

FISHES IN NORTH AMERICAN DESERTS

Edited by

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5 Effects of Habitat Size on Species Richness and Adult Body Sizes of Desert Fishes

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ABSTRACT

A comparison of samples from deserts in the United States and the Paraguayan Chaco shows that species richness, life history patterns, and evolution of desert fishes are strongly influenced by habitat size and drainage directions with respect to habitat stability. In the intermountain (United States) desert, streams head in relatively stable habitats and flow onto deserts where conditions are frequently more variable and habitat may disappear. Chaco streams originate in low, flat headwaters where wet-season precipitation collects in temporary swamps and drains to a large stable river with a rich fauna. Species richness ranges from 0 to more than 40 species per sample in the Chaco, depending on habitat size. Annual extinction is high

locally, but recolonization rate is also high and long-term extinction rates are probably low. This pattern contrasts with that in the intermountain desert where the annual cycles are part of a longer postpluvial desiccation and extinction cycle. Here barriers to recolonization are imposed by basin and range topography and species numbers range from 0 to 11 per sample.

The pluvial fluctuations in the Great Basin might have cyclicly disrupted evolutionary trends before they produced species-level adaptations to deserts or pluvial great lakes. Chaco aridity is not so old as in the intermountain desert, but colonization from tropical, humid forest streams has introduced fishes with diverse adaptations for air breathing and for surviving dry seasons as aestivating adults. Selection has produced annual life-history adaptations that include survival of eggs in desiccated substrate.

Body size is also related to habitat size in most nonbenthic freshwater fishes. Many intermountain minnows, suckers, and trouts are selected locally for large size by increased adult survival and consequent late reproduction in large habitats. Annual fluctuations that reduce habitats seasonally, thus causing heavy mortality, lead to persistence of phenotypes that reproduce early at the expense of later growth. Fossil evidence suggests that late Cenozoic species richness and body size in intermountain fishes were generally correlated with habitat size. Most desert fishes belong to widespread groups apparently adaptable to a broad size range of habitats.

INTRODUCTION

Latitudinal variation in species richness has been shown by Fischer (1960) to be strongly influenced by long- and short-term stability of environment. Pianka (1966) and Emery (1980) summarized the influence of environmental stability as well as spatial heterogeneity, productivity, and aspects of community structure on species richness. Barbour and Brown (1972) showed that surface area and latitude account for 90 percent of the variation in numbers of species of fishes in lakes.

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The number of species of fishes at a freshwater stream locality depends on the volume, temporal stability, and spatial heterogeneity of habitats (Evans and Noble 1979; Gorman and Karr 1978; Sheldon 1968). The species richness in a drainage is influenced by the same factors and also by the nature of habitat connections that allow colonization among localities and drainages (Horwitz 1978; MacArthur and Wilson 1967). Volume and connectedness affect species richness indirectly by their effect on habitat diversity and colonization rate.

Desert fishes provide an opportunity to examine the relative effects of these ecologic and biogeographic factors because fish habitats in arid lands are subject to extreme reduction and fluctuation. The deserts of western North America offer an additional dimension for study: parts of the evolutionary and ecological history can be inferred from paleontological and geological evidence.

This study tests several propositions about the interaction of habitat volume, climate, geography, and time in the regulation of fish species richness, life histories, and body size in arid lands:

1. Habitat volume is a dominant determinant of species richness in fluvial freshwater fishes. It is controlled by interaction of precipitation, evaporation, groundwater geology, and geographical relief.

2. Fluctuations in volume cause local extinctions, but colonization enables species numbers to approach equilibrium in proportion to the volume and persistence of habitats that connect the localities. This is a form of the extinction-colonization hypotheses of MacArthur and Wilson (1967). It and the preceding postulate must be considered in the context of the species-area relationship (Levins and Heatwole 1963; MacArthur and Wilson 1967).

3. Two contrasting life-history responses to fluctuating aquatic environments in arid regions are reduction of adult body size because of increased early investment in reproduction and increased adult body size because of uncertain offspring survival relative to adult survival.

COMPARISONS

The fish fauna studied here is that of the cold deserts of the US intermountain west. [The warm-desert fishes are treated by R. R. Miller and M. L. Smith in this volume.] For comparison, observations of fishes and habitats of the Paraguayan Chaco are also presented. The Chaco of Paraguay is one-fourth the size of the intermountain cold desert; each is a part of a larger arid region. The Chaco is warm; the intermountain cold desert is defined to exclude its warmer extension to the south. The Chaco is flat and connected to a great fluvial system; the intermountain cold desert is traversed by rows of north-south trending mountain ranges and shows corresponding isolation among its basins. The dry seasons of the two regions are similar in length and precipitation but the wet seasons in the Chaco receive more rain. The species richness in the two areas is similar in the dry but different in the wettest sections.

The Intermountain Cold Desert

For the purposes of this study this region is defined as those lowland areas of the Basin and Range Province of the western United States in which the annual rainfall is less than 40 cm, the mean January temperature is less than 0°C, and the mean annual number of days with a minimum temperature as low as 0°C ranges from 60 to about 210. Included are the lowlands of California east of the Sierras and south to Death Valley, Nevada north of Las Vegas, northern Arizona, northwest New Mexico, western Colorado, Utah, southwest Wyoming, the Snake River Plain of Idaho, southeast Oregon, and the strip of central Oregon and Washington east of the Cascades (Figure 1). The elevation generally ranges from 600 to 2400 m, with extremes from -85 to 4000 m (but areas above 2400 m are excluded from most of this analysis). Most of the area is between 35° and 45° N latitude.

From the Climatic Atlas of the United States (US Department of Commerce 1968, pp. 1-23) we can characterize the dominant climatic feature of the region as

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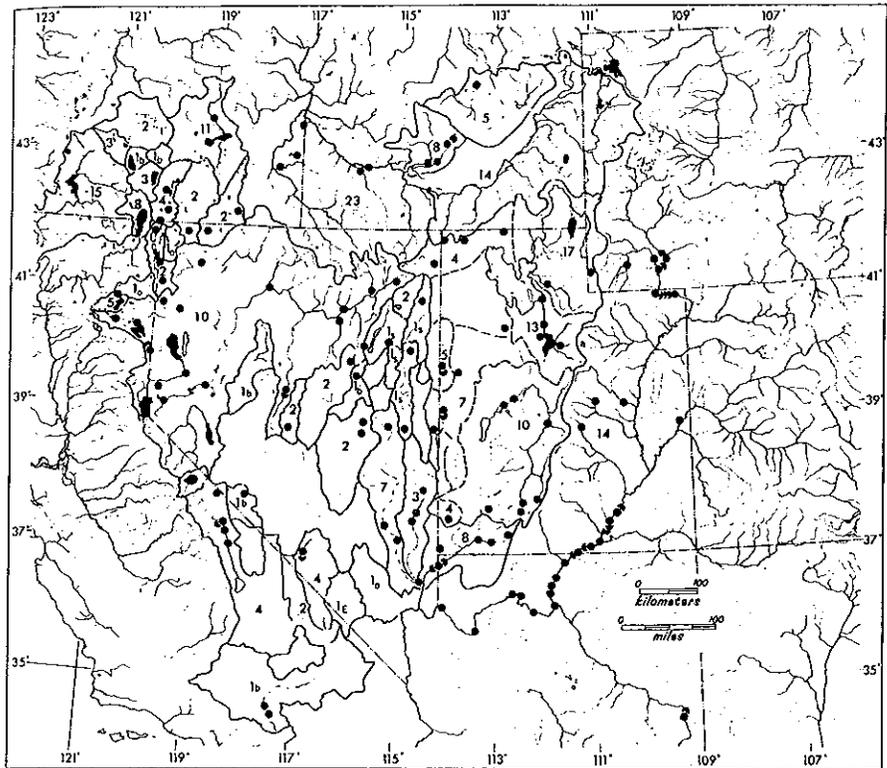


