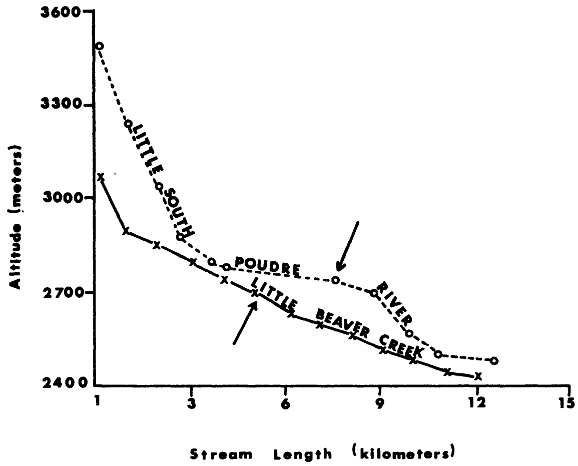

FIG. 2. Longitudinal profile of Little South Poudre River and Little Beaver Creek. Arrows mark upstream limit of brown trout distribution.

ter months. Length of time that water is above a certain minimum temperature, however, may well be limiting.

No distinct upper altitude limited brook trout distribution. Upstream distribution was independent of altitude but dependent on stream size. For instance, Little Beaver Creek at 3,050 m elevation and 1.0 km above the upper limit of brook trout had flows as low as 0.015 m^3/sec.

Vegetative type was not related to altitudinal distribution of fishes. The transition zone between montane and sub-alpine is 2,900 m, 150–300 m higher than the brown-brook trout separation zone.

Fish distribution in the watershed is unstable and is changing because of annual introductions of rainbow trout, downstream range extension of suckers, and upstream movement of brown trout. Three examples are available to illustrate the upstream movement of brown trout. In Pennock Creek a section of stream approximately 1.2 km upstream from the mouth was electrofished in 1956, 1964, and 1967. Species composition ratio was 3:1, 12:1, and 20:1 respectively, brown trout to brook trout. In Little Beaver Creek the same number of brook and brown trouts were found at 2,600 m in 1964. In 1967 only brown trout were present. This later shift was accelerated by opening of the area to increased fishing pressure, thus selectively removing the more easily catchable brook trout. Fry, 8–10 cm yearlings, and adult brown trout were present in 1968 in the Little South Poudre River at 2,750 m. Formerly only a lingering population existed. Apparently this peripheral segment of the population is now reproducing.

The fish population of the Little South Poudre River drainage is distinctive in that cutthroat trout is the only native species. Small cyprinids and cottids frequently found in head waters of Rocky Mountain streams have never been reported. Although some of these native fishes are present in the main Poudre River, it appears that only cutthroat trout moved upstream; other species became established through introductions.

Distribution of brown trout is expanding upstream slowly. The relationship between altitude and upstream distribution of brown trout is similar in five of the tributary streams. Although temperature is a likely controlling factor, others should not be precluded. Brown trout are aggressive biological competitors; high altitude climates of the Rocky Mountains are influenced by long-term warming of the post-Pleistocene period; and there is selective fishing mortality on the easier-to-catch brook trout.

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EQUITABILITY INDICES: DEPENDENCE ON THE SPECIES COUNT

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Abstract. Three measures of equitability or relative diversity are shown to be dependent on the species count component of total diversity. This dependence limits the use of equitability indices as comparative statistics.

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Lloyd and Ghelardi (1964) introduced an equitability index which was intended to partition the Shannon-Wiener species diversity into a component depending on the species count and a component of equitability depending on the distribution of relative abundances among the species in a sample. More recently a number of ecologists including Barrett (1968), Buzas and Gibson (1969), Hairston et al. (1968), Kohn (1968), and Pulliam, Odum and Barrett (1968) have used the equitability index or similar measures in studies of community structure. The equitability concept is a useful one and permits considerable refinement in diversity studies. However, the measures of equitability or relative diversity now in use have characteristics which may invalidate their use for comparative purposes.

Lloyd and Ghelardi (1964) defined their index as

$$\varepsilon = S'/S$$

where S is the observed number of species and S' is the theoretical number of species which would yield the observed diversity H if their relative abundances followed the broken-stick model of MacArthur (1957). Diversity $H = -\sum^{S} p_i \ln p_i$ where the p_i are the proportion of the i^{th} species. A similar measure, here called E, is $E = e^H/S$ where H is the observed diversity and e is the base of the natural logarithms. The quantity e^H is the minimum number of equally common species which could yield the observed diversity H. A third measure is H/H_{max} where H is the observed diversity and $H_{max} = \ln S$ or the maximum possible diversity for a sample of S equally abundant species.

The equitability concept is based on the assumption that ε and the other measures partition total diversity into an effect of the species count and an effect of variations in relative abundance. If the separation is incomplete so that ε depends on S, then differences in equitability could result from differences in the species count rather than any fundamental change (or lack of change) in organization. Equitability $\varepsilon = S'/S$ is obviously a function of S whose form suggests a hyperbola, although the precise shape will depend on the values of S'.

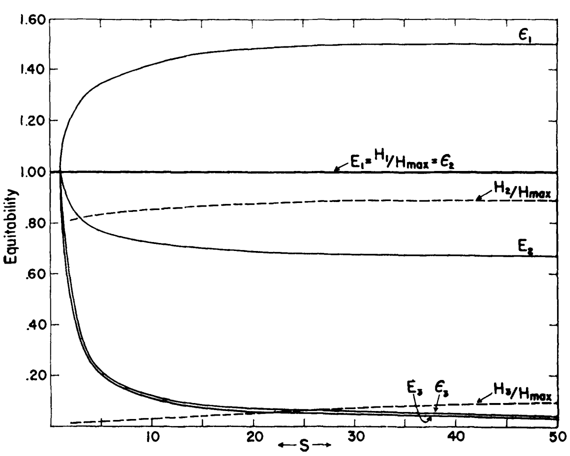

FIG. 1. Relationship of three equitability indices to the species count for three patterns of relative abundance. 1. All species equally abundant. 2. Abundances given by the MacArthur distribution. 3. All species except the first represented by single individuals in samples of 1,000.

Figure 1 shows the relationship between equitability and the species count for the three indices and three patterns of relative abundance. The first abundance pattern is the case where all species are equally common, and the second is given by the MacArthur model. The third set of curves represents a situation of low diversity and low equitability where, in samples of 1,000 individuals, all species except the first are represented by single individuals. Each of the equitability measures is dependent on the species count to some degree although all are fairly stable for $S > 20$. The indices ε and E are strongly dependent on S for $S < 10$, and this dependence increases as equitability deviates from unity.

Figure 1 suggests that the dependence of equitability on the species count is not very important, since it operates most strongly when the species count is low. However, this is precisely the situation in which diversity and equitability measures are likely to be used. Most diversity studies include at least some samples with low species counts. The same effect can be obtained by splitting a large assemblage into smaller taxonomic or ecological groups or by comparing samples from normal and disturbed environments. In each case, differences in S can lead to spurious changes in equitability.

Of the equitability measures discussed here, H/H_{max} appears the most stable and best suited for general use. Equitabilities ε and E should be compared only when S is large or, if S is small, when the species counts are equal.

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