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Growth and predation activity at deep-sea hydrothermal vents along the Galápagos Rift

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ABSTRACT

Growth rates of unclassified mussels collected from hydrothermal vents on the Pacific Ocean (2500 m) are among the highest recorded for deep-sea species. Mature mussels have mean growth rates of about 1 cm yr\(^{-1}\) which are comparable to growth rates of shallow water mussels. The largest mussel collected (18.4 cm) is estimated to be 19 ± 7 years old based on results of a mark and recapture experiment. Growth rates of mussels depend on their location around the vents and may vary by factors of 2 to 3. Food concentrations, rather than low ambient temperature and high ambient pressure, appear to be the major limiting factor for growth. Mussels from the vent area called “Rose Garden” appear to synchronously change their growth rates every 6 to 10 months. This phenomenon may reflect changes in vent activity on this time scale.

The vent decapod Bathograea thermydron is apparently responsible for inflicting damage to the mussel shells. Analysis of this damage suggests that predation activity is intense on specimens below 2.0 cm in length. We suggest that the mussels obtain a refuge from predation by growing rapidly to a size larger than 2.0 cm. The growth rates and predation patterns of the Galápagos mussels are remarkably similar to shallow-water mussel beds.

1. Introduction

Before discovery of the Galápagos hydrothermal vent faunal assemblages in 1977, knowledge of the biology and ecology of deep-sea benthic organisms came mainly from soft bottom sediment habitats characterized by low densities of small deposit feeders. Biological processes in these deep-sea communities (e.g., rates of metabolism, growth, colonization, birth and death) are known to be very low compared with similar processes in shallow water ecosystems (Grassle and Sanders, 1973; Jannasch and Wirsen, 1973; Smith and Teal, 1973; Turekian et al., 1975; Grassle, 1977).

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The Galápagos assemblages are different from all earlier studied deep-sea communities as they are dominated by dense aggregations of large epifaunal suspension-feeding organisms which live on hardened lava around thermal vents (Lonsdale, 1977). Temperatures in the vent areas are on the order of 12 to 17°C while the surrounding ambient water is about 2°C. The apparent food sources for all of the suspension feeders are dense suspensions of chemosynthetic bacteria which obtain energy from the earth’s interior; oxidation of metal sulfides which emanate from the vents (Jannasch and Wirsen, 1979; Rau and Hedges, 1979).

A major goal of the Galápagos research program is to compare rates of biological processes at the vents with rates in more normal deep-sea communities and in shallow water ecosystems. To this end, we have attempted to measure growth of, and predation on, a presently unclassified mussel from the Galápagos vents. Mussels, all apparently belonging to the same species, dominate the fauna in both numbers and biomass (Corliss and Ballard, 1977; Lonsdale, 1977; Ballard and Grassle, 1979; Corliss et al., 1979; Grassle et al., 1979).

We have examined shells of living mussels collected by the DSRV Alvin from two extensively studied thermal vent areas: “Mussel Bed” and “Rose Garden” (Corliss and Ballard, 1977; Lonsdale, 1977; Ballard and Grassle, 1979; Corliss et al., 1979; Grassle et al., 1979). These organisms were singled out for growth study because molluscan shells contain a nearly complete record of their growth which, in turn, allows one to reconstruct ontogenetic growth rates, population growth, and skeletal evidence of predator attack (Rhoads and Lutz, 1980). Although our data are limited to the mussels, we believe that the results have broad implications for understanding biological processes in the thermal vent assemblages as a whole.

2. In situ growth measurements

In situ growth rates of mussels from the vent area called “Mussel Bed” were determined from shells that were abraded along their posterior margins using a small file held by the manipulator arm of the deep-sea research submersible Alvin. After a period of 294 days, Alvin returned to recover the same file-marked specimens. From size-specific increases in shell length beyond the file mark on each shell, we constructed an ontogenetic growth curve using the von Bertalanffy growth equation (Rhoads et al., 1981). These data were obtained from mussels greater than 3.5 cm in length. Growth rates of juvenile mussels (< 3.5 cm) were estimated from individuals which apparently colonized microbiological sampling equipment deployed at “Mussel Bed” (Rhoads et al., 1981).