FIGURE 1. The intermountain cold desert (sampling area marked with round symbols). Numerals indicate numbers of native in each basin.

its extreme daily temperature fluctuation; the variation is 10 to 20°C (usually 14 to 17°C) in the spring and 14 to 25°C (usually 17 to 22°C) in the summer. The normal daily ranges are consistently the highest in the United States. The mean annual lake evaporation ranges from 86 cm on the Snake River Plain to 218 cm in Death Valley and usually between 100 and 150 cm over most of the region. Summer precipitation is low, usually 0.5 to 1.5 cm/month (in contrast to the monsoonal deserts to the southeast, which have about four times that amount). The winter precipitation is slightly higher but still usually less than 2.5 cm month⁻¹. The mean annual runoff is generally less than 2.5 cm except in the uplands (Langbein et al. 1949).

The Paraguayan Chaco

The Chaco is the northwest portion of Paraguay, an area of 246,925 km² west of the Paraguay River (Figure 2). It lies between 19 and 25°S latitude and merges to the south with the Chaco Austral of Argentina. The flat topography ranges from 64 to 350 m in elevation. Most of the fish occur in the east below 100 m. Topsoil is derived from sandy alluvium and the vegetation is xerophytic.

Mean annual temperatures range from 24 to more than 26°C; the extremes are -5 to 44°C (Sanchez 1973). The warmest months are December to February. The mean annual rainfall is 30 to 145 cm, graded from the dry northwest to the moist lowlands along the Paraguay River. Drought occurs annually from May to September, with a peak in August. Records show a range of 15 to 367 days per season with no recorded rainfall; zero precipitation is shown for 38 percent of the August entries and less than 2 cm precipitation is recorded for 75 percent of the August entries (Gorham 1973).

Low dry-season precipitation (0.5 to 6.5 cm) and high temperature fluctuations are aspects comparable to the intermountain desert of the United States. Important differences in the Chaco are the higher winter temperatures, the greater summer precipitation, and the summer connections of all habitats to the Paraguay system because of the flat topography. The last distinction has the most important impact on fish distribution and species richness.

GEOLOGIC AND CLIMATIC HISTORY

Intermountain Cold Desert

Two distinct geologic provinces make up this region: the Basin and Range (and associated Snake River Plain), and the Colorado Plateau. These are partly separated by the Wasatch Mountains in central Utah. The Rocky Mountains form the eastern boundary, the Idaho batholith a part of the northern boundary, and the Sierras and Cascades make up the western boundary

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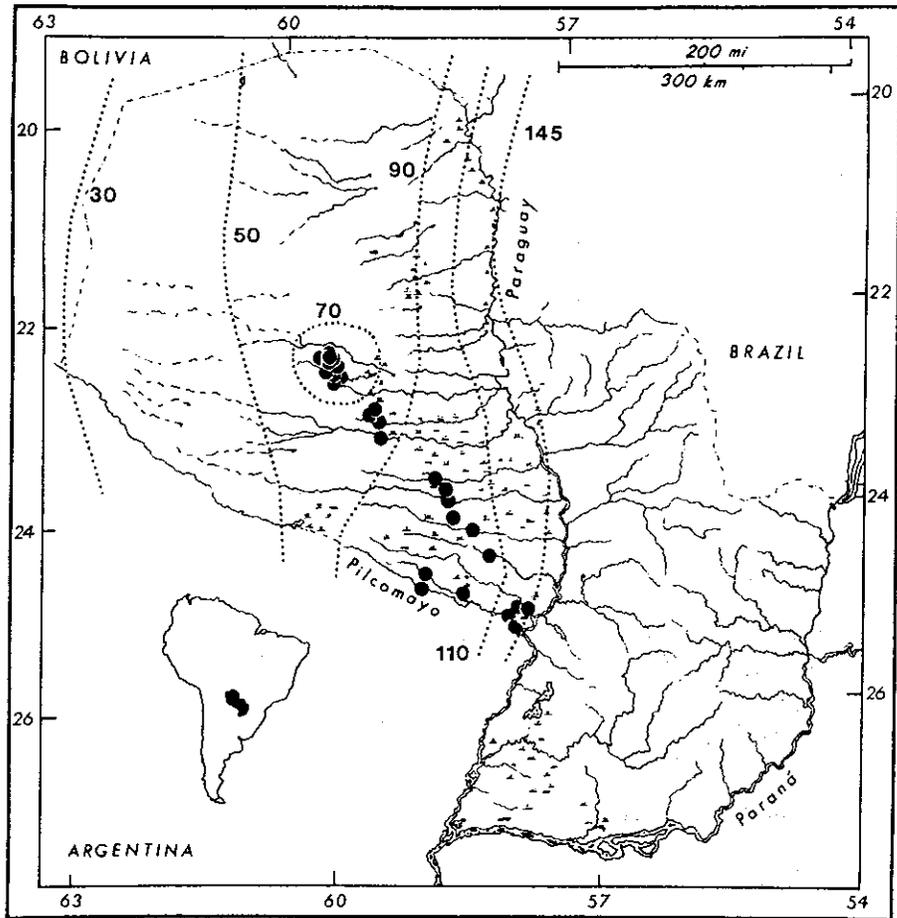


FIGURE 2. Map of Paraguay. Round symbols indicate sampling localities in the Chaco (west of the Paraguay River). Dotted lines show rainfall isoclines (in cm precipitation).

and the all-important barrier to the moisture of Pacific air masses. The present topography of the Great Basin and Snake River Plain began with rifting and extensional faulting 14 to 17 million years ago (Zoback and Thompson 1978). A significant shift toward a cooler, drier climate occurred at about the same time according to paleobotanical evidence (Axelrod 1950,

1956, 1968; Chaney 1944; Dorf 1930; Smiley 1963). Western US fossil fish records from the same time indicate broader distribution patterns than in any subsequent period (Smith and Miller in press).

Differentiation of the Colorado Plateau and Basin and Range Provinces began with basin and range faulting accompanied by uplift and (probably) increased precipitation in western Colorado (Larson et al. 1975). Connection of the upper Colorado drainage with the lower Colorado drainage to the Gulf of California occurred at least 3.3 million years ago (Lucchitta 1972). The time and location of connections of upper Colorado River waters to the lower Colorado (above the Lake Meade area) in the intervening period is problematical (Hunt 1969; Lucchitta 1972). Pliocene lakes, however, were important features of the drainage in northern Arizona (Uyeno and Miller 1965).

