhance the contrast of the microstructures. Valves were ultrasonically rinsed in deionized water after each polishing step to remove grinding powder.

A caliper was used to measure the distances between major growth lines (i.e., annual increments) in radial cross-sections of 16 *Chione (C.) cortezi* and 18 *Chione (C.) fluctifraga* specimens (North Orca and Isla Montague material) to the nearest 10 µm using a reflected light binocular microscope. Cumulative growth curves were calculated from the annual increment data, and each curve was fitted with a sigmoidal non-linear regression model referred to as "MMF model" in the software package CurveExpert Vs. 1.34 (available as shareware at <http://www.ebicom.net/~dhyams/cvxpt.htm>):

$$P(t) = (ab + ct^d)/(b + t^d),$$

where $P(t)$ is the predicted increment width at time t and a , b , c , and d are fitted constants.

Thirty *Chione* (*C.*) *cortezii* specimens from North Orca and one *Chione* (*C.*) *cortezii* specimen from Isla Pelicano were etched in a NaOH-buffered EDTA solution (0.25 M, pH 7.9) for 1 to 2 hours, carefully rinsed in water and acetone, and allowed to air dry. Etching increased the contrast of the growth increments.

In addition, we prepared polished thin sections (thickness 30–50 μm) of five *Chione* (*C.*) *cortezii* specimens from North Orca and stained them with a 0.5% Rhodamine B solution for 3 minutes in the microwave at 50°C. This method stained the organic-rich microgrowth increments and made their recognition easier.

Microgrowth increment widths (i.e., higher order increments, from a few μm to 300 μm thickness) of one *Chione* (*C.*) *cortezii* specimen (IP1-A1R) from Isla Pelicano were measured to the nearest 5 μm in radial cross sections under a reflective light microscope using an eyepiece scale. We used linear regression (growth increment width versus growth increment number) to estimate how increment width changed through 1 year. The purpose of linear regression is to remove the age trend (Cook & Kairiukstis, 1990). The growth index was calculated by dividing the observed increment width by the predicted increment width. These procedures are known as detrending and indexing in dendrochronology (see Fritts, 1976; Cook & Kairiukstis, 1990). The growth index is a dimensionless measure of how growth deviates from the average trend. A value of 1 indicates no deviation; values greater than 1 indicate more rapid growth than expected; values less than 1 indicate slower growth than expected. Jones et al. (1989) have applied this technique to inter-annual growth variation of bivalve mollusks. Here, we apply the technique to intra-annual growth variation.

Specimen IP1-A1R was rinsed several times ultrasonically with deionized water prior to sampling for isotopic composition. The outer shell layer was sampled using a 300 μm drill under a binocular microscope. The number of increments sampled varied from three to 40. Each of the 22 drill holes yielded 50 to 200 μg of carbonate for isotopic analysis. A micromass automated carbonate extraction system was used to process the samples. $\delta^{18}\text{O}$ is reproduced relative to PDB on a NBS-19 value of -1.92‰ . Precision is better than 0.1 ‰ .

RESULTS

Annual Growth Patterns and Growth Breaks

We observed two seasonally distinct interruptions in growth in both species. Samples collected in late February show a growth break (GB1, dark line, Figure 2d) near the ventral margin on the exterior shell surface as well as in radial cross sections. This pattern is more clearly developed in *C. (C.) cortezii* than in *C. (C.) fluctifraga*. No growth break occurs near the margin on specimens

collected in November or December. At greater magnification ($\times 100$), the higher order increments preceding GB1 continuously decrease in width (Figure 2d). The nature of these higher order increments is described below in further detail.

A striking feature in both *Chione* species is a several millimeter-thick purple zone consisting of numerous, very narrow (approx. 1–5 μm) higher order increments (Figure 2c, e). In older specimens, there is a growth break (GB2, Figure 2b) visible within this purple zone that is expressed as a dark line on the outer shell surface. The thickness of this purple band varies with age and species. It is broader and less distinct in young specimens and it is more obvious in *C. (C.) fluctifraga* than in *C. (C.) cortezii*. The purple band is not seen after the last GB1 in May samples, but can be identified unequivocally at the ventral margin in specimens that were collected in early August. In these specimens, the purple band is thinner than in previous years recorded in the shell, suggesting that the GB2 was being deposited in early August.

