ing depends not only on initial porosity but also on the relative time scales for soil deformation and pore pressure diffusion (*18*). If fluid pressure can diffuse into or away from contracting or dilating soil as quickly as the soil deforms, pressure equilibration keeps pace with deformation and the effects of porosity change diminish. However, the time scale for pore pressure diffusion is h^2/D, where h is the typical thickness of the deforming soil mass and D is its typical hydraulic diffusivity. Even sandy soils with high diffusivity commonly have $D < 100$ cm^2/s (Table 1). Thus, the time scale for diffusive pore pressure equilibration in deforming soil masses with $h \sim 1$ m typically surpasses 10 s. In comparison, the time scale for landslide acceleration in response to basal pore-pressure change is $\sqrt{h/g}$ (*21*), which yields values <1 s for $h \sim 1$ m. We conclude that pore pressure diffusion can seldom keep pace with soil deformation and that relatively small variations in porosity can influence landslide behavior profoundly.

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9. On the scale of individual grains and pores, the coupling of fluid pressure and displacement of adjacent solids is described by viscous lubrication theory. On a continuum scale involving millions of grains and pores, the same coupling can be described by porosity change and attendant development and diffusion of pore fluid pressure.
10. Soil strength typically obeys the Coulomb-Terzaghi equation $\tau = (\sigma - p)\tan\varphi + c$, where τ is mobilized shear strength, σ is total normal stress, and p is pore fluid pressure, all on the same failure plane; φ is the soil angle of internal friction; and c is soil cohesion. Increased pore fluid pressure therefore reduces soil strength if all other factors are constant.
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16. Tiltmeters were Crossbow model CXTA01-CAN, rigidly mounted in smooth cylindrical tubes 2.5 cm in diameter, fitted with rough exterior vanes 1 cm high to provide good frictional contact with soil. Extensometers were Celesco model PT101-250AS, attached to anchors embedded in the soil surface. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.
17. Dynamic piezometers were fabricated to have a configuration that promoted rapid dynamic response and minimal signal attenuation (*11*). The sensing elements in these piezometers were Honeywell Microswitch differential pressure transducers (model 26PCCFA3D, with nominal range 0 to 15 psi). Identical pressure transducers mounted to the pressure ports of Soil Moisture Equipment Jet-Fill tensiometers (model 2725, equipped with porous ceramic tips with nominal 1-bar air entry pressures) were used to measure pore water pressures less than atmospheric.
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20. As illustrated in Fig. 2, dense soils generally display a prominent peak in strength (due to dilation), which impedes landslide initiation. After peaking, the strength of dense soils gradually decays. With sufficiently large deformations, dense soils and loose soils hypothetically approach a state of constant porosity (the critical state) and constant (residual) strength. Breakage of soil aggregates complicated this behavior in our ring-shear experiments (Fig. 2).
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Rapid Evolution of Reproductive Isolation in the Wild: Evidence from Introduced Salmon

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Colonization of new environments should promote rapid speciation as a by-product of adaptation to divergent selective regimes. Although this process of ecological speciation is known to have occurred over millennia or centuries, nothing is known about how quickly reproductive isolation actually evolves when new environments are first colonized. Using DNA microsatellites, population-specific natural tags, and phenotypic variation, we tested for reproductive isolation between two adjacent salmon populations of a common ancestry that colonized divergent reproductive environments (a river and a lake beach). We found evidence for the evolution of reproductive isolation after fewer than 13 generations.

Ecological speciation occurs when organisms exposed to divergent selective regimes evolve reproductive isolation as a by-product of adaptation (*1–3*). Mechanisms contributing to ecological speciation include mate choice based on traits under divergent selection (*4*, *5*), hybrid or backcross inferiority (*2*), and reinforcement of assortative mating when hybrids are inferior (*6*, *7*). Ecological speciation appears to be relevant in allopatry and sympatry and has been supported by theoretical models, laboratory experiments, and studies of natural systems (*1–9*). Here we focus on an unknown aspect of ecological speciation: How quickly can reproductive isolation evolve?

Rapid evolution of adaptive traits often occurs in populations exposed to divergent ecological environments (*10*, *11*). Although this implies that reproductive isolation may also evolve rapidly, the best examples of ecological speciation are seen in groups that began diverging thousands of years ago (*12*, *13*). Unfortunately, inferring evolutionary rates on the basis of long-standing groups is questionable, because averaging disparate rates across time will obscure biologically important short-term evolution (*11*). Thus, reproductive isolation might evolve in only a few generations, or it may require a long and gradual accumulation of isolating mechanisms. Some insects that colonized new host plants 100 to 200 years ago have evolved ecologically mediated reproductive isolation (*14*, *15*). We ask whether reproductive isolation can evolve even faster by testing for evidence of intrinsic barriers to gene flow between two populations of sockeye salm-

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on (*Oncorhynchus nerka*) derived from a common source less than 13 generations previously.