Subtropical climates were gradually replaced by warm temperate climates during the late Miocene through the Pliocene (Dorf 1959) as basin and range faulting continued to increase the isolation and internal drainage of the Great Basin and parts of the Colorado system. The elements of intermountain desert vegetation were assembled by response to aridity, at least in the lowlands and on drier slopes, through the Miocene to late Pliocene (Axelrod 1950, 1956).

Glaciers existed 3 million years ago in the Great Basin headwaters of the Sierras (Curry 1966). Because the paleobotanical evidence indicates warm temperatures accompanied by dry climates, the contemporary existence of widespread lake deposits and onset of montane glaciation seem to require much lower local evaporation rates; specifically, cool summers. Geological evidence (Longwell 1928; Mannion 1962) also indicates dry climates. Even during the subsequent Pleistocene pluvial episodes the precipitation was less than twice that of today (Snyder and Langbein 1962). Many studies of pluvial cycles in relation to lower temperature and higher precipitation are reviewed by Morrison (1965) and refined by Brakenridge (1978). In general, it is clear that lake waters were not derived from glaciers; it seems likely that precipitation was modestly increased and that low summer temperatures and lower

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evaporation were important factors. Northern occur-
 rences of cold-intolerant fossil reptiles also support
 the conclusion that climates were more equable than
 today until late in the Pleistocene (Hibbard 1960; Van
 Devender and Spaulding 1979; Van Devender and Wiseman
 1977).

A climatic mechanism offered by Bryson and Wend-
 land (1967) involves the exclusion of arctic air from
 middle latitudes by continental ice sheets and local
 adiabatic warming of drainage winds off the ice.
 Morrison (1965), on the basis of evidence of weathering
 profiles, erosion, and surficial deposits in relation
 to pluvial and glacial evidence, suggests that the
 typical cycle began with cool-dry conditions at the be-
 ginning of an interpluvial-interglacial and progressed
 through warm-dry, warm-wet, cold-wet (beginning of
 pluvial-glacial), cool-moist, then back to cool-dry.
 Examination of O^{18} curves (Emiliani 1972) has sug-
 gested that glacial episodes were several times as long
 as interglacials. Paleolacustrine data assembled by
 Morrison (1965) seem to suggest that pluvials were
 often shorter than interpluvials. Certainly pluvials
 were frequently interrupted by desiccation episodes and
 stable lacustrine habitats were of relatively short
 duration, possibly less than 20,000 years (Emiliani
 1972). Pliocene lake deposits are more continuous than
 Pleistocene, which indicates longer duration of stable
 habitats, at least on the Snake River Plain (Glenns
 Ferry Formation, Malde and Powers 1962) and in parts of
 the western and northern Great Basin.

In summary, despite evidence of remarkable fresh-
 water lakes, arid conditions have been at least as fre-
 quent: for fishes the history has been marked by scores
 of oscillations between pluvial- and aridity-dominated
 habitats.

The main effects of this instability on intermoun-
 tain fish distributions have been severe extinctions
 and barriers to colonization (Smith 1978). Species
 richness is unusually low in small drainages in rela-
 tion to large drainages (i.e., the species:area curve
 is steep) which indicates (1) higher extinction of spe-
 cies that were restricted to small populations during
 interpluvials and (2) low colonization because of

relief- and aridity-induced barriers to dispersal among basins. Interpluvial extinctions were more severe in the south than in the north. Northern and peripheral drainages have more species than southern and central basins and species distributions are much broader in the northern parts of the region; this indicates freer dispersal. These conditions hold despite the fact that because of the relationship of temperature to elevation and latitude mountain barriers were (effectively) higher in the north and lower in the south (Smith 1978).

The Chaco

The first unmistakable evidence of desert and semidesert conditions in southern South America occurs in the Pliocene (Solbrig 1976). At this time the final uplift of the Bolivian Cordillera Central completed the topographic relief that began in the Miocene (Harrington 1962). Miocene climates represented continuing trends toward lower temperature and precipitation, but the climate was more humid than today. Grasslands were increasing, forests decreasing (Solbrig 1976). With the establishment of the vast alluvial plain in the rainshadow of the Andes by the end of the Pliocene the present setting was nearly complete. At least three major montane glacial stages constituted Pleistocene interruptions, but the effect on fishes in the Chaco was probably minor because of the distance and difference in elevation. Examination of numerous exposures along the southeastern trans-Chaco highway in August 1979 revealed no lacustrine beds. In all probability the present pattern of annual flood cycles that swell the Paraguay tributaries in the wet season, then dry them in the winter, also characterized the Pleistocene. Long-term variations in temperature and habitat persistence no doubt occurred but probably did not cause long-term isolation and extinction of fish species as in the Great Basin. From the standpoint of the fishes the most important aspects of the Chaco environment are continuous connections to a central habitat system and the seasonal existence of widespread, shallow, nutrient-rich swamps.

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Fossil Fishes

About 25 Miocene, Pliocene, and Pleistocene fish localities in the intermountain cold desert offer an opportunity to compare past environments and diversity with the present. High diversity evolved only in a few intermountain lacustrine environments, the richest being the Miocene and Pliocene lakes on the Snake River Plain (Kimmel 1975; Smith 1975). Historical data permit the evaluation of long-term ecology and evolution of species richness in the intermountain area.

CLIMATE, GEOGRAPHY, AND FISH SPECIES RICHNESS

Variables that influence fish species richness in streams are temperature, oxygen concentration, salinity, habitat volume, and heterogeneity, as well as (indirectly) precipitation, evaporation, elevation, stream order, and discharge. The extremes and predictability are probably more significant than averages (Fischer 1960).

Temperature

An unexpected result in the early stages of this study was the failure to find a major correlation between temperature (or its variance) and species number. The effect of elevation and temperature in the Basin and Range Province is not reflected in patterns of species richness. A major effect of temperature variation on fish species richness is probably demonstrable along a latitudinal gradient in the Mississippi basin but does not appear in the intermountain deserts because the effect of topographic relief on temperature, precipitation, and evaporation causes a strong negative correlation between temperature and habitat permanence (discussed below). In the Chaco temperature is higher in the north and species richness increases to the east. Scanty data on temperature extremes suggest a negative correlation between range of temperature and species richness.

There is no doubt that temperature is an important factor that affects the growth, metabolism, and distribution of fishes. Failure to find a positive temperature effect on species richness in the intermountain desert might reflect the history of extinction by desiccation in the south and substantial colonization by coolwater forms from the north (Smith 1978). The major effect of temperature on species richness is the local elimination of narrowly adapted species by extreme variations in temperature. The evolutionary significance of this phenomenon has been investigated by Brown and Feldmeth (1971) and Hirshfield et al. (1980).

Salinity

Salinity is important to desert fishes because of the high evaporative accumulation of dissolved salt. High salinity environments in both the Chaco and the intermountain deserts show reduced faunas, which usually consist mainly of cyprinodontids (e.g., Miller 1948). Extreme effects of salinity are seen in the fishless waters of the Great Salt Lake (Utah) and the middle Rio Pilcomayo of the Chaco.

Cyprinodontids are the most salinity-tolerant desert fishes (Renfro and Hill 1971). Their derivation from estuarine sister groups suggests that they are technically "preadapted" rather than "desert-adapted" to salinity (M. L. Smith, this volume).