Figure 1 shows the age-length relationship for both adult and juvenile mussels. This ontogenetic growth curve indicates that the mussels apparently continue to grow throughout life, i.e., experience indeterminant growth. The maximum age of the largest mussel collected (18.4 cm) was estimated to be 19 ± 7 years old. The
Figure 1. The ontogenetic growth curve for mussels from "Mussel Bed" based on age-specific growth rates. Squares represent juvenile mussels retrieved from microbiological sampling equipment. Triangles represent clearly file-marked mussels and circles represent probably file-marked mussels. Data from Rhoads et al., 1981. The von Bertalanffy growth equation was used to generate this curve. Dashed lines delimit the standard deviation of the age estimate.

The long-term growth rate of this sampled population appears to be ca. 1 cm/yr\(^{-1}\) (Rhoads et al., 1981).

One might assume that mussel growth could vary depending on the location of mussels around the vents. Gradients in the density of food or other factors influencing growth could lead to a wide range of growth rates. To investigate this possibility we examined mussels transplanted from one location to another.

3. Transplant experiment

Dr. Kenneth Smith retrieved mussels with Alvin from an area of dense mussel growth, placed these mussels into a wire mesh cage, and transplanted them to a peripheral area of low mussel density. The submersible also transplanted mussels from peripheral areas to a densely populated mussel bed. Both transplantations took place on January 26, 1979 on dive 885 at "Mussel Bed." These mussels were collected 312 days later on December 4, 1979.

The primary purpose of the transplant experiment was to see how mussel respiration and chemistry of soft tissues varied spatially. The major apparent difference
Figure 2. The time of mussel transplantation (arrow) and change in shell growth after transplantation ($x$) as inferred from changes in shell curvature. (A) Single valve of a mussel shell resting on a horizontal plane. An increase in shell growth rate is marked by a decrease in the rate of shell curvature. The length of the shell is being increased relative to its width. (B) A decrease in shell growth rate results in an increase in the rate of shell curvature. Shell width is increasing relative to length.

between high and low density mussel growth areas was the abundance of suspended microbial food.

After soft tissues had been removed from the transplanted mussels, we utilized the shells to make growth estimates. In this experiment, the shell edge was not marked with a file at the time of transplantation. The influence of the change in location on mussel growth was deduced from changes in shell curvature as shown in Figure 2. Figure 3A-B shows the apparent changes in mussel growth following transplantation. Sample sizes are small and the mean specimen sizes of the two populations are different. Also, the exact location on the shell of a change in shell curvature is open to subjective judgment. This may account for the apparent anomalous data point (specimen 17) in Figure 3A. In spite of these problems, the transplantation experiment suggests that the location of mussels is an important factor in controlling growth rates. If we choose the regression slope with the best fit ($R^2$) in Figure 3A (specimen 17 excluded), mussels in densely populated areas may be growing two to three times faster than those in peripheral areas.

4. Shell growth patterns

Many of the Galápagos mussels have growth rings on the external surface of the shell. These rings, in most cases, correspond to changes in shell curvature which, in turn, mark changes in the rate of shell growth (Fig. 2). Some rings, however, are apparently formed by a period of mantle withdrawal related to damage of the shell
Figure 3. Changes in mussel growth rates after transplantation. (A) Transplantation of 6 mussels from a densely populated area to a low density peripheral area. Numbers by data points refer to specimen numbers. Two regressions are plotted as specimen 17 appears to be anomalous. Regression \((R1, N = 6)\) gives a correlation coefficient of \(-0.76\). If specimen 17 is excluded from the data set, the correlation coefficient improves to \(-0.90\) \((R2, N = 5)\).

(B) Transplantation of 3 mussels from a low density peripheral area to a densely populated area. Numbers by data points refer to specimen numbers. The correlation coefficient is \(-0.93\).
Figure 4. Length-frequency distribution of mussels collected at “Rose Garden” at the base of the vestimentiferan wall on dives 983 and 984 ($N = 205$). Specimens used for the shell growth pattern study ($N = 139$) fall within the cross-hatched area (see Fig. 5).

Margins (and mantle?) by predators. These “damage rings” are recognized by extensive chipping of the posterior and ventral shell margin. The resulting notches and irregular indentations show evidence of subsequent shell repair.

We have investigated the periodicity of major nonpredatory rings among a population of mussels collected from the “Rose Garden” vent area on dives 983 (November 30, 1979) and 984 (December 1, 1979). Figure 4 depicts the shell length-frequency relationship for the total mussel population collected and the subpopulation (68% of the total) used in the shell growth pattern study.