Sockeye salmon form distinct reproductive "ecotypes," with adults breeding in streams or along lake beaches (*16*, *17*). After continental glaciers receded about 10,000 years ago, sockeye salmon colonized hundreds of new lake systems, many of which now contain reproductively isolated populations that are adapted to beaches and streams (*16*). Postglacial reproductive isolation was presumably achieved through natal homing, divergent sexual ornamentation, and ecological selection against hybrids. Parallel evolution of these ecotypes within many different lake systems provides a robust interpretive framework.

Introductions of salmon to new locations have provided excellent opportunities to study rates and patterns of evolution (*18–21*). Sockeye salmon were introduced into Lake Washington, Washington, from Baker Lake, Washington, between 1937 and 1945. These introductions gave rise to a large (currently 100,000 to 350,000 breeders) self-sustaining population in the major tributary to Lake Washington (Cedar River). In 1957, a new population was first documented breeding along a Lake Washington beach (Pleasure Point) about 7 km north of Cedar River. The beach site was apparently colonized by fish from the river or, if not, both populations are at least of the same introduced lineage [inferred from historical records and allozyme variation (*18–20*)]. The two populations have been diverging for a maximum of 56 years (1937 to 1992), which is equivalent to approximately 13 generations (*20*), and the beach population is less abundant by about two orders of magnitude (*22*). As a starting point for divergence, we adopted 13 generations (from 1937) rather than 8 generations (from 1957) because the former is unambiguous and conservative.

We examined reproductive isolation between the beach (Pleasure Point) and river (Cedar River) populations on the basis of collections of breeding adults (*23*). We used population-specific natural marks to identify river fish that were immigrants to the beach, DNA microsatellite loci to estimate genetic differentiation between river and beach residents, population-genetic models to infer the relative reproductive success of immigrants, and adult life history and morphology to consider the ecological basis for isolation.

We quantified immigration of river-born adults to the beach using natural marks that are produced on otoliths (calcareous ear stones) while embryos incubate in the gravel. Because the incubation environment is isothermal at the beach but variable in the river (*22*), we could examine the otoliths of adults to determine whether each had been born (incubated) at the beach or river (*24*). This analysis, conducted blind with respect to collection location, microsatellite variation, and phenotypic traits, revealed that most breeding adults collected from the river had indeed incubated under a variable thermal regime (34 of 35 in 1992 and 30 of 38 in 1993) but that many adults collected from the beach had also incubated under a variable thermal regime (14 of 32 in 1992 and 12 of 34 in 1993). Thus, approximately 39% of adults breeding at the beach (48% of females and 34% of males) were immigrants from the river (*22*).

This estimated immigration rate of river fish into the beach population is so high that unless reproductive isolating mechanisms had evolved, the two populations could not have diverged at neutral genetic loci. We used allelic variation at six microsatellite loci (*25*) to quantify genetic differences between three groups categorized by otolith patterns and breeding location: beach residents (born and breeding at the beach), river residents (born and breeding in the river), and beach immigrants (born in the river but breeding at the beach). River residents and beach immigrants showed no evidence of genetic divergence (Table 1), which is consistent with the expectation that immigrants to the beach were from the river. In contrast, beach residents were genetically distinct from river residents and from beach immigrants (Table 1). This pattern of genetic differentiation could only have arisen if beach immigrants have reduced reproductive success relative to beach residents.

We considered the extent of reproductive isolation by comparing the proportion of immigrant breeding adults in the beach population (adult migration, determined from otoliths) to the proportion of immigrant genes (gene flow, determined from microsatellites). If gene flow were less than adult migration, we would have evidence for the evolution of reproductive isolation. The standard approach to estimating gene flow from genetic data requires assumptions that most natural populations violate (*26*). We therefore estimated gene flow using recursion equations that avoided these assumptions, allowing for two populations of different sizes, asymmetric gene flow, and nonequilibrium conditions (*27*). Gene flow from the river to the beach was less than adult migration (39%), as long as the beach effective population size was not exceptionally low ($N_e > 8$; Fig. 1). Breeding population sizes range from 100 to 8180 at the beach (*20*), suggesting that $N_e \gg 8$. Thus, the reproductive success of river fish breeding at the beach must be lower than that of beach residents, despite their recent common ancestry.