Oxygen

One of the most discussed adaptations of arid-land fishes is the use of accessory respiratory structures to make use of atmospheric oxygen. Most of the species in the arid part of the Chaco show such adaptations (Carter and Beadle 1930, 1931). Examples include lungfish (Lepidosiren paradoxa), catfish (Hoplosternum, Pterygoplichthys), and characins (Hoplias). Even the cichlids when stressed readily lie at the surface to bathe their gills in oxygen-rich water. No similar adaptations, except physiological tolerances (Hirshfield et al. 1980) and behaviors for obtaining surface oxygen occur in desert fishes of North America despite

temperature is an important factor in metabolism, and distribution of a positive temperature in the intermountain region of extinction by substantial colonization north (Smith 1978). The species richness is the adapted species by extinction. The evolutionary significance has been investigated by Hirshfield et al. (1980).

desert fishes because of the presence of dissolved salt. Both the Chaco and the reduced faunas, which include minodontids (e.g., Millerichthys) are seen in the Salt Lake (Utah) and the Colorado.

most salinity-tolerant species (Miller 1971). Their derivation suggests that they are more than "desert-adapted" (Miller 1971).

adaptations of arid-land fishes include respiratory structures that allow them to breathe oxygen. Most of the species in the Chaco show such adaptations. Examples include lungfish, catfish (*Hoplosternum*), and minnows (*Hoplarias*). Even the minnows lie at the surface to breathe oxygen-rich water. No similar adaptations or physiological tolerances (Hirshfield 1978) are known for obtaining surface oxygen in the deserts of North America despite

their equal or greater antiquity. Furthermore, temperatures are higher in the Chaco and warm, shallow waters conducive to oxygen stress occur in all seasons: in the organic-rich swamps during the summer wet season and the drying pools of the (warm) winter. In the North American deserts drying pools and (high temperature) oxygen stress are generally restricted to the summer and moving (oxygen-enriched) waters are more constant in all seasons. In both regions, but especially in North America, recolonization after local extinction comes from oxygen-rich environments.

A possible historical reason for the absence of special desert adaptations in North American fishes, in contrast to mammals, for example (Mares 1976), is that their exposure to cool pluvial lakes at frequent geologic intervals and long-term persistence of cool running-water habitats has precluded consistent selection for such traits.

Habitat Size

The amount and persistence of fluvial habitat depends on the balance between precipitation and evaporation as well as groundwater and topographic control of discharge rate. Elevation is related to species richness only insofar as it is correlated with habitat size, temperature, and gradient. Stream order is equally indirect as a causal variable because its relation to species richness depends on its correlation with habitat volume, stability, and dispersal connections (Evans and Noble 1979; Horwitz 1978).

A test of the hypothesis that habitat size is a dominant determinant of species richness in streams might be conducted with measurements for many localities over all seasons. Presently available data (C. L. Hubbs seine collections from western United States, 1925-1945, and seine, electrofishing, and rotenone collections by the author and colleagues in western United States and Paraguay) allow examination of the effects of habitat size (estimated by habitat width) and a general index of regional water supply (precipitation and evaporation data from weather station summaries, the Climatic Atlas of the United States and Gorham

1973). Stream width is consistently related to other dimensional parameters (Leopold et al. 1964). Samples were taken in the dry season in both areas and include collections from streams, springs (US), and ponded sections of streams. Effects of springs and ponds on variations in width do not differ between the two areas. Introduced species are included in the totals because the question is ecological rather than historical. They are limited to North American samples, where except in trout streams their numbers are generally correlated with native species (Smith 1978).

Species number is significantly correlated with habitat width in both areas (Figures 3, 5). The number of species increases steeply in larger habitats, especially in the Chaco. There is considerable scatter in the data, especially in the Colorado drainage (Figure 3). The combined samples show a correlation of .58 ($p < .01$) between species number and stream width. The correlation is .71 ($p < .01$) in the Great Basin and Snake River drainage. On the other hand, the samples associated with the Colorado River drainage have a correlation coefficient of only .46 ($p < .01$). These samples include small streams near their confluence with the main river, sometimes with an inflated species number, as well as samples in the main channel of the Green and Colorado rivers, where species number is often limited by sand substrate and strong current.

Species number is not correlated ($r = .1$, $p = .3$) with precipitation in the Great Basin (plus Snake River Plain) and Colorado drainages (Figure 4). Nevertheless the graph is instructive. A few relatively high species numbers are found in the low-precipitation area of the graph, in large streams that flow out into the most arid sections of the region (upper left of Figure 4). By contrast there are 50 samples from small headwater streams in the moist upland watersheds (lower right part of Figure 4).

The role of evaporation in the interaction between precipitation, habitat size, and species number was tested by regression of species richness on a surface-water index. The index was computed as annual precipitation minus the square root of annual lake evaporation because evaporation is 2 to 10 times larger than

stently related to other (Smith et al. 1964). Samples in both areas and include springs (US), and ponded seeps (US), and ponded seeps (US) differ between the two areas included in the totals. The relationship is historical rather than historical. In the Great Basin and Snake River American samples, where the number of species is generally higher (Smith 1978).

Significantly correlated with stream width (Figures 3, 5). The number of species in larger habitats, especially in the Colorado drainage (Figure 3), shows a correlation of .58 between stream width and stream width. The relationship is significant in the Great Basin and Snake River drainage have a correlation of .46 ($p < .01$). These samples are near their confluence with an inflated species number in the main channel of the stream where species number is high and strong current.

Correlated ($r = .1$, $p = .3$) in the Great Basin (plus Snake River drainage) (Figure 4). Nevertheless, the few relatively high species numbers in the low-precipitation area of the Great Basin (at flow out into the most upper left of Figure 4). Samples from small headwater watersheds (lower right

show the interaction between stream width and species number was not significant on a surface-precipitation computed as annual precipitation minus annual lake evaporation (about 10 times larger than

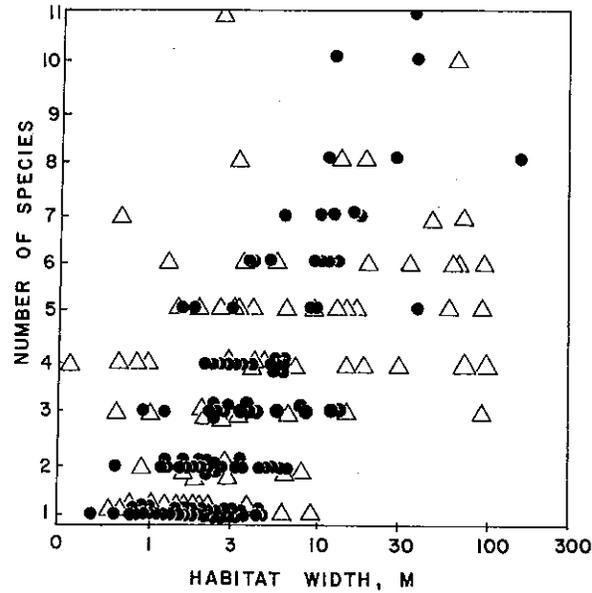


FIGURE 3. Number of species as a function of stream width for 183 localities in the intermountain cold desert. Great Basin and Snake River localities are solid circles, Colorado and adjacent localities are triangles. The overall correlation coefficient is .58 ($p < .01$).

precipitation in this region. The index is conformable with regional surface water but the relationship was not significant ($r = -.07$, $p = .3$).