The width of higher order increments increases continuously after GB1, reaches a maximum of 230 μm about midway between GB1 and GB2, and then decreases slightly before the purple zone. This pattern is characteristic for specimens smaller than 3 cm. There is an additional small growth break in some larger specimens (> 4 cm) usually somewhere between GB1 and the purple band. Growth rate decreases suddenly before this break and increases soon after.

The interval between the end of the purple band and GB1 is characterized by wider (up to 120 μm) microgrowth increments. Microgrowth increment width increases rapidly at the end of the purple zone. In specimens collected in early December, the higher order increments near the ventral margin are considerably smaller than those in specimens collected in November.

Growth Rate

Increment widths between GB1's of both *Chione* species decrease from the umbo to the ventral margin, indicating that growth rate decreases with age. However, the growth curves are distinct for each species (Figure 3). Note that growth data from different localities from specimens living at different times are included in this diagram. Therefore, despite varying environmental influences, the overall growth patterns for each species remain essentially the same. Fitting the data with a sigmoidal growth function (MMF-model) returns very high correlation coefficients ($r = 0.997$, $P < 0.05$). Similar correlation coefficients have been reported from investigations of other species (Jones et al., 1989).

The two species differ in their maximum ages. Whereas the maximum observed age of *C. (C.) cortezii* specimens is 8 years, the oldest *C. (C.) fluctifraga* specimens are almost 16 years old. The oldest *C. (C.) cortezii* spec-

