Evolution of Sockeye Salmon Ecotypes

RAPID EVOLUTION OF REPRODUCTIVE isolation is proposed by A. Hendry and colleagues to be the cause of the genetic differences between two adjacent populations of Washington State sockeye salmon (Reports, 20 Oct., p. 516). These two populations or "ecotypes," one living in a tributary (Cedar River) and the other along a beach (Pleasure Point) of Lake Washington, are suggested to have evolved after introductions of sockeye into Lake Washington from Baker Lake between 1937 and 1945 (within about 13 generations) and in spite of high estimated migration rates. Hendry *et al.*'s conclusions, however, depend on several assumptions.

Lake Washington neighbors: male beach (left) and river (right) salmon.

First, they assume that the hatchery population used for the introductions was genetically homogeneous. However, the hatchery population, in fact, included both beach and river ecotypes (as well as other gene pools) in its ancestry in various proportions in the five brood years used for the introductions (*1*). Although some mixing of the ecotypes undoubtedly occurred in the hatchery, natural segregation based on different spawn times could have maintained much of the diversity between them until the time of the introductions. Therefore, the current diversity of ecotypes in Lake Washington, and any reproductive isolation, could reflect divergence much older than 13 generations.

Another assumption the authors make is that the "beach immigrants" are derived from the Cedar River population, on the basis of temperature-sensitive otolith (a calcareous ear stone) banding patterns. However, some or all of these immigrants could have come from other beach-spawning sites in Lake Washington that have temperature profiles similar to that of Cedar River (*2*).

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Hendry *et al.* also assume no founder effect and a constant migration at the high rate estimated for 1992–93. More plausible scenarios involving a founder effect and low initial migration could explain their genetic data without postulation of any reduced reproductive success of immigrants. Finally, the genetic data, based on small samples ($N = 12$ for the key sample of beach immigrants) for a single year, should be corroborated with data for subsequent years before any meaningful conclusions are drawn.

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2. J. G. Woodey, thesis, University of Washington (1996).

Response

WE REPORTED THAT TWO NEW SALMON populations within Lake Washington have diverged in response to natural selection and are now partially reproductively isolated. Gustafson and colleagues suggest some alternative scenarios.

First, they point out that both beach and river ecotypes contributed to the initial Baker Lake hatchery stock used for introductions into Lake Washington. This is true, but, as we have discussed elsewhere (*1*), the hatchery propagated all (or nearly all) of the fish as a single mixed stock for up to eight generations. As a result, any preexisting genetic differentiation would have been homogenized before the introductions. Furthermore, salmon did not colonize Pleasure Point Beach until after the introductions from Baker Lake had ceased (*2*), suggesting that the Pleasure Point population was secondarily derived from the population of Cedar River. Reproductive isolation, therefore arose de novo and in situ. A mix of genes from beach and river ecotypes in the introduced group would simply have provided genetic variation to facilitate rapid divergence.

Second, Gustafson *et al.* suggest that some of the Pleasure Point immigrants could have come from other beach populations. This is unlikely because the immigrants were genetically similar to Cedar River fish, and because most of the beach-spawners at the time of our study were at Pleasure Point. In shoreline surveys by boat, we found only five spawning pairs elsewhere.

Third, they propose that the observed genetic differences could have resulted from founder effects. Although possible, this is unlikely, given the observed high rates of adult movement (any founder effect would be rapidly destroyed by gene flow unless reproductive isolation had evolved). The alternatives offered by Gustafson *et al.* are contradictory: they suggest that genetic differences were present before the introduction and then suggest that genetic differences arose in situ.

In conclusion, our explanations remain the most consistent with the data. Although our study was the first to document the evolution of reproductive isolation on such a short time scale, we expect that other studies will reveal analogous situations.