In the Chaco the number of species is far greater and the contrast between small, fishless ponds and streams and large, species-rich habitats is more pronounced (Figure 5). The correlation coefficient between species number and habitat width is .32 ($p = .04$). The correlation is lower in the flat Chaco region because drying streams and their remnant, isolated ponds do not conform to the normal close relationship among channel dimensions in flowing streams. Furthermore, the samples were taken during the period of accelerated local extinction.

Precipitation is a more forceful factor in the Chaco. The correlation coefficient between species

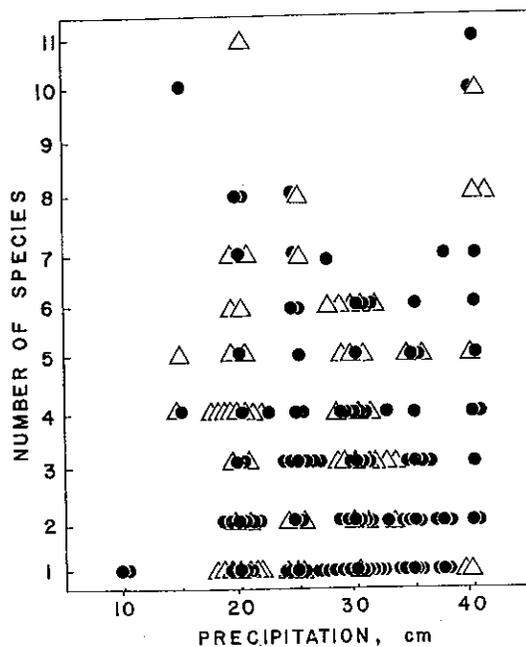
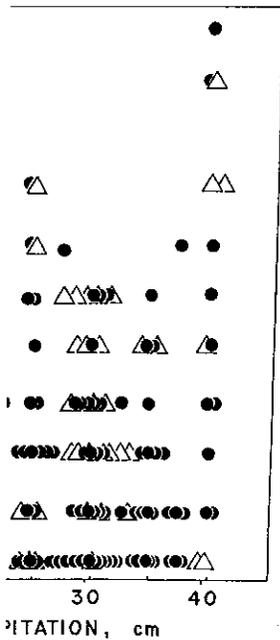


FIGURE 4. Number of species as a function of mean annual precipitation in the intermountain cold desert. Solid symbols are Great Basin and Snake River Plain localities; triangles represent localities in the Colorado and adjacent drainages.

number and precipitation is .77 ($p < .01$). A comparison of Figures 5 and 6 reveals that the smallest habitats, with few species, are in the driest areas sampled. (The slope of both Chaco regressions should probably be steeper; our samples underestimate the true species numbers in the largest waters.) When the log of habitat width is added to a stepwise multiple linear regression model, the partial correlation between precipitation and species number drops from .76 to .68, which indicates correlation of the independent variables. The coefficient of causation (multiple R^2) increases from .59 to .63. Species richness in the Chaco was also studied in relation to precipitation in the dry season, but the relationship was not significant ($r = .15$, $p = .36$).



ies as a function of mean intermountain cold desert. basin and Snake River Plain present localities in the ages.

.77 ($p < .01$). A comparison that the smallest habitats are in the driest areas with Chaco regressions should samples underestimate the true (largest waters.) When the log to a stepwise multiple linear correlation between precipitation drops from .76 to .68, of the independent variable of causation (multiple R^2) Species richness in the relation to precipitation in relationship was not signifi-

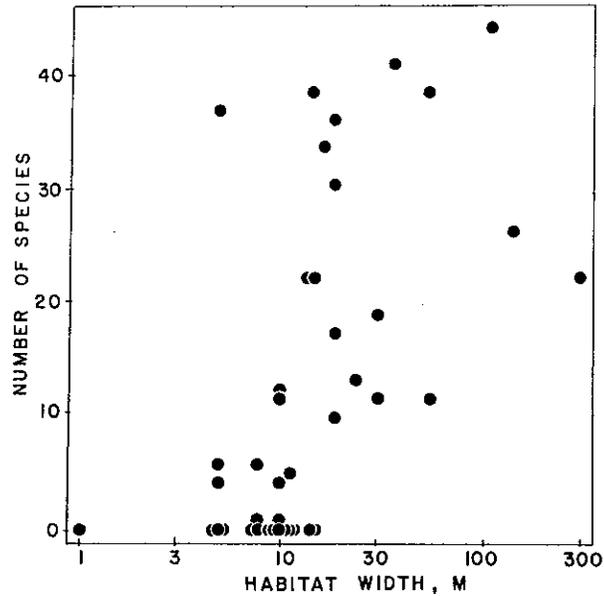


FIGURE 5. Number of species as a function of habitat width for 41 localities in the Paraguayan Chaco. The correlation coefficient is .32 ($p = .04$).

In summary, there is a strong relationship between habitat size and species number in both systems but the explanation is incomplete. The role of habitat size is complex in a way that involves dispersal and colonization.

Fluctuations in habitat size cause local extinctions, but recolonization occurs in proportion to the size and persistence of connecting habitats. That species richness in the intermountain region is low because of barriers to colonization is suggested by the steep species:area curve ($z = .59$ in Smith 1978, Figure 8). A similar line of evidence is the relative absence of rare species in truncated species-abundance curves for desert communities (Smith, unpublished data), demonstrated by Hubbell (1979) in a study of dry-forest trees.

The striking contrast in patterns of species richness between the Chaco and the intermountain samples is related to a simple but little recognized geographical

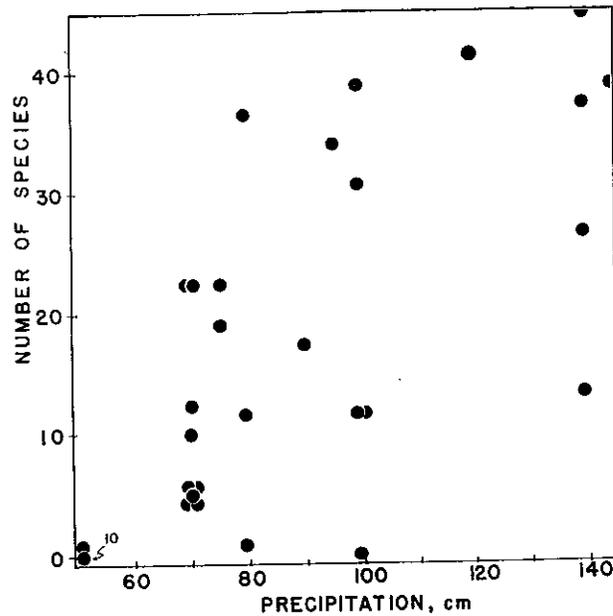
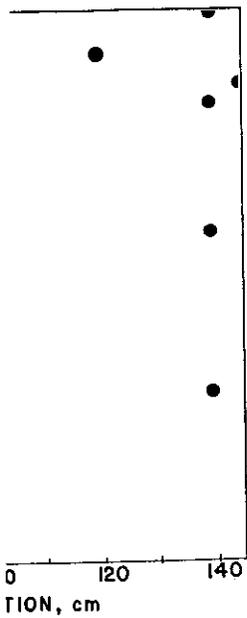


FIGURE 6. Number of species as a function of mean annual precipitation in the Paraguayan Chaco. The correlation coefficient is .77 ($p < .01$).

factor. In the intermountain deserts streams collect their waters in mountains with high precipitation and flow out onto low-precipitation alluvial plains and playas. In such cases the lower reaches are often the least stable and the least predictable with respect to their habitats and inhabitants. Local extinctions cannot be recolonized from a stable, main-trunk refuge because of the double isolation by desert and mountain barriers.

