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15 May 1981; revised 8 September 1981

Growth of Bivalves at Deep-Sea Hydrothermal Vents Along the Galápagos Rift

Abstract. *Direct measurements of shell growth of an unclassified mussel from active hydrothermal vents along the Galápagos Rift reveal growth rates of approximately 1 centimeter per year for mature specimens. The largest mussel collected (with shell length of 18.4 centimeters) was estimated to be 19 ± 7 years old at the time of sampling. Recorded growth rates are among the highest documented for deep-sea species.*

Most communities of abyssal benthic organisms from soft, bottom sediment habitats are characterized by low densities of small deposit feeders. In these communities biological processes, such as metabolism, growth, colonization, and birth, are known to be slow in comparison with processes in shallow-water ecosystems (*1*, *2*). The faunal assemblages discovered in 1977 around deep-sea hydrothermal vents along the Galápagos Rift are different from all earlier studied deep-sea communities; they are dominated by dense aggregations of large epifaunal suspension-feeding organisms that live on hardened lava around active thermal springs. Many of the organisms encounter temperatures of 12° to 17°C and apparently feed on dense suspensions of chemosynthetic bacteria that obtain energy from the earth's interior through oxidation of metal sulfides which emanate from the vents (*3*, *4*).

A major goal of the Galápagos Rift research program is to compare rates of biological processes at the vents with rates in other deep-sea and shallow-water ecosystems. In this report, we summarize results of the first direct measurements of growth of an organism from the hydrothermal vent areas. The studied organism is a presently unclassified mussel (Bivalvia; Mytilidae), a species which dominates the vent fauna in both numbers and biomass (*5*, *6*).

Two techniques exist for obtaining growth rates in skeletonized deep-sea benthos: radiochemical dating (*2*, *7*) and mark-recapture. For this study we employed the mark-recapture technique for the first time in the deep sea. The shells of living mussels at the vent area known as Mussel Bed (*6*) were abraded with a file along their posterior margins on 12 February 1979 with the use of the manipulator arm of the deep-sea research vessel *Alvin* (dive 887). All file-marked specimens were located within a single clump of mussels that was identified with a cube-shaped wire marker and recovered by *Alvin* on 3 December 1979 (dive 986) after 294 days. The filing resulted in different degrees of marking success. Some mussels showed definite evidence of rasp grooves on the abraded region of the shell, and these are identified in Fig. 1A as clearly marked specimens. Mussels with an abraded shell edge but without evidence of grooves cut by the file are labeled as probably marked specimens (Fig. 1A). Mussels from the