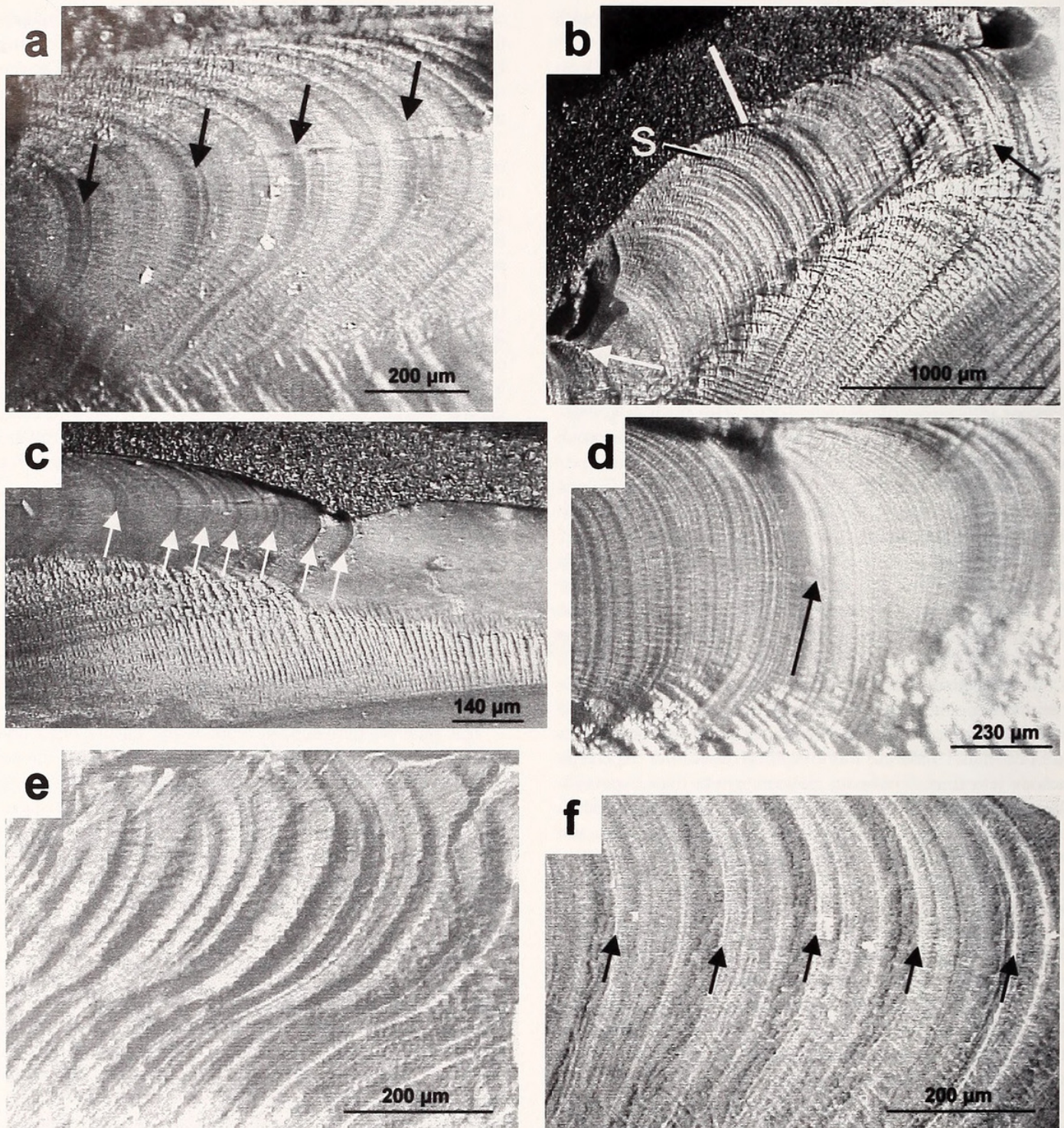


Figure 2. Microgrowth patterns of *Chione (Chionista) cortezi* (Figures 2a–d; sample no. IP1-A1R, Isla Pelicano) and *Chione (Chionista) fluctifraga* (Figures 2e, f; sample no. NO3-A6L, North Orca) as seen on etched surfaces under reflected light microscope (a–d) and SEM (e, f). Growth direction is always to the right. a. Lunar day increments produced during spring of the 3rd year. Each lunar day increment is bordered by thick ridges (arrows). Faint ridges are sometimes visible between two thicker ridges. b. Arrows mark an annual increment in a later ontogenetic stage (6th year). The white line indicates the summer break (GB2). The spawning break is indicated by “s.” c. Slowdown of growth in the summer in an early ontogenetic stage (3rd year). Fortnightly cycles are indicated by arrows. d. Winterbreak (GB1, arrow) in the 3rd year. Note the narrow increments preceding the break and their increasing width after the break to the right. e. Growth slowdown during hot summer. Lunar day increments are about $\frac{1}{4}$ the width of those earlier in the spring of the same year. (shown in Figure 2f). The etch-resistant increments are broader than during the spring and fall. f. Lunar day increments (see Figure 2a for description).