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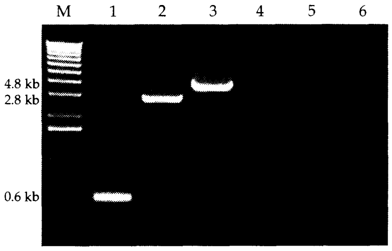

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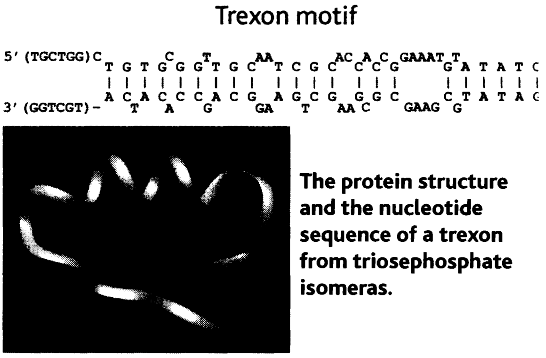
Selfish DNA and the Origin of Genes

A PALINDROMIC REPEAT OF ABOUT 150 BASE pairs was found by H. Ogata and colleagues to be inserted into many protein-coding genes of *Rickettsia conorii*, the bacterium that causes Mediterranean spotted fever (Reports, 13 Oct., p. 347). The corresponding amino acids encoded by these repeats are thought to be expressed in the mature proteins. The authors suggest that the amino acid segments in the DNA conform to a general motif—an α helix flanked by turns or loops. Finally, Ogata *et al.* propose that these *Rickettsia* palindromic elements (RPEs) represent an example of selfish DNA (DNA that has no apparent cellular function) participating directly in the creation of new protein sequences.

The findings confirm my earlier work in which I arrived at many of the same conclusions, but starting from a different perspective. Instead of examining DNA sequences, I analyzed protein sequences, specifically the amino acid sequences of proteins from multi-gene families (such as thionin and transforming growth factor–β) (*1*). These proteins appear to have evolved from smaller modules that I called duplication units, which have a characteristic structure: an α helix and a short turn or loop. There were also amino acid sequence similarities among these various segments from diverse proteins. Two of these segments, GBP-4 from galactose/glucose binding protein and neurophysin-3 (*1*), show striking similarity (nearly 50% homology) to the central conserved region described by Ogata *et al.*

I also found that the duplication unit was encoded by a short inverted repeat segment of DNA that resembled transposable genetic elements (see the figure). I termed these segments "trexons," for transposable exons. The RPEs described by Ogata *et al.* appear to be very similar to trexons. I proposed that the trexons arose from the initial building blocks of RNA and suggested that these segments represented "selfish DNA" acting at the level of the exon rather than the intron (*1*). It is rewarding to see that this work has been confirmed in convincing fashion by another group. In view of the different research approaches that led to such similar conclusions, it may be time to reconsider the idea that exons were static gene elements that gained mobility only by association with introns.

I would submit that trexons and RPEs are modern-day vestiges of the earliest phase of sequence creation in a highly mobile RNA world. Certain features of *Rickettsia* (for example, their close similarity to mitochondria and their slow-paced growth) may have helped these segments survive through evolution more or less intact. I have suggested that these mobile genetic elements encoded protein segments that were specialized for participating in protein-protein and protein-polynucleotide interactions (*1*). The RPEs from *Rickettsia* may serve similar roles and define either a protein interaction domain or a polynucleotide-binding motif.



The protein structure and the nucleotide sequence of a trexon from triosephosphate isomeras.

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Response

STRUCTURAL AND FUNCTIONAL MODULARITY of proteins is well established. Occurrences of homologous domains in otherwise different proteins suggest the recurrent use of modular units in evolution. The combinatorial advantage of modular units to design diverse proteins is obvious, but the precise relation between evolutionarily successful modules and mobile sequence units is not yet clear. The "trexon" hypothesis proposed by Dwyer (*1*) and the palindromic element (RPE) that we discovered in several *Rickettsia* species (*2*) provide an interesting al-

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