In contrast, the tributaries of the Paraguay head in flat, arid alluvial plains where the dry season reduces the apparent species number to zero. The streams then flow through increasingly wetter regions into the Paraguay River, a large stable habitat with potential for recolonizing almost any local extinction. Thus direction of flow relative to the precipitation gradient interacts with the effect of habitat volume to produce an impoverished fauna where the flow direction is



as a function of mean precipitation in the Paraguayan Chaco. The correlation coefficient is $r = 0.91$ ($P < .01$).

In the arid deserts streams collect water only during high precipitation and flow only on alluvial plains and floodplains. These reaches are often the most variable with respect to habitat characteristics.

Local extinctions can occur in the main-trunk refuge because of the desert and mountain habitats.

Species of the Paraguay headwaters are absent where the dry season reaches zero. The streams flow only in the wetter regions into the floodplains. The habitat with potential for local extinction. Thus the precipitation gradient of habitat volume to produce the flow direction is

wet-to-dry and a rich fauna where the direction is dry-to-wet.

Late Cenozoic Species Richness

The Late Cenozoic fossil record of fishes from the intermountain cold desert permits the examination of the effects of long-term and large-scale fluctuations in habitat size on species richness. Most of the fossil occurrences (Figure 7) are in lake deposits, whereas the comparisons emphasized above involve streams. Because lakes and streams in the same basins share most species, the comparison of species richness in and among basins is generally valid.

The hypothesis is that large habitat size promotes increased species richness by increased species packing and lower extinction rates. Instability of habitat volume causes local extinctions, whereas restriction of aquatic connections increases the likelihood of extinctions and decreases colonization. On the other hand, seasonality promotes selection for special life-history adaptations and semiisolation promotes evolutionary fixation of genetic traits. Therefore on the basis of the known geologic and climatic history we might predict high extinction rates or evolution of special adaptations and speciation, depending on the frequency of the fluctuations in volume of aquatic habitat. Seasonal fluctuations should have caused local extinctions and strong selective pressures; long-term fluctuations should have increased the breadth of the extinctions and the rate of speciation.

Two patterns, one geographic and one temporal, are shown in Figure 7 (and by comparison with Figure 1). First, there is a strong latitudinal gradient in species richness but its trend is opposite that of most such gradients. Second, the pattern of high species richness in the north (or at least in the Snake River Basin) has been characteristic of the region for all the Late Cenozoic. It has been shown that the present species richness at localities is correlated with habitat volume. This conclusion is strengthened by the historical trends in Figure 7.

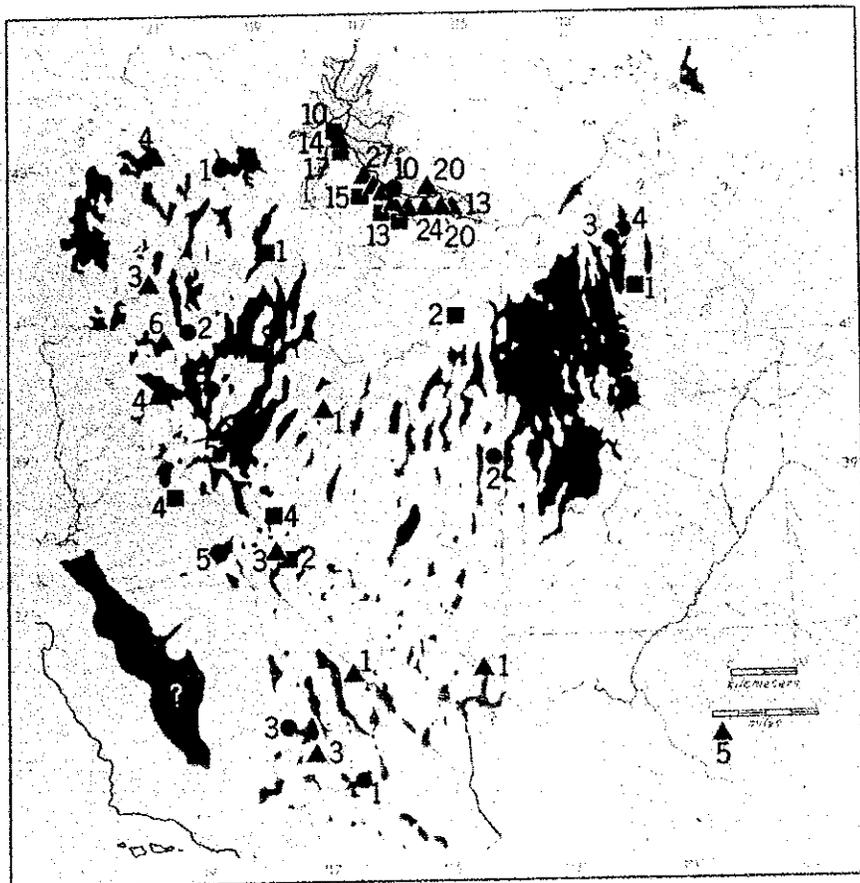
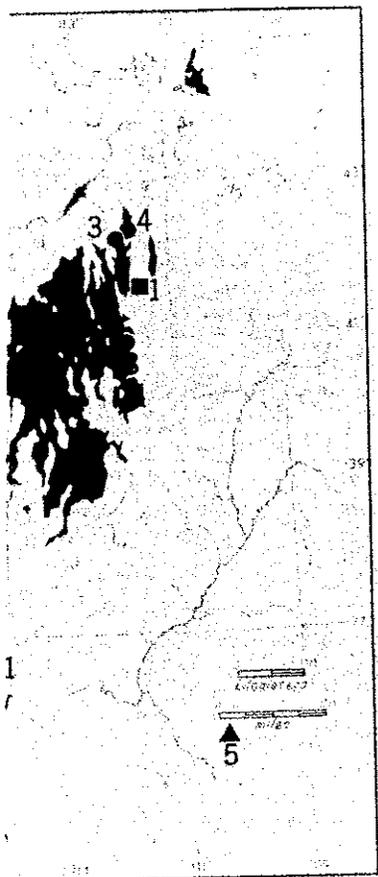


FIGURE 7. Maximum extent of Pleistocene pluvial lakes and some Pliocene lakes with estimates of species numbers in selected fossil lakes and stream systems. Data from published sources and work in progress (Table 1). Numbers are underestimates, probably by two or more species each, because small forms such as *Rhinichthys* and *Richardsonius* are rarely collected, although they were probably present.