Specimens smaller than 60 mm in length were not used in the growth pattern study because young specimens either had no rings or the rings were difficult to identify. Specimens larger than 112 mm were not used as there were too few specimens to generate a growth-ring frequency diagram.

If growth-ring sequences can be correlated between individuals, one may assume that environmental factors are operating that affect each individual of the population in a similar way and that the environmental factor is operating uniformly over the population’s area of distribution (Dillon and Clark, 1980). If rings cannot be correlated between individuals, one may assume that the rings are produced by factors which are temporally and spatially variable.

The posterior margin of the shell marks the same time of collection for all individuals and is therefore the origin for all growth-ring measurements. The distance between growth rings was measured along the axis of maximum shell growth (sensu Rhoads and Pannella, 1970). Because the distance between growth rings is a
Figure 5. Frequency distributions of the distance from the posterior margins of mussel shells to major growth rings. (A) Size class 59.9-77.0 mm ($N = 36$). (B) Size class 77.1-11.2 mm ($N = 103$). Values above peaks give the range in time in years before collection ($\pm 1$ standard error) that these rings were produced. Corresponding growth ring frequency peaks between the small and larger size classes are identified with arrows.

function of age and growth rate, we have divided the population into two size classes (Fig. 5). By using the length-age data of Figure 1, we have identified the time of formation of each major growth-ring mode for both the small and large mussel size classes. The equation used is derived from the inverted von Bertalanffy equation:

$$T = \text{age at time of collection minus the age when the nonpredatory ring was produced.}$$

$$= \frac{1}{r} \ln \left[ \frac{x_{\text{max}} - x}{x_{\text{max}} - \bar{x}} \right]$$

where

$T =$ time (years) ago that a ring was produced.

$r = 0.135 \text{ yr}^{-1}.$

$x_{\text{max}} =$ extrapolated maximum attainable length = 19.92 cm.

$\ln =$ natural logarithm

$x =$ shell length at the time when a specific growth ring is produced.

$\bar{x} =$ sample mean.
The value of $x$ was obtained by subtracting the mean modal length from the sample mean. For the small size class this sample mean is 69.7 mm; for the larger size class, it is 93.8 mm.

In Figure 5 we have assigned an age for each growth-ring peak. This allows us to temporally correlate clusters of growth rings between the small and large mussels. Most of the growth rings tend to occur at intervals between 0.5 and 0.8 years (i.e., 6 to 10 months) (Fig. 6).

5. Predator activity

Some of the growth rings in the mussels show evidence of shell damage and repair. This damage is in the form of small v-shaped notches, generally along the posterior region of the growth ring, or shell edge damage localized in the region of the byssal notch. The probability that such shell edge damage is due entirely to mechanical abrasion by water turbulence at these sites is unlikely. We suggest that this damage is caused by unsuccessful predator attacks. The most likely predator is the brachyuran crab, *Bathograea thermydron* (Williams, 1980).

We have analyzed the distribution of these predator marks over the surface of the mussel shells and determined the length of a mussel when a particular predator mark was made at its shell edge. Several predator marks can be present on a specimen; thus, older individuals contribute more information to a predation-frequency dis-
Figure 7. Normalized frequency distribution of shell length when predator damage was inflicted on the shell edge. Data based on 139 specimens which yielded 205 measurements. (A) Shell edge damage exclusive of the byssal notch area. (B) Byssal notch damage only. Dark bars represent original (prenormalized) sample sizes. The distribution was normalized with the formula:

\[ f' = \left( \frac{f \times 1000}{\sum_{i=1}^{\infty} n_i} \right) \]

where

- \( f_i \) = the original frequency of the \( i \)th size class
- \( f'_i \) = the normalized frequency of the \( i \)th size class
- \( n_i \) = the number of individuals in the \( j \)th size class

Distribution than do smaller, younger individuals. In order to correct for this bias, we have prepared a normalized predator-damage frequency diagram (Fig. 7A, B).

Figure 7A gives the frequency distribution of shell edge damage (exclusive of byssal notch attacks). Two major modes are present; a broad distribution about a mode at 4.0-5.0 cm and a narrowly distributed population with a mode of 10.0-11.5 cm. Figure 7B shows that byssal attacks are limited to mussel sizes less than 9 cm in length and about 90% of these attacks occurred before the mussels reached
a length of 7 cm. About 24% of the 139 specimens show no evidence of shell predator damage. Figure 8 illustrates the pattern of shell damage observed in the byssal notch region.

