

immune responses are required for therapeutic benefit". If only a single product is tested, how are we ever going to know?

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■ See *Nature* **362**, 277; 25 March 1993 for an account of MicroGeneSys's withdrawal of its vaccine from the US Army's trial.

Molluscan shell growth and loss

SIR — Shell growth rings are the principal source of information on the age and growth of molluscs. A growth annulus is assumed to be deposited each year^{1,2}, and microscopic rings are thought to record the length of lunar, daily and tidal cycles¹. The assumption that shell material, once laid down, is never removed, has not been adequately tested. Some studies have used marks on shells that would disappear if shells decrease in size^{3,4}; it is known that molluscs can remain living for long periods without detectable growth⁵; and some studies have recorded negative growth but dismissed it as apparent error. If molluscan shells can decrease in size, then growth rates of molluscs could be overestimated and growth annuli would not reliably estimate age.

We investigated changes in shell size in populations of the common freshwater mussels *Anodonta grandis grandis* and *Lampsilis radiata siliquoides* at two sites

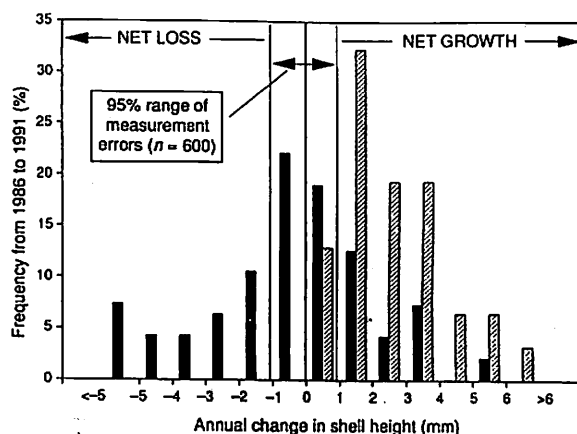
in a well buffered, oligotrophic lake⁶. The rate of shell growth was determined by measuring and marking the edge of the shell at a recorded time, returning the mussels to their natural habitat, then remeasuring the shell dimensions after 1-5 years of *in situ* growth.

Seventy-three *Lampsilis* and 56 *Anodonta* were measured and marked during August 1986 and 1988. We removed animals from the lake briefly, used non-toxic dental cement to glue a pointed, rigid, plastic label at the posterior-ventral margin of one valve of each mussel, and returned animals to the water within 1 hour of collection. Shell dimensions were determined independently by W. L. D. and an experienced field assistant for each mussel relocated during August of 1987-91.

The initial height of each mussel and the height in subsequent years were measured exactly perpendicular to the shell hinge at the umbo using a digital caliper (± 0.01 mm). Mussels were handled gently and kept at lake temperature in ambient lake water during measurement. Measurement error found in blind repeated trials was less than 1 mm in 95% of the 600 trials (see figure).

More than 35% of marked mussels decreased in size. Decreases were commonly 10% and sometimes as much as 20% of total shell height. Although *Lampsilis* showed the most frequent and radical rates of shrinkage, *Anodonta* shells also decreased significantly in size. Decreases in shell size are not due to our marking method or the general water quality in this lake, but vary among sites and populations. For example, *Lampsilis* at the sandbar site grew at rates (average 2.6 mm per yr) similar to those found for the same species in other lakes^{7,8}, whereas less than 1 km away, in the same basin of the same lake, the average rate of growth of marked *Lampsilis* was -0.3 mm per yr.

Changes in shell size were significantly greater than measurement errors (see figure for the example of *Lampsilis*). Most negative measurement errors were between 0 and -1.1 mm; the greatest found in 600 trials was -2.5 mm. At the sandbar site, all *Lampsilis* showed growth, but at the bay site shell height in *Lampsilis* frequently decreased at rates greater than 5 mm per yr. A Kruskal-Wallis comparison of the 52 estimates of annual *Lampsilis* growth that were ≤ 0



Growth rates of *Lampsilis* determined *in situ* by mark and recapture techniques at two sites in Wabana Lake, Minnesota, from 1986 to 1991. Frequencies, number of mussels showing an annual change in shell height that is less than the upper bound of the interval indicated on the abscissa, but greater than or equal to the lower bound of the interval. Vertical broken lines, limits of 95% of all measurement errors determined by remeasuring 10 *Lampsilis* and 10 *Anodonta* of a range of shell sizes 30 times each, in random order. The average estimated size of each shell was calculated and the remeasurement errors estimated as the differences between the average height of each shell and each individual estimate of the height of that shell. Black, bay site ($n=95$); hatched, sandbar site ($n=31$).

with the 247 estimates of measurement error ≤ 0 shows that shell shrinkage is much greater than would be expected from measurement errors alone ($n=299$, $P<0.0001$). Shrinkage was not caused by exterior shell erosion⁹ because the outside periostracum was largely unbroken in shrinking shells and the nacre and crystalline layers inside had been removed, leaving the excess periostracum.

The erasure of shell growth we found has not previously been reported in the longstanding literature on molluscan growth. We hope that people trying to read the shell-growth record will now be aware that part of it may have been erased.

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