We considered potential isolating mechanisms by examining two adult traits that are subject to divergent selection between rivers and beaches. Male body depth is sexually selected (*28*) and reaches extremes in beach populations where it is unopposed by predation, water flow, or water depth (*29*). In rivers, males have shallower bodies (*29*), presumably owing to selection for increased swimming efficiency. Female body size differs between beaches and rivers because large

Table 1. Genetic differentiation at six microsatellite loci (*25*) between beach residents ($N = 22$), river residents ($N = 35$), and beach immigrants ($N = 12$). Nei's unbiased genetic distance (D) and F_{ST} (bootstrapped 95% confidence intervals are shown in parentheses) were calculated with TFPGA (*35*). The significance of genotypic differentiation (*GD*) was determined with GENEPOP (*36*). Observed differentiation cannot be attributed to linkage of any one locus to a locus under divergent selection, because even after deletion of the locus that best differentiated river residents from beach residents (Ssa85, $F_{ST} = 0.054$), divergence was still substantial.

Comparison	F_{ST}	F_{ST} (no Ssa85)	D	*GD* (*P* value)
River residents versus beach immigrants	0.008 (0.002–0.013)	0.008	0.010	0.365
River residents versus beach residents	0.025 (0.008–0.042)	0.017	0.054	0.002
Beach residents versus beach immigrants	0.015 (0.001–0.033)	0.012	0.026	0.030

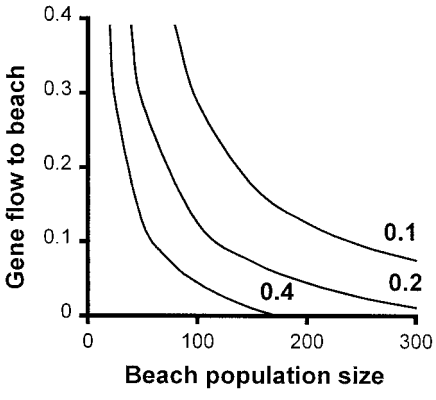

Fig. 1. Estimated rates of gene flow from the river to the beach. Curves were determined with recursion equations (*27*) to estimate gene flow (m_1) that would lead to the observed F_{ST} (0.025) after 13 generations. We assumed that beach colonizers were representative of the river population (that is, founder effects were minimal), that all gene flow was from the river to the beach ($m_2 = 0$), and that $N_e = 10{,}000$ in the river. Recursions were started with an IBD of 1/10,000. Curves represent a range of possible N_e/N ratios (0.1, 0.2, and 0.4).

females dig deeper nests, thereby protecting their eggs from disturbance during flooding (*30*). Flooding is absent from beaches, and females are correspondingly smaller (*17*, *29*). In our study, beach males had deeper bodies (standardized to average body length) and beach females were shorter, with beach immigrants somewhat intermediate for both traits (Fig. 2). These results suggest that beach immigrants are not as well suited for the beach environment as are beach residents, perhaps contributing to reduced mating success or offspring survival. Many other traits are subject to divergent selection between beaches and rivers (*20*), and beach immigrants are probably also compromised for those traits.

Significant reproductive isolation (albeit partial) after fewer than 13 generations implies that much of the isolation observed in ecological speciation can arise soon after initial divergence.

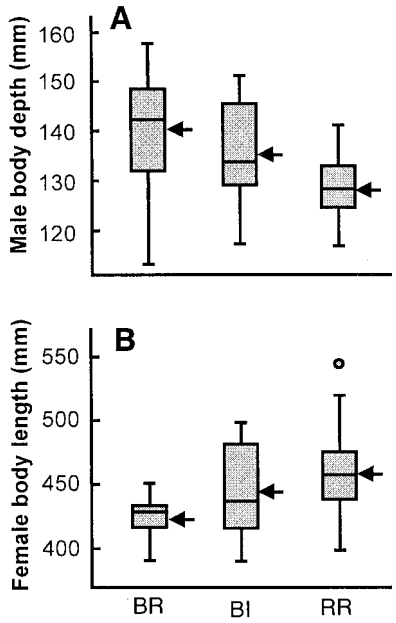

Fig. 2. Differences in (**A**) standardized male body depth and (**B**) female body length (*37*) between beach residents (BR), beach immigrants (BI), and river residents (RR). Boxes contain 50% of the data and bars contain the remainder; horizontal lines indicate medians, arrows indicate means, and the circle indicates an outlier. On the basis of Tukey tests, river residents and beach immigrants had similar female lengths ($P = 0.365$) and male body depths ($P = 0.076$), river residents and beach residents had different lengths ($P = 0.003$) and body depths ($P < 0.001$), and beach residents and beach immigrants had similar lengths ($P = 0.256$) and body depths ($P = 0.289$). The morphological intermediacy of beach immigrants could arise because of phenotypic plasticity (if swimming in rivers reduces body depth), morphology-influenced site selection (if smaller river females and deeper bodied river males are more likely to breed at the beach), or site selection by hybrids (if hybrids were produced in the river and then bred at the beach).

