Thin sections of a compact, internal structure projecting from the hinge region of the bivalve *Mya arenaria* reveal the presence of tidal and seasonal patterns. This is the first demonstration that microgrowth increments are formed in a structure not associated with the growing edge of the shell. The clarity and simple orientation of these extensive patterns, combined with the resilience of the hinge region to disturbance and damage, suggests that detailed examinations of internal shell structures will prove valuable in ecological, archaeological, and paleoecological studies.

Ecologists, archaeologists, and paleoecologists share an interest in the calcined layers of animals, because such layers can be preserved and can record growth variations. The shells of bivalve mollusks consist of two or more calcified layers that can differ considerably in composition and structure. These layers are formed by the mantle tissue in different regions of the shell. The outer layer is deposited at the ventral or growing margin. The innermost layer forms in interior regions generally behind the pallial line (1), a region where the mantle tissue attaches to the shell. As one might expect, growth patterns within the shell are also preserved to a different degree in these layers. Several investigators have suggested that the finest, most detailed growth records are formed in the outer layer, while only major patterns in growth can be resolved in the innermost layer (2, 3). Experience to date has borne this out. Daily and tidally produced growth increments have been documented in the outer shell layer of a variety of species (2, 4–7). Only annual and seasonal patterns have been identified in the inner shell layer (3, 8–13).

Here we report, for the first time, the presence of tidally deposited growth increments within an inner shell layer and within a structure associated with the hinge region rather than the ventral margin of the shell. We also describe the occurrence of well-defined seasonal patterns in this species and suggest that, when present, detailed microgrowth records in the inner shell layer may more accurately reflect the physiological state of a bivalve than comparable patterns within the outer layer. The species studied is the soft-shell clam, *Mya arenaria*, which is widely distributed along the coastal areas of the North Atlantic and North Pacific Oceans.

Searching for growth patterns in the inner shell layer is not a common procedure, but tends to occur only after it has been determined that growth patterns are for some reason poorly preserved in the outer layer of the species being studied (13). This is the case for *Mya arenaria*. The shell of this species is thin and always shows signs of considerable damage, abrasion, and erosion. The ventral margin is usually chipped, irregular, and frequently repaired. Growth records are poorly preserved in cross-sections of the valve and are unreliable for estimating the age of individuals (8, 14). Instead, investigators have concentrated on examining the chondrophore, an internal, spoon-shaped shelf projecting from the hinge region of the left valve (Fig. 1a). Using thin sections or acetate peel replicas of the chondrophore, several prior studies established the presence of annual patterns (8, 14–16), and in one case (17), the presence of intra-annual features was noted.

Samples of *Mya arenaria* were collected bimonthly in 1986–87 and monthly during 1988–89 at an intertidal location in Stony Brook Harbor, Long Island, New York. Thin sections were produced according to the methods described in detail by Clark (18), and the shells were prepared as follows. First, the chondrophore, along with a portion of the left valve, was sectioned from the umbo to...
Figure 1. Microgrowth patterns in the chondrophore of Mya arenaria. (a) View of left valve with associated chondrophore. Line A–B shows orientation of thin sections. (b), (c), and (e) Optical micrographs of thin sections illustrating the detailed microgrowth increment patterns. Note the seasonal variations in increment thickness and morphology. All three micrographs to same scale. (d) Composite optical micrograph of a thin section of the chondrophore and hinge region of a 4+ year old individual. Distinct summer (S) and spawning features (R) are evident. Spring (Sp) and fall/winter (F/W) appear as dark (opaque) regions in thin sections. Specimen collected in March 1989. (f) Counts of the number of microgrowth increment pairs occurring after the spawning band versus day number during 1988–89 (n = 46). Based on monthly sampling, the spawning band was produced in individuals after 13 May and prior to 8 June, the first date plotted in the figure. For the regression, 1 June is defined as the origin. The segmented or two-phase linear function was fit by least squares under the assumptions that the location of the join point was unknown and error variances in the two segments were unequal. Detailed methods for this regression may be found in Hudson (30). Slope of the first line segment verifies the semidiurnal rate of increment deposition (95% CI: 0.94 < b₁ < 1.04 pairs of increments per day). Rate of increment production decreases in fall/winter as shown by the slope of the second line segment (95% CI: 0.28 < b₂ < 0.41 pairs of increments per day).

the chondrophore edge (Fig. 1a). Specimens were then mounted onto petrographic slides, sectioned a second time, ground, and polished by hand. Thin sections of 231 specimens were examined under transmitted light using a compound microscope at low magnification (12.5–100×). We analyzed growth patterns primarily by characterizing how features present at the edge of the chondrophore changed from one sampling date to the next. Unless otherwise noted, the specific features described below occurred in 90% or more of the specimens that were examined and that had been properly prepared.