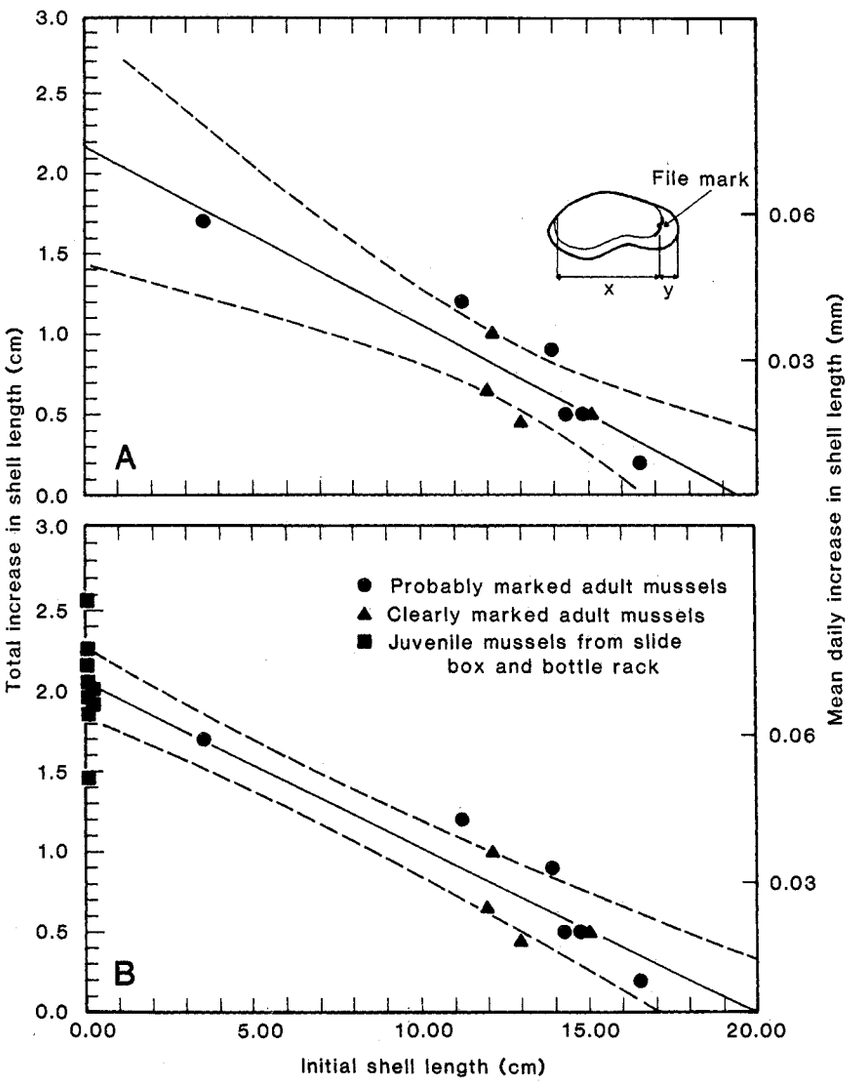

Fig. 1. Total and mean daily increase in shell length for mussels of different sizes. (A) Growth of adult mussels: a plot of the relation of shell length at the time of marking (abscissa) and the increase in shell length after 294 days (N = 10). Inset drawing defines the measurements for the x and y coordinates. Dashed lines are the 95 percent confidence limits for the regression line. (B) Increase in shell length of adult mussels (as above) and juvenile mussels (N = 9) recovered from microbiological sampling equipment deployed for 297 days. An initial settling size of 400 μm is assigned for the juvenile specimens. Dashed lines are the 95 percent confidence limits for the regression.

0036-8075/81/1120-0911$01.00/0

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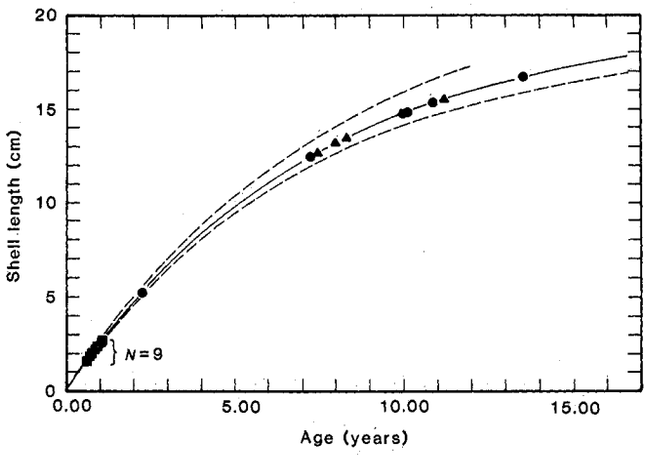

Fig. 2. The ontogenetic growth curve for mussels from Mussel Bed based on the size-specific growth rates summarized in Fig. 1B. Symbols are the same as those used in Fig. 1. The curve was generated by use of the von Bertalanffy growth equation and includes data for both clearly and questionably file-marked mussels (N = 10) recovered after 294 days, as well as the nine largest juvenile specimens recovered from the microbiological equipment. Dashed lines delimit the standard deviation of age estimate.

marked population did not include specimens less than 3.5 cm in length. We estimated juvenile growth rates by projecting the slope of the regression line into the y intercept. This intercept predicts a growth rate of 0.074 mm per day (*8*).

An independent source of information about juvenile growth rates may have been provided by a fortuitous experiment. Small mussels 8 to 25 mm long were recovered from a slide box (N = 25) and bottom rack (N = 9) that were placed at the vents for 297 days for microbiological sampling experiments. If we assume that the mussels arrived by primary settlement (pediveliger larvae), juvenile growth rates can be determined. (We have no independent evidence, however, to exclude the possibility that these mussels represent a secondary colonization.) Nine of the 34 juvenile specimens, ranging in length from 1.5 to 2.6 cm, are considerably larger than the rest and should represent the earliest settling spat. If they settled on the equipment soon after it was deployed, mean juvenile growth rates would be about 0.07 mm per day (Fig 1B). If only the largest juvenile (25 mm) is used to obtain a growth estimate, the value is closer to 0.09 mm per day. These estimates are close to our extrapolated juvenile growth rate (Fig. 1A). Although these data do not prove that these juveniles represent a primary settlement, they suggest that this possibility is tenable.