Our results may seem exceptional but are clearly biologically possible, as evidenced by laboratory studies in which reproductive isolation often evolves over similar time frames (*8*). Our study was based on indirect methods (patterns of genetic variation), which measure total isolation (postzygotic and prezygotic). Direct tests of reproductive isolation, such as mate preference, would be complementary because they quantify the prezygotic contribution to isolation (*9*). Experimental demonstrations of speciation in the wild have been considered intractable because isolation is assumed to require a long period. Our findings suggest that when organisms colonize different environments, experimental studies of speciation may prove feasible.

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23. In 1992 and 1993, breeding adult fish were collected at a weir 10.4 km upstream from the mouth of the Cedar River; at Pleasure Point, fish were collected with fishing gear (*18*, *19*). Fish were killed by a blow to the head and measured for length [from the middle of the eye to the hypural plate (*19*)]. Males were also measured for body depth [from the anterior insertion of the dorsal fin to the bottom of the abdomen (*19*)]. Otoliths were removed (*22*), and tissue samples were frozen (*18*).
24. Characteristic dark and light otolith banding patterns are influenced by variations in diurnal water temperature. When temperatures fluctuate, increments are dark and highly contrasted against their background. When temperatures are constant, increments are less distinctive and weakly contrasted (*31*). We processed otoliths to reveal banding patterns in the core region that correspond to the incubation period (*22*). Blind trials were then used to classify each otolith as having been produced by a variable (river) or constant (beach) thermal regime (*22*).
25. DNA was extracted from frozen tissue, and six dinucleotide microsatellite loci (Oneμ1, Oneμ2, Oneμ8, Oneμ11, Oneμ14, and Ssa85) were amplified as described elsewhere (*32*). Microsatellite alleles were separated with an Applied Biosystems 373A automated DNA sequencer and were analyzed with GeneScan 672 and Genotyper software (*33*, *34*). Only 1992 samples were analyzed, because 1993 samples were destroyed by a freezer failure. Loci were in Hardy-Weinberg equilibrium, except for Oneμ2 locus in river residents ($P = 0.023$), and locus pairs were in linkage equilibrium, except for Oneμ2 versus Oneμ14 ($P = 0.046$) and Oneμ8 versus Oneμ11 ($P = 0.041$) in beach residents. These deviations were not significant after sequential Bonferroni corrections.
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$$f_1' = \frac{1}{2N_{e1}} + \left[1 - \frac{1}{2N_{e1}}\right][(1 - m_1)^2 f_1 + 2m_1 (1 - m_1) f_{12} + m_1^2 f_2$$

$$f_2' = \frac{1}{2N_{e2}} + \left[1 - \frac{1}{2N_{e2}}\right][(1 - m_2)^2 f_2 + 2m_2 (1 - m_2) f_{12} + m_2^2 f_1]$$

$$f_{12}' = (1 - m_1)(1 - m_2) f_{12} + m_1(1 - m_2) f_2 + m_2(1 - m_1) f_1 + m_1 m_2 f_{12}$$

$$F_{ST} = \frac{\frac{f_1 + f_2}{2} - \frac{f_1 + f_2 + 2f_{12}}{4}}{1 - \frac{f_1 + f_2 + 2f_{12}}{4}}$$

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37. Female body length differed ($F = 6.02$, $P = 0.004$) among beach residents ($N = 13$), river residents ($N = 42$), and beach immigrants ($N = 12$). Analysis of covariance (ANCOVA) revealed that male body depth/body length ($\log_{10}$) slopes were homogeneous ($F = 1.08$, $P = 0.347$) among beach residents ($N = 27$), river residents ($N = 22$), and beach immigrants ($N = 14$). After removal of the interaction term, body length ($F = 107.26$, $P < 0.001$) and group ($F = 9.05$, $P < 0.001$) had significant effects on body depth. Body depth was standardized to average body length (444.7 mm) using $D_{std} = D_o(444.7/L_o)^{1.346}$, where D is body depth, L is body length, 1.346 is the ANCOVA slope, and subscripts std and o refer to standardized and observed measurements.
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