The resolution of growth patterns in the chondrophore depends to a large extent on the thickness of the section (Fig. 2). Distinct variations in transparency are found in thin sections ground to 150–250 microns (Fig. 1d). At some time during May–June of each year, a thin trans-
lucent band is formed at the edge of the chondrophore (Fig. 2b); this event coincides with the spawning season, which was identified by Brousseau (19) for several nearby populations. This translucent band occurs infrequently in one-year-old individuals (32%). It is, however, readily apparent at all other ages up to the oldest individuals examined (91% of specimens 2–5 years old).

The translucent spawning band is followed by a seasonal cycle consisting of an opaque (optically dense) region formed in spring, a broad translucent region in summer, and a second opaque region in fall-winter (Fig. 2a–e). No discernible change differentiating fall from winter is apparent at the edge of the chondrophore, but an opaque layer does begin forming in January on the inner surface of the region where the chondrophore joins with the umbo (large arrow in Fig. 1d). This opaque layer is initially patchy and thin but increases in size and thickness during the winter.

When sections are ground thinner to 80–150 microns, extensive series of microgrowth increments become evident (Fig. 1b, c, e). These also vary seasonally with broad, regularly shaped increments in spring, grading into closely spaced, regular increments in summer. Regularly shaped increments also tend to be deposited during early fall, but by mid-fall, and throughout the winter, the increments appear irregular in form (e.g., see transition in Fig. 1e). In addition, increment widths may be variable during early fall, but they gradually decrease in thickness during this season and remain thin throughout the winter.

The number of microgrowth increments in the interval between the most recent spawning band and the edge of the chondrophore can be related to the date of sample

![Figure 2. Optical micrographs illustrating both seasonal changes at the edge of the chondrophore and the effect of section thickness on the resolution of microgrowth patterns. All micrographs to same scale. (a) Late winter collection. Opaque region with irregular microgrowth increments present at the edge of the chondrophore. Thin section is about 120 microns in thickness. (b) Spring collection. Newly formed spawning band (R) at the edge of the chondrophore. Opaque region in interior is previous winter, 180 micron thin section. (c) Early summer collection. Translucent region characteristic of summer growth (S) is just beginning to form at edge. Note spawning band (R) in interior and opaque spring region (between R and S), 180 micron thin section. (d) Early fall collection. Opaque region forming at edge. Note translucent summer region in interior, 100 micron thin section. (e) Early winter collection. Opaque region with irregular microgrowth increments occurs at edge. Interior region includes previous fall, 120 micron thin section. (f) Same individual as in (c) but with chondrophore ground to about 130 micron thickness. In general, microgrowth increments become evident but the contrast between opaque and translucent regions is lost as the section is ground thinner.](image-url)
collection (Fig. 1f). Increments are produced at a semi-
diurnal tidal frequency during the warmer months (i.e.,
water temperatures above 15°), when a one-to-one cor-
respondence is found between pairs of increments and
day number. By mid-fall, the number of increment pairs
produced per day falls below 1.0, but some increment
production continues through the winter. We do not know
whether this decline is due to a decrease in the rate of
increment production, to periods of growth interruption,
or to shell dissolution. The decline does, however, coincide
with the formation of irregularly shaped microgrowth in-
crements. We have also observed that older, slower grow-
ing individuals (4–5 years) tend to form irregular micro-
growth increments, even during the warmer months, and
increment production in these individuals no longer oc-
curs at a semidiurnal tidal frequency.