Because of uncertainties about the data on the "probably marked" adult mussels and the juvenile population from the microbiological equipment, growth curves were generated for the following data subsets: (i) only specimens with definite file marks, (ii) only specimens with questionable file marks, (iii) both definitely and questionably marked specimens, and (iv) these same three variations plus data for the juvenile mussels. These six subsets yielded essentially the same growth curve; we thus chose the curve fit to the entire data set depicted in Fig. 1B to represent the general ontogenetic growth curve (Fig. 2).

Data from the marking experiment indicate that mussels increase their shell lengths throughout life. No mussels larger than 18.4 cm were collected, suggesting that our populations are less than 19 ± 7 years old. This maximum age estimate assumes that the length-age relation of Fig. 2 can be generally applied. Using the 18.4-cm maximum size and our age estimate, we calculate the long-term growth rate of mature mussels to be approximately 1 cm per year.

The thermal vent mussels have an ontogenetic growth curve that is similar to curves for shallow-water mytilids, especially ribbed mussels (*Geukensia demissa* Dillwyn) from productive temperate salt marshes (*9*). Both *G. demissa* and the vent mussel have relatively long mean life-spans and continue to grow throughout life.

Few comparative growth data exist for deep-sea molluscs. The growth rate for a single specimen of a large (22.6 cm long) vesicomyid clam, *Calyptogena magnifica* (*10*), was determined in another Galápagos vent area known as Clambake I (*6*). The shell age was determined from the $^{228}Th/^{228}Ra$ ratio contained in the shell (*7*). A growth rate of 4 cm per year was obtained, and the age of the specimen at the time of death was estimated to be between 3.5 and 11.5 years (*7, 11*). This growth rate is about four times greater than that estimated for the Galápagos Rift mussels and is also high when compared with reported growth rates for shallow-water bivalves. The growth rate of another deep-sea clam, *Tindaria callistiformis*, was determined radiochemically to be 0.0084 cm per year, with a life-span of about 100 years (*2*). *Tindaria callistiformis* is a small (≤ 8.4 mm) deposit-feeding bivalve inhabiting soft sediments in nonhydrothermal areas of the Atlantic. The Galápagos Rift clam and mussels have yearly growth rates which are, respectively, 500 and 120 times faster than that of *T. callistiformis*.

The bivalves associated with hydrothermal vents have yielded the highest growth rates known for deep-sea organisms. These high growth rates are apparently supported by either dense suspensions of chemosynthetic microbes associated with the vents or by photoautotrophically produced material from surface waters that is concentrated by convection cells created by the vents (*3, 4, 12*). One of the most significant aspects of this growth data is that food, rather than low ambient temperature and high ambient pressure, appears to be the major limiting factor for growth and productivity in the deep sea.

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8. The ontogenetic growth rate data (Fig. 1) indicate that the rate of change of shell length is a linear function of initial shell length. We used

the von Bertalanffy equation $X(T) = X_{max} - (X_{max} - X_0)e^{-RT}$ to generate ontogenetic growth curves; $X(T)$ is shell length at age T, X_0 is the settling size, assigned a length of 400 μm [R. A. Lutz, D. Jablonski, D. C. Rhoads, R. D. Turner, *Mar. Biol.* **57**, 127 (1980)], where X_{max} is the maximum shell length, and R is a time constant. The parameters X_{max} and R were obtained from the von Bertalanffy equation, rewritten as $\Delta X_T = X(T + \Delta T) - X(T) = AX + B$, where $A = -(1 - e^{-R\Delta T})$, where $B = X_{max}(1 - e^{-RT})$ and ΔX_T is the total measured increment in shell length during the period ΔT. The regression coefficients in Fig. 1B yielded estimates of A and B. The parameters X_{max} and R were then computed from $X_{max} = -B/A$ and $R = -M(1 + A)\Delta T$.

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9 April 1981; revised 15 September 1981

Hanford-Derived Plutonium in Columbia River Sediments

Abstract. *Mass spectrometry data on plutonium isolated from Columbia River sediments exhibit mean ratios of plutonium-240 to plutonium-242 consistent with those observed for integrated global fallout. Ratios of plutonium-240 to plutonium-239 show marked deviations from accepted fallout values, suggesting a second source of plutonium-239. This additional plutonium-239 arises from the decay of neptunium-239 produced in reactor effluent water from the old plutonium production reactors located on the Hanford Reservation. An estimated 20 to 25 percent of the total plutonium inventory in sediments behind McNary Reservoir, the first downriver site of fine sediment accumulation below the Hanford Reservation, is ascribed to reactor operations.*