6. Biological and geological implications

The rate of change in shell growth of the file-marked mussels is comparable to mussels transplanted to peripheral areas but lower than the rates observed for mussels transplanted to high population density areas. The shell length-age curve of Figure 1 would therefore overestimate the age of densely aggregated mussels. The Galápagos mussels have an ontogenetic growth curve which is similar to curves for shallow-water mussels, especially *Geukensia demissa* (Lutz and Castagna, 1980) (Fig. 9). Both the thermal vent mussel and *G. demissa* have relatively long mean life spans and continue to grow throughout life.

The apparently synchronous change in mussel growth at “Rose Garden” every 6 to 10 months may reflect a change in vent output on this time scale. Such a
periodic change in temperature and nutrient conditions could affect mussel growth. We have analyzed mussels from “Mussel Bed” for synchronous changes in growth and found none. This may be related to the small sample size of mussels from this site which does not allow us to construct a meaningful frequency distribution. Alternatively, thermal pulsing, if existent, may be operating at only certain vent areas.

Few comparative growth data exist for deep-water molluscs. The growth rate for a single dead specimen of a large (22.6 cm long) vesicomyid clam, *Calyptogena magnifica* (Boss and Turner, 1980), was determined in another Galápagos vent area known as “Clambake I.” The shell was aged using $^{228}\text{Th}/^{228}\text{Ra}$ contained within its shell (Turekian *et al.*, 1979). A growth rate of 4 cm yr$^{-1}$ was obtained and the age of the specimen at the time of the death was estimated to be between 3.5 and 11.5 years. This growth rate is about 4 times greater than that estimated for the Galápagos mussels and is also high when compared with shallow water bivalve growth.

The growth rate of another deep-sea clam, *Tindaria callistiformis*, was determined radiochemically to be 0.0084 cm yr$^{-1}$, with a life span of about 100 years (Turekian *et al.*, 1975). *Tindaria callistiformis* is a small (< 8.4 mm) deposit-feeding bivalve inhabiting soft sediments in nonhydrothermal areas of the Atlantic. The Galápagos clam and mussels have yearly growth rates which are, respectively, 500 times faster and 119 times faster than *T. callistiformis*.

The clams and mussels associated with the hydrothermal vents have yielded the highest growth rates known for deep-sea organisms. These high growth rates are supported by dense suspensions of chemosynthetic microbes associated with the vents (Jannasch and Wirsen, 1979; Rau and Hedges, 1979; Arp and Childress, 1981; Cavanaugh *et al.*, 1981; Enright *et al.*, 1981; Felbeck, 1981; Jones, 1981; Rau, 1981; Wittenberg *et al.*, 1981). One of the most significant aspects of these growth data is that they suggest that food, rather than low ambient temperature and high ambient pressure, is the major limiting factor for growth and productivity in the deep sea.

Evidence of shell edge damage, tentatively attributed to the crab *B. thermydron*, is rarely encountered in specimens below 2 cm in length. Presumably, if mussels below this size are attacked, they are consumed. Most of the unsuccessful predator attacks occur in mussels having shell lengths between 2.0 and 5.5 cm. The frequency of shell attack falls off at larger sizes except that a curious subordinant peak is seen at the largest sizes. By obtaining a large size rapidly, the mussels apparently attain a refuge from predation. This phenomenon is well known for some shallow-water invertebrates (e.g., Paine, 1976). Shallow-water crabs (e.g., *Carcinus maenus*) tend to selectively prey on smaller mussels in order to maximize prey energy content while minimizing the time required to manipulate and open shells (Elner and Hughes, 1978). This phenomenon may be operating at the vent sites.

The apparently high frequency of shell damage of mussels $\geq$ 10 cm in length could reflect the fact that the shell is being accreted slowly at these sizes. The dis-
tance between damage rings may be small, but the time interval between chance encounters with crabs may be relatively infrequent. From these predation data one would expect a mussel survivorship curve that was initially concave (high juvenile mortality), leveling off above a length of 2 cm. The shape of the curve at larger sizes is uncertain. It is interesting to note that, if predation is primarily responsible for truncating the survivorship curve at 18 cm, this predation is not manifested in a large death assemblage of mussel shells. Even with shell dissolution at these water depths, one would expect to encounter a large number of empty shells in various stages of dissolution. Although empty shells are noted, a large time-averaged death assemblage has not been observed at these vents.

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