Another common feature supports our semidiurnal tidal
interpretation; i.e., in portions of the chondrophore of
almost every specimen examined, pairs of increments
are separated by a diffuse, rather than a distinct boundary
and appear coupled (e.g., spring periods in Fig. 1b, c).
This type of pattern has been observed in the outer shell
layer of other species, and in each instance has been shown
to be tidal in origin (2, 4, 7, 20, 21). In these prior studies,
investigators have found that the alternating diffuse and
sharp boundaries between increments are formed either
when the semidiurnal tides are mixed (i.e., unequal) (2,
7, 21) or when they are accompanied by large diurnal
temperature variations (4, 20).

While we have demonstrated that detailed tidal patterns
occur in the chondrophore, we do not generally expect
that a direct correspondence will be found between mi-
crogrowth records produced in the inner and outer shell
layers of bivalves. Increment deposition at the ventral
margin is influenced by a wide variety of environmental
conditions, including perturbations due to abrasion during
movement, unsuccessful predator attacks, storms, and any
other disturbances that may cause local injury or with-
drawal of the mantle tissue (22). On the other hand, the
inner shell layer, and the chondrophore in particular, is
removed from direct contact with the external environ-
ment. The disturbance threshold required to affect incre-
ment deposition should be higher, and we expect that
only environmental changes that cause a systemic phys-
iological response will tend to be recorded. Thus, micro-
growth patterns in the inner shell layer should contain
less environmental noise due to minor disturbances and
should be more integrated with, and more accurately re-
lect, the physiological processes of a bivalve than com-
parable patterns deposited in the outer shell layer.

Supporting this view is the sharp contrast between the
distorted, highly disturbed form of the outer shell layer
in Mya arenaria and the detailed, and at times very uni-
form, patterns preserved in the chondrophore. Another
indication is the prominence of features in the chondro-
phore associated with the two periods of greatest physi-
ological stress for Mya arenaria, i.e., summer and spawn-
ing. The soft-shell clam is a boreal species, and summer
represents an extended period of energetic stress due to
high water temperatures and potentially low food supplies
on Long Island’s tidal flats. During July and August, water
temperatures in protected, intertidal areas consistently
reach 26–28° (23), and chlorophyll-a concentrations in
both the water (24) and surficial sediments (23) can un-
dergo mid-summer declines. Kennedy and Mihursky (25)
have shown that the metabolic requirements of Mya con-
tinue to increase with temperature up to 30° and have
suggested that high temperatures can lead to starvation if
food supplies are scarce. Above 30°, Mya suffer significant
mortalities (26). In Mercenaria mercenaria, the occurrence
of a similar translucent region in the middle shell layer
has been termed a “stress zone” by Clark (27) and has
been observed to form when water temperatures exceed
25° (28), the upper limit for optimal shell growth in this
species (29).

The second stress period, associated with spawning,
appears as a prominent translucent band consisting of
four or more closely spaced microgrowth increments
(Fig. 1b, 2b, c, f). The morphology of this feature is very
similar to the spawning band in the outer shell layer of
Mercenaria mercenaria (22). However, in Mercenaria
mercenaria, the spawning band is less prominent than
growth interruptions produced by discrete environmental
disturbances (22).

The hinge region in bivalves is the most resilient part
of the shell, and it is also the only part containing a com-
plete record of growth. These characteristics make the
presence of detailed patterns in the hinge region partic-
ularly valuable in archaeological and paleoecological ap-
lications. For example, we are currently analyzing 1200-
year-old, shell-bearing, archaeological deposits in which
fully intact specimens of Mya arenaria are rare. However,
complete chondrophores are commonly recovered, and
both seasonal and microgrowth increment patterns are
well preserved. These patterns are allowing us to recon-
struct detailed aspects of growth in Mya, as well as to infer
seasonal shellfish-harvesting practices for this species.

Chondrophores, cardinal platforms, and other internal
structures associated with the hinge occur in many bivalve
taxa but have been overlooked as potential sources of de-
tailed microgrowth increment records. Our observations
suggest that the microgrowth records preserved in these
structures are not simply reflections of patterns found in
other parts of the shell. As in the case of Mya, internal
structures may contain the only usable growth patterns.
At the very least, these patterns should have less environ-
mental noise and should be more closely coupled to sys-
temic physiological processes. Given the clarity and simple
orientation of the microgrowth increments found in the chondrophore, these structures will also be quite amenable to microprobe and image analysis examination.

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Literature Cited


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