The lower Columbia River received large amounts of artificial radioactivity during the period from 1944 to 1970 as a consequence of the operation of single-pass plutonium production reactors located on the Hanford Reservation in Washington State (*1*, *2*). Although much information has accumulated concerning the absolute activity levels and geochemical behavior of elements with short and moderately long-lived radioisotopes in the river system, the same cannot be said for the very long-lived transuranic radionuclides, that is, ^{239}Pu (half-life $t_{1/2}$ = 24,131 years), ^{240}Pu ($t_{1/2}$ = 6570 years), and ^{242}Pu ($t_{1/2}$ = 376,300 years) (*3*). We report here the results of mass spectrometry and absolute activity determinations of plutonium isolated from Columbia River sediments for the period from 1944 to 1977. The data indicate that reactor-derived plutonium constitutes between 20 and 25 percent of the integrated plutonium inventories in sediments 100 km downstream of the reactors. Furthermore, the plutonium contributed by the reactors appears to have been only ^{239}Pu.

Sediment cores were raised during August 1977 from McNary Reservoir on the Columbia River (*4*) and from Ice Harbor Reservoir on the Snake River (Fig. 1). The Ice Harbor samples served as controls since the plutonium present in these sediments is derived entirely from atmospheric fallout. The absolute amounts of $^{239, 240}$Pu in our samples were determined by the addition of known amounts of ^{242}Pu to 10 to 20 g of dry sediment prior to processing and subsequent α-spectrometry measurements; no plutonium isotopes were added to portions of the same sediment (50 g) from which plutonium was isolated for mass spectrometry measurements. These latter samples were leached three times with 6*N* HCl, and the plutonium was isolated and purified by our standard laboratory procedures. Further purification at the Savannah River Laboratory entailed small-column (0.4 ml), ion-exchange chromatography, the plutonium being finally concentrated onto two or three AG 1 × 4 resin beads (50 μm in diameter). The dried beads were then loaded into the mass spectrometer V filaments for analysis. The mass spectrometer used was a surface-ionization, three-stage instrument constructed at the Savannah River Laboratory.

Table 1 lists the absolute concentrations of $^{239, 240}$Pu at the various horizons sampled and the isotopic composition of the plutonium in both our Ice Harbor Reservoir and McNary Reservoir cores as of November 1980. The mean sedimentation rate at the McNary Reservoir coring site (~ 1.4 to 1.5 cm year^{-1}) was determined from the position of the $^{239, 240}$Pu subsurface maximum observed at 19 to 20 cm, which we attribute to maximum fallout delivery in mid-1963 (*5*). We observed a marked increase in the ratio of ^{238}Pu to $^{239, 240}$Pu between 13.5 and 16.5 cm (Table 1), which we attribute to the arrival of SNAP-9A (Systems for Nuclear Auxiliary Power) in the Northern Hemisphere in mid-1966 (*6*).

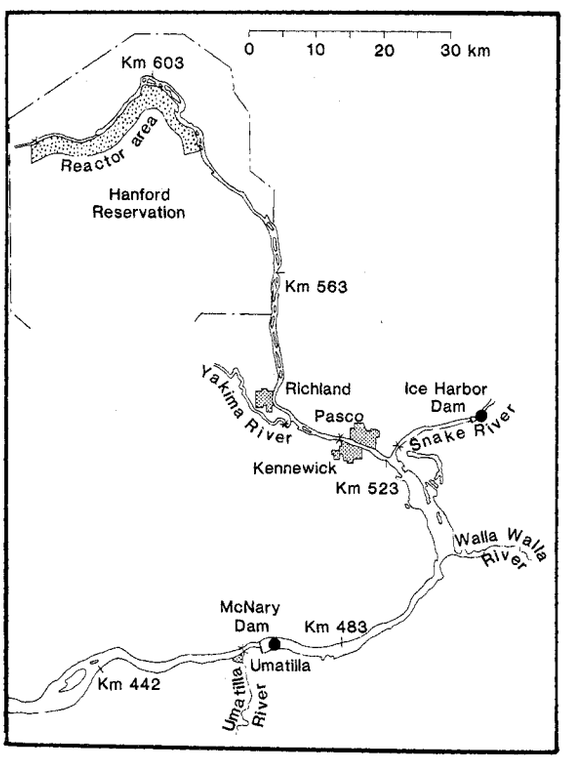

Fig. 1. Sampling sites for sediment cores raised from the Ice Harbor Reservoir and McNary Reservoir.

0036-8075/81/1120-0913$01.00/0

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