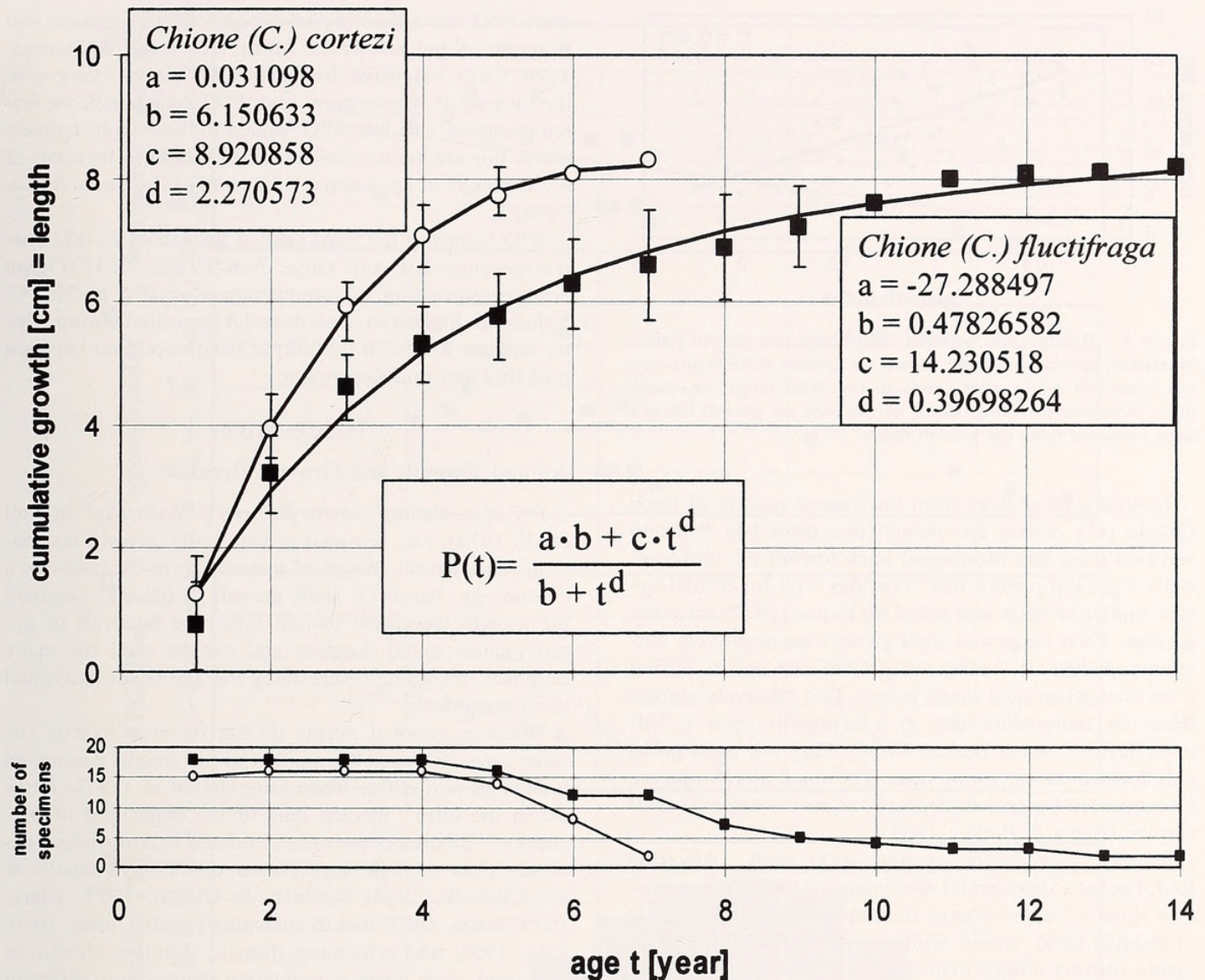


Figure 3. Growth curves of *Chione (Chionista) cortezi* and *Chione (Chionista) fluctifraga*. Maximum observed ages in *Chione (Chionista) fluctifraga* are lower than in *Chione (Chionista) cortezi*. *Chione (Chionista) cortezi* grows faster than *Chione (Chionista) fluctifraga*.

imens, however, are generally $\frac{1}{3}$ larger than the oldest *C. (C.) fluctifraga* specimens. The ventral margins of the oldest *C. (C.) fluctifraga* specimens are bent to the inside: the growth direction in this species changes from an anterior-posterior direction to growth directed toward the opposite margin along the commissure. With increasing age, the shell margin of *C. (C.) fluctifraga* becomes obtuse, and the convexity of its shell increases sharply as has been demonstrated by Zolotarev (1980) for other species. As a result, the length/height relationship of old specimens is higher than that of young specimens.

Higher Order Growth Increments

Cross-dating (matching increments in different specimens, see Fritts, 1976) of the most recently produced increments on the ventral margin of 14 *Chione (C.) cortezi*

and eight *Chione (C.) fluctifraga* specimens collected at North Orca in early December 1999 indicates that every high-low tidal cycle results in a couplet of one narrow etch-resistant and one broader, deeply etched increment. A high-low tidal cycle comprises approximately 12.4 hours. In specimens collected during the morning low tide, the etch-resistant increment at the commissure is considerably less distinct than in specimens collected during afternoon low tide. The time interval between two thick etch-resistant growth increments is approximately 24.8 hours. In the paleontological and biological literature, the term lunar day is often used to describe the time interval between these microgrowth increments (e.g., Evans, 1972; Pannella, 1976). A lunar day is the amount of time required for one rotation of the Earth on its axis, with respect to the Moon.

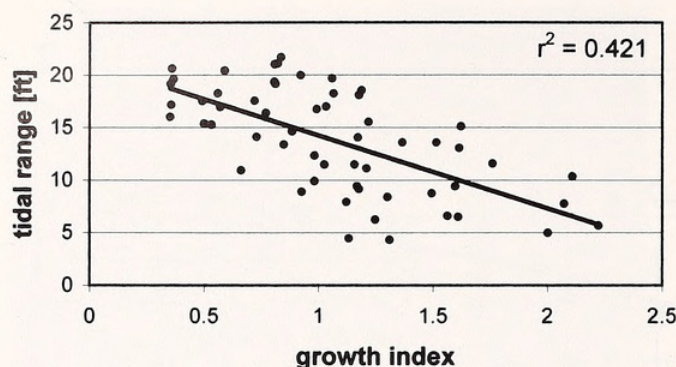


Figure 4. Relationship between tidal range and growth index. Maximum growth rate (here shown for *Chione (Chionista) cortezi*, shell IP1-A1R) corresponds to low tidal range, i.e., neap tides. Note that the influence of temperature on growth has not been extracted from the growth index.