Miocene localities in the Great Basin have one to four species, including trouts, minnows, and a sunfish. In the Snake River Plain we find 10 to 17 species (additional trout, salmon, *Esox*, minnows, suckers, and



Pleistocene pluvial lakes and stream systems. Data in progress (Table 1). Probably by two or more forms such as Rhinichthys collected, although they

Great Basin have one to 10, minnows, and a sunfish. find 10 to 17 species of minnows, suckers, and

sculpins). The Miocene Deer Butte and Chalk Hills formations on the Snake River Plain (Kimmel 1979) are extensive, thick sections which indicate large, long-term depositional environments and probably large, long-term lacustrine and fluvial habitats. The Miocene deposits in the Great Basin are less extensive and indicate smaller, less persistent bodies of water (Table 1). (An exception is a fauna, described by P. H. McClellan from the Salt Lake Group, which is related to the Chalk Hills fauna.) The rather limited depositional systems are probably due in part to the low Miocene relief.

Pliocene localities in the Basin and Range Province (5.5 to 1.7 million years ago) are also poor in species compared with the fauna of the Snake River Plain (Table 1). Glens Ferry lacustrine sites (Smith 1975) have up to 27 species; fluvial sites have 10 to 13 species. Again, the Basin and Range sites represent less extensive depositional systems. The Pliocene faunas differ from the Miocene by the addition of genera and species of whitefish, suckers, minnows, and sculpins. Boreal forms, such as Prosopium, Myoxocephalus, and other sculpins become conspicuous by their relative abundance in some deposits on the Snake River Plain, thus indicating cooler climates and aquatic connections to the north (compare with Axelrod 1968). At this time the number of species of fishes in the Glens Ferry Formation reached the maximum known for Late Cenozoic western North America. Geological evidence (Kimmel 1979) reveals that the Glens Ferry lacustrine system persisted at least one million years.

The close of the Pliocene on the Snake River Plain is marked by regression of lacustrine Glens Ferry deposition (Kimmel 1979) and depletion of fish species richness (Smith 1975), perhaps as the Glens Ferry lake began draining into the Columbia River system (previous drainage to the Pacific at least occasionally passed through southern Oregon or California (Kimmel 1975; Smith 1975; Taylor 1960; Wheeler and Cook 1954). Whatever the cause, the decrease in aquatic volume and species richness was roughly synchronous.

Pleistocene faunas (Table 1, Figure 7) are richer in association with large waters. Pleistocene deposits of the Bruneau Formation and the Glens Ferry Formation

TABLE 1. Known Species Richness of Late Cenozoic Fossil Localities in the Intermountain Cold Desert^a

State	Location	Formation	Species	Authority
Pleistocene				
California	Afton	Manix Lake	1	2
California	China Lake	?	3	3
California	Mono Lake	?	5	3
Idaho	Grandview	Bruneau and Glenns Ferry	10	1
Idaho	Swan Lake	-	3	1
Idaho	Lake Thatcher	Main Canyon	4	4
Nevada	Duck Valley	-	2	3
Nevada	Smith Creek Cave	-	2	1
Nevada	Pyramid Lake	-	3	1,3
Oregon	Fossil Lake	Unnamed	4	3
Oregon	Harney Lake	?	1	1
Utah	Bonneville	Bonneville? Draper?	8	6
Pliocene				
Arizona	Bidahochi	Bidahochi	5	7
California	Crowder Flat	Alturas	3	1
California	Furnace Creek	Titus Canyon	3	8
California	Honey Lake	Unnamed	4	9
California	Mohave Desert	Unnamed	1	8
California	Secret Valley	Unnamed	6	1
Oregon	Fossil Lake	Unnamed	4	3
Oregon	Adrian	Chalk Hills [Deer Butte Kimmel, 1975]	14	10
Idaho	Fossil Creek	Glenns Ferry	27	11
Idaho	Castle Creek	Glenns Ferry	24	11
	Browns Creek			
	Birch Creek			
	Shoofly			
	Poison Creek			
	Horse Hill			
Idaho	Sand Point	Glenns Ferry	20	11
	Bennett Spring			
Idaho	Hagerman	Glenns Ferry	13	11
Nevada	Esmeralda	Esmeralda	3	12
Nevada	Jersey Valley	Unnamed	1	13
Nevada	Logandale	?	1	1
Nevada	Mopung Hills	Upper Truckee	4	9

ite Cenozoic Fossil
Desert^a

ion	Species	Authority
ie		
Lake	1	2
	3	3
	5	3
u and Ferry	10	1
	3	1
anyon	4	4
	2	3
	2	1
	3	1,3
id	4	3
	1	1
ville? ?	8	6
ochi	5	7
as	3	1
Canyon	3	8
ed	4	9
ed	1	8
ed	6	1
ed	4	3
Hills Butte	14	10
[1, 1975]		
s Ferry	27	11
s Ferry	24	11
is Ferry	20	11
is Ferry	13	11
alda	3	12
ned	1	13
?	1	1
Truckee	4	9

TABLE 1. (Continued)

State	Location	Formation	Species	Authority
Miocene				
California	Bear Valley	Unnamed	4	1
Oregon	Trout Creek	Trout Creek	1	15
Oregon	Sand Hollow	Deer Butte	10	15
Oregon	Adrian	Chalk Hills	17	10
Idaho	Browns Creek	Poison Creek?	15	1
Idaho	Shoofly	Chalk Hills	13	10
Idaho	Horse Hill	Chalk Hills	13	10
Nevada	Esmeralda	Esmeralda	2	1,16
Nevada	Humboldt	Humboldt	2	1
Nevada	Rabbithole	?	1	17
Nevada	Stewart Spring	?	4	1
Nevada	Truckee	Truckee	5	14
Utah	Cache Valley	Salt Lake	1	18

^aSources: (1) unpublished data; (2) Blackwelder and Ellsworth (1936); (3) Miller and Smith (1981); (4) Bright (1967); (5) Meade and Van Devender collection; (6) Smith et al. (1968) and Madsen collection; (7) Uyeno and Miller (1965); (8) Miller (1945); (9) Taylor and Smith (1981); (10) Kimmel (1975); (11) Smith (1975); (12) LaRivers (1962); (13) Lugaski (1979); (14) Bell (1974) and subsequent collection; (15) Smith and Miller (in press); (16) LaRivers (1966); (17) LaRivers (1964); (18) Uyeno and Miller (1963).

near Grandview on the Snake River Plain, although depauperate, are the richest observed in the intermountain area. Pleistocene lakes in this area were not so permanent as the earlier lakes. Lake Bonneville was the largest and has the richest fauna outside the Snake River Plain. Nevertheless it is depauperate for its size, no doubt because of its long-term instability. Lake episodes were usually too short to permit extensive evolution and (or) interpluvials were arid enough to cause severe extinction. The species richness associated with other Pleistocene pluvial lakes indicates the same restrictions.

The negative effect of isolation on species richness is seen in the low numbers at southern localities, but not in historical trends. There is no evidence of more species in southern Miocene samples, even though distributions of Miocene species indicate fewer barriers and the paleobotanical record indicates more precipitation and moisture. Southern localities are consistently poor in species (Figure 7). The Miocene vegetation of southeastern Nevada was an oak sclerophyll woodland that implies a cool temperate climate with perhaps 760 mm annual precipitation (Axelrod 1956, 1979). The elevation was possibly 760 to 915 m, with low relief (Axelrod, 1956, 1979). The low fish species richness in the Miocene suggests seasonal aridity and perhaps isolation from the rich fauna of the Snake River Plain.