Counting lunar days from the ventral margin of three *Chione (C.) cortezi* specimens (one from Isla Pelicano and two from Isla Montague) back toward the umbo reveals a growth pattern that coincides with lunar tidal cycles similar to what was noted by Evans (1972) for other species. Tidal range and shell growth are negatively correlated (Figure 4). Maximum growth rate occurs during neap tides when tidal range is low. Two relatively narrow lunar day increments form in a fortnightly cycle ("3rd-order layers" *sensu* Barker, 1964). They are most probably formed during spring tides. The small increments are accompanied by growth depressions on the external shell surface (Berry & Barker, 1968).

Twenty stained (tetracycline 1000 mg/L, Alizarine Red; bucket experiments) specimens of both *Chione* species show a yellow-orange (tetracycline under UV-light) or reddish band, whose widths correspond to the increments formed during exposure to the stains. These experiments confirm the results found by field sampling on consecutive tides (described above). Only specimens of age-class one and two, however, showed noticeable shell growth in December 1999 when these experiments were conducted.

All these findings enabled us to date the major events in the shell with precision to the nearest fortnightly cycle. However, the total number of lunar days within an annual increment was always less than the expected number (353.25) of lunar day increments in a solar year. The total number of lunar day increments in three specimens of *C. (C.) cortezi* was 253, 291, and 307.

Stable Isotope Variation

The oxygen isotope composition of a shell is a function of the ambient temperature and $\delta^{18}\text{O}$ of the water (which in turn is determined by evaporation rate and the amount of freshwater input) in which the individual is living. Shells were collected at times when the Colorado River did not flow into the Gulf of California. Thus changes in

shell $\delta^{18}\text{O}$ are a function of changes in temperature and evaporation but not fluvial influx (see Dodd & Stanton, 1990, for an extensive discussion). $\delta^{18}\text{O}$ values vary with the inverse of temperature: high $\delta^{18}\text{O}$ values indicate low temperatures and low $\delta^{18}\text{O}$ values indicate high temperature. For aragonitic mollusks a temperature increase of 4.7°C results in an isotopic shift of 1‰ (Grossman & Ku, 1986).

$\delta^{18}\text{O}$ values in the third year of growth of *C. (C.) cortezi* specimen IP1-A1R range from 0.91 to -2.47 (Figure 5c), corresponding to a temperature of 15.5 to 30.5°C. Values are highest in shell material deposited during winter and are lowest in the purple band deposited between mid July and mid September.

DISCUSSION

Annual Growth and Growth Breaks

Periodic, distinct growth patterns ("biochecks" of Hall et al., 1974), i.e., seasonal growth halts, growth retardation, or structural change of material form the basis for a chronology, based on shell growth. Biochecks segment the growth increment pattern into time intervals of approximately equal duration and can be used for many purposes, including determining the age of an individual bivalve mollusk.

Because seasonal events do not recur at exactly the same time each year, the number of increments per annual increment may differ. Therefore, Hall et al. (1974) introduced the term "median date of the deposition of biochecks." Biochecks are usually related to temperature extremes (low or high; e.g., Davenport, 1938; Pannella & MacClintock, 1968; Kennish & Olsson, 1975; Clark, 1975; Jones, 1983) and to spawning events (Jones, 1980; Sato, 1995; and references therein). Caution should be exercised when using reproduction biochecks in different specimens for dating. The dates of reproduction breaks in *Chione (C.) fluctifraga* vary considerably between individuals (Martínez-Córdova, 1988). This has also been shown for other bivalve mollusks (e.g., Coe, 1948; Coe & Fitch, 1950; Sato, 1995).

Depending on the seasonal temperature cycles, one or two temperature-mediated biochecks can be present: a summer break and/or a winter break (e.g., Koike, 1980; Clark, 1979; Sato, 1995; Jones & Quitmyer, 1996). The specimens studied here show both a winter and a summer biocheck (compare Koike, 1980 and references therein). The winter break represents a cessation of growth. The summer break represents a slowdown and/or a cessation.

The growth slowdown in summer is macroscopically expressed as a purple band (summer band). In some shells a growth halt is present within the purple band (summer break, GB2). The shutdown of growth in the cold season is called a winter break (GB1). Additional support for this interpretation comes from counting the lunar day increments in specimens collected during different seasons to

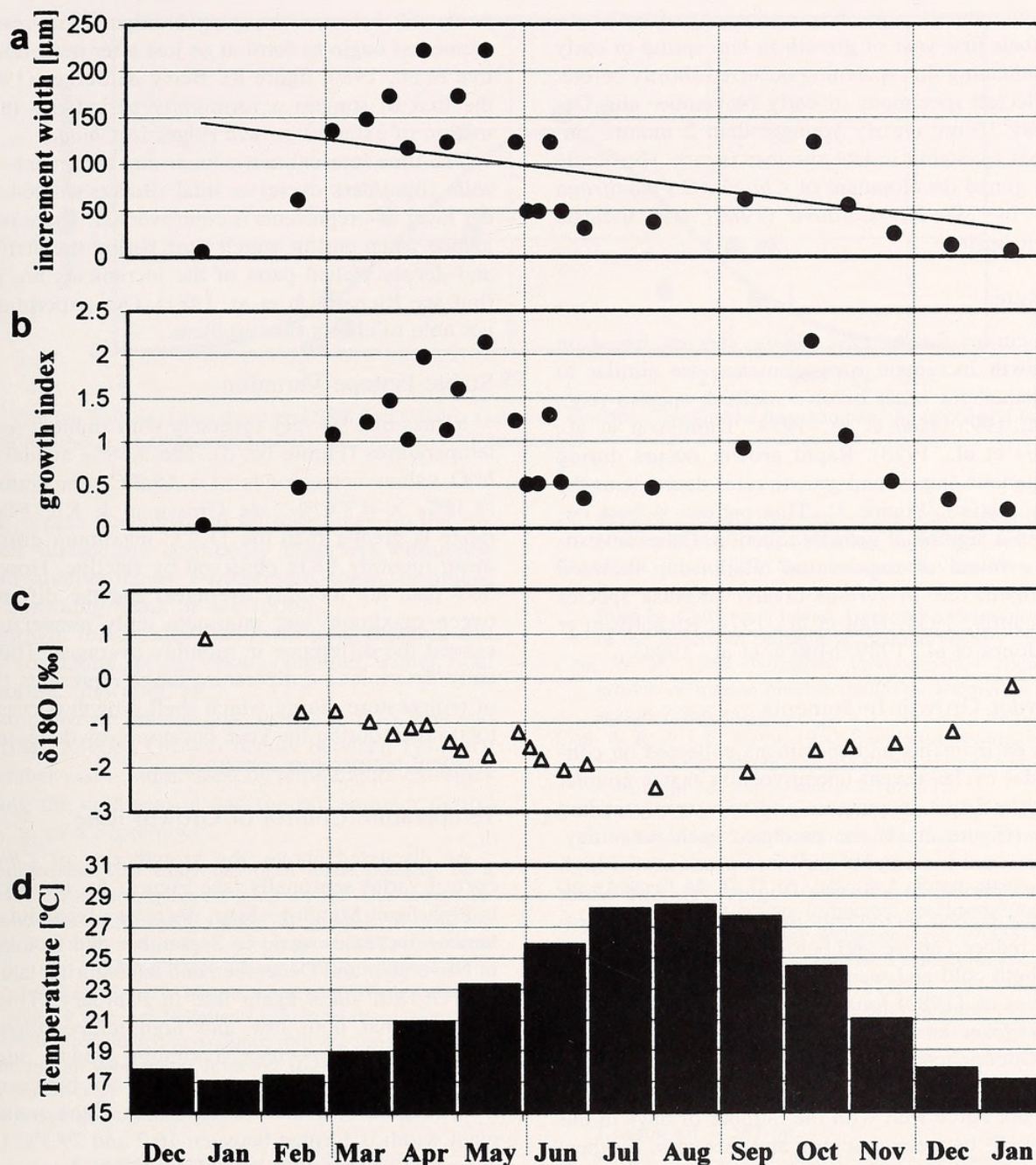


Figure 5. Comparison of growth rate and oxygen isotope composition of *Chione* (*Chionista*) *cortezi* (IP1-A1R) and sea surface temperatures. a. Microgrowth increment width (lunar day increment width). Only those data are depicted for which oxygen isotope composition has been determined. A linear fit has been applied to the raw data in order to extract the inherent age trend. b. Age-detrended growth data. The residuals were calculated from the data in Figure 5a by dividing the measured by the predicted (linear fit) data. c. Oxygen isotope data of selected increments. d. Monthly sea surface temperatures (SST) based on satellite observations of the sampled region during growth of *Chione* (*Chionista*) *cortezi*.

date the biochecks. In the Gulf of California, unfavorable temperature extremes for *Chione*'s growth are reached during both summer and winter. Because these temperatures can be reached more than once during each season, there may sometimes be several growth halts within a winter or summer band.

Annual reproduction breaks occur in specimens 3 years

old or older. These show the characteristic microgrowth pattern described by Kennish & Olsson (1975) and Sato (1995) for reproduction breaks, namely abruptly smaller increment widths that preceded the break followed by broad increments afterward (Figure 2b). The interpretation of these late spring or early summer growth biochecks as reproduction events is reinforced by counting

lunar day increments, e.g., most specimens of both species start their first year of growth in late spring or early summer, indicating that spawning occurred shortly before. Of all collected specimens in early November and December only 10 are clearly younger than 2 months, indicating that spawning in late summer is rare. Histologic studies on gonad development of *Chione* (*C.*) *fluctifraga* specimens by Martínez-Córdova (1988) also indicate spawning in spring.

Growth Rate