By Pliocene time some aquatic connections had occurred between the northwest and southwest Great Basin with the establishment of *Chasmistes* as far south as China Lake (Miller and Smith 1981; Taylor and Smith 1981). The biogeographic track from the southwest Great Basin northward along the Sierras, eastward across the Snake River Plain, and south into northern Utah was described by Taylor (1960) on the basis of the distribution of mollusks and *Chasmistes*. This pattern requires at least brief absences of topographic barriers, and therefore establishes the significance of ecological barriers to southern dispersal of many northern species that did not move south. The ecological barriers probably involved low, unstable, warm-water habitats. Large-scale fluctuations characterized the

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pleistocene. The pluvial lakes were surely stable habitats, optimal in almost every way. Their low species richness can be explained only by barriers between basins and failure of pluvial conditions to persist long enough to permit much species evolution.

The Recent fauna includes some taxa that apparently were evolved locally at some unknown time in the late Cenozoic; for example, the Prosopium species flock in Bear Lake; species differentiation in Gila, Ptychocheilus, Richardsonius, Catostomus, and Chasmistes; the endemic genera of minnows, Iotichthys, Eremichthys, Relictus, Moapa, and the Plagopterinae; the cyprinodontid genera, Empetrichthys and Crenichthys; and the species diversity in Cottus and Cyprinodon. Of this diversity three large groups contain some possible examples of Pleistocene isolation and speciation: the Great Basin and related Catostomus (subgenus Catostomus), the species of Lepidomeda (Miller and Hubbs 1960), and the species of Cyprinodon (Miller 1948). In each of these cases the species are similar, allopatric, and probably lacking in genetic isolating mechanisms. Data that indicate a basis for questioning the level of species evolution in Cyprinodon were presented by Turner (1974), Turner and Liu (1977), Cokendolpher (1980), and Stevenson (1981). The karyotypes of Lepidomeda were shown by Uyeno and Miller (1973) to be similar. Many species pairs of Catostomus in and around the Great Basin are not completely separable by known characters even though intermittent geographic separation surely dates back into the Pliocene or early Pleistocene (M. L. Smith, this volume). These observations do not detract from the importance of the differentiation in Cyprinodon, Lepidomeda, and Catostomus. If these genera provide examples of Pleistocene speciation, it is critical that the amount of differentiation be documented.

HABITAT VOLUME AND BODY SIZE IN INTERMOUNTAIN FISHES

It is a common observation that individuals of many species reach larger sizes in larger streams. Not only is growth potentially faster when greater input

from upstream provides more ration but individuals in larger, more stable waters may live longer because they are less subject to seasonal mortality. Some fishes may also respond to restrictive living space by growing less, regardless of ration. Although it is unclear how much of the correlation between body size and habitat size is due to faster growth and how much to longevity, it is even less clear how much of the observed pattern is heritable adaptive variation in age or size of maturity and how much is opportunistic adaptation to local resources.

It may be assumed that the supply of ration in a stream is proportional to the normal volume of habitat upstream (minus food extraction by competitors). The density of food and competitors is not precisely proportional to volume because the seasonal fluctuations in fish and invertebrate biomass are not coincident with each other or volume. Two additional qualifications affect productivity in desert streams. First, input of terrestrial leaf litter and insects is less than in mesic climates. Second, streams in arid lands carry more sand and consequently provide less favorable substrate for bacteria, algae, diatoms and invertebrates. Extreme cases occur when discharge is sufficiently high, in relation to channel dimensions, to move bedload; thus eliminating habitat for periphyton and benthos (e.g., in the Colorado River). The fishes that occupy these streams are subject to low ration, swift current (relatively unavoidable in the main channels of the Green and Colorado), and large seasonal fluctuations. Here, in contrast to most streams, gradients in productivity and stability may be reversed: density of benthic organisms is higher at higher elevations (and steeper gradients) because of more organic input and more stable substrate and also because rainfall, evaporation, oxygen, and groundwater supply (and its effect on temperature) are usually more stable nearer the mountains.

A consequence of the steep ecological gradient is sharp species segregation. Higher elevations require adaptations to low temperatures, short growing season, current, and low ratio of living volume to substrate. By contrast, lower, seasonally larger habitats have

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more species, higher temperatures, and a longer growing season but lower food density. Optimal habitat for most species occurs in intermediate reaches in the zone of transition of gradient, substrate, and temperature.

In light of these considerations, some influences on body size may be explored: (a) ration and temperature are major determinants of growth rate (Brett et al. 1969); (b) length of the growing season determines yearly increments (Gerking 1966). The first year's growth is especially important to survival and reproduction. Growth during the second and subsequent years depends on the effects of survival probability on reproductive investment (Hirshfield and Tinkle 1975; Murphy 1968; Williams 1966).

1. High adult density is unfavorable for juvenile survivorship, especially when both eat the same food (e.g., microvores) or when cannibalism is common. When these or other factors contribute to relatively low juvenile survivorship selection favors later reproduction, iteroparity, and long-term investment in large numbers of potential offspring.

2. Low adult survivorship caused by seasonal reduction in habitual size favors individuals that reproduce early in life.

3. Intermediate responses might be favored in intermediate environments or under irregular schedules of seasonal fluctuation, but divergence from intermediacy is caused by positive feedback effects within the two alternatives: In (1) longevity leads to larger size, which in turn increases longevity in the presence of factors (such as predators) that disadvantage small individuals. In (2) low adult survival favors early reproductive investment, which subtracts from future growth and leads to small size and shorter life span (Constantz 1979).

Body Size and Habitat Width

Maximum adult size was recorded for samples of several stream species in the University of Michigan Museum of Zoology. (Minimum adult size is more important but harder to measure reliably in late summer

samples; thus the amount of available data is reduced. Average adult size is difficult to for the same reason. Maximum adult size is less ambiguous and was not significantly related to sample size in the examples given.)

C. L. Smith (1980) presented evidence of interaction between maximum size (per species) and community structure in fishes inhabiting patch reefs. This interaction is not demonstrable in my data. Instead maximum adult size is usually correlated with habitat dimensions (Table 2, Figure 8). The variation in body size attributable to stream width (log transformed) ranges from 8 to 5 percent (R^2) in the significant samples. In those species that display the correlation the strength of the response is proportional to adult body size: the smallest species (e.g., Rhinichthys) remain relatively small in large streams (where they are common); larger suckers (Catostomus) are larger at maturity and show a proportionally larger response to increase in habitat volume. Adults of the larger species are rarely present in small tributaries, although young are usually found in the same streams as their parents (often in shallower waters).

The large species are absent from most small isolated drainage units in the Great Basin. The fossil record suggests that the species remaining in these units are the survivors of postpluvial extinctions. Thirteen single-species survivors in drainage basins (Figure 1) are small fishes: six Gila bicolor, four Relictus solitarius, and three Rhinichthys oculus. This evidence indicates disproportionate extinction of large-bodied species in small habitats and small basins.

Recent samples demonstrate a plasticity that implies selection against large individuals in small habitats. Gila bicolor (including G. alvordensis) and Gila atraria show nearly identical responses to habitat size (Table 2, Figure 8). These species are ecologically and morphologically similar, but their lineages have been separated since the late Miocene, which suggests parallel environmental control of body size in these forms. These species are capable of maturing at small size in small creeks and springs (35 and 62 mm SL; Table 2). In large rivers and lakes, however, they

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