Growth curves for the two *Chione* species, based on annual growth increment measurements, are similar to those published for other bivalve mollusk species (e.g., Sato, 1994, 1995; Hall et al., 1974; Thompson et al., 1980; Jones et al., 1978). Rapid growth occurs during early ontogenetic stages, and growth rates decrease as the individuals mature (Figure 3). This pattern is best described with a sigmoidal growth equation. Other investigators have found an exponential relationship between age and growth rate in various bivalve mollusk species (von Bertalanffy, 1934; Hall et al., 1974; Richardson et al., 1980; Jones et al., 1989; Mutvei et al., 1994).

Higher Order Growth Increments

Staining experiments and specimens collected on consecutive tidal cycles reveal unequivocally that a couplet of two etch-resistant increments and two deeply etched increments (Figure 2a, f) are produced each lunar day. The etch-resistant increments are more prominent if high temperatures prevail at low tide (Figure 2e). The width of the deeply etched increments increases with temperature, but is reduced above and below specific temperature extremes, both cold and warm (see below).

Crabtree et al. (1980) found that growth increments in *C. (C.) fluctifraga* are a poor indicator of time. Crabtree et al. (1980) conducted notching experiments on *C. (C.) fluctifraga* specimens. They concluded that "the line counts did not agree well with the number of days in the growth period" between notching and recovery. Furthermore, they found that there was no "consistency in growth line counts" both between different counters and between specimens of different age classes. However, a careful re-examination of the young specimen depicted in figure 8 of their paper shows 45 to 47 couplets consisting of two dark and two light increments. This should correspond to 45 to 47 lunar days consisting of 90 to 94 dark growth lines, although the six persons in their experiment counted only 56 to 74 lines (i.e., 23 to 37 lunar days). Our recounts match the expected number of increments (~48 lunar days) very well.

Furthermore, recalculation of the tidal increment cycles (with wxtide25, Windows program available at http://www.geocities.com/Silicon_Valley/Horizon/1195/wxtide32.html) indicates that the slight depressions (= deeply etched in-

crements) between the growth ridges (etch-resistant increments) begin to form at or just after neap tides (Crabtree et al., 1980: figure 8). Berry & Barker (1968) were the first to suggest a fortnightly periodicity in the formation of external growth ridges in *Chione*.

The time interval that a lunar day increment—whether solar (light/dark cycle) or tidal (Barker's, 1964, "4th-order layer")—represents is controversial. There is little evidence when and in which time period the etch-resistant and deeply etched parts of the increments are produced (but see Richardson et al. 1981). Our experiments were not able to clarify this problem.

Stable Isotope Variation

Values of $\delta^{18}\text{O}$ vary inversely with ambient sea surface temperatures (Figure 6c, d). The 3.38‰ annual range in $\delta^{18}\text{O}$ values corresponds to a 15.9°C temperature range ($3.38\text{‰} \times 4.7\text{°C/‰}$, see Grossman & Ku, 1986). This range is greater than the 11.4°C maximum difference in mean monthly SSTs observed by satellite. However, the SST data are monthly averages, and the difference between maximum and minimum daily temperatures will exceed the difference in monthly averages. The isotopically determined temperature range represents the range of temperature during which shell growth occurs, not the total range during the year, because growth ceases during seasonal temperature extremes.

Temperature Control of Growth Rate

As discussed above, the growth rate of *Chione* (*C.*) *cortezi* varies seasonally (see Figures 5a, b). Growth rate is high from March to June, decreases from July to September, increases again in September and October, slows in November and December, and halts during late December. Growth starts again late in February. This pattern suggests that both low and high temperatures inhibit growth in this species. Maximum growth rates occur when monthly average temperatures are between 21 and 24°C (Figure 6). Ninety-five percent of the annual increment width is formed between 16.7 and 29.3°C (monthly average SST, satellite data, Figure 5d). Isotopically derived estimates of temperature confirm this range. Winter growth breaks (GB1) occur when temperatures drop below this range and summer breaks (GB2) occur when temperatures exceed this range.

SUMMARY AND CONCLUSIONS

Specimens of *Chione* (*C.*) *fluctifraga* and *Chione* (*C.*) *cortezi* show both a winter and summer biocheck. Both biochecks are useful for ontogenetic age determination. The maximum observed age for *Chione* (*C.*) *fluctifraga* is higher (15 years) than that of *Chione* (*C.*) *cortezi* (8 years) even though *Chione* (*C.*) *cortezi* grows to a larger size. *Chione* (*C.*) *fluctifraga* grows much more slowly than *Chione* (*C.*) *cortezi*.

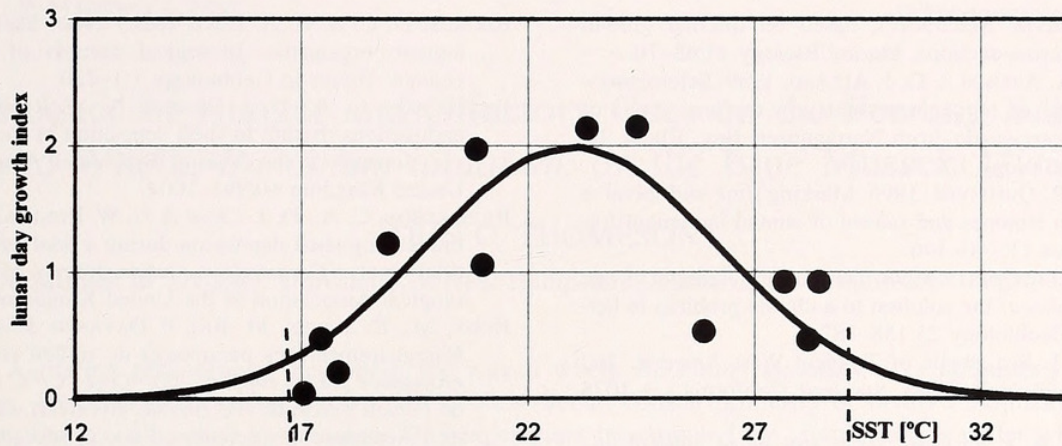


Figure 6. Growth indices (lunar days) and SST fitted with a Gaussian function. The dashed lines indicate the upper and lower growth temperature thresholds in *Chione (C.) cortezi* and *Chione (C.) fluctifraga*.

Growth breaks accompanied by dark lines on the exterior shell surface are commonly observed within the winter and summer bands. Furthermore, some specimens exhibit a spawning break in late spring.

Microgrowth increments form with tidal rhythms and are useful for dating special events (summer, winter, tidal cycles, storms, spawning, etc.).

Maximum growth rates occur during April to June and again during October. Growth occurs between February and December and is suppressed by temperature extremes both during the cold season and the hot summer period (mid July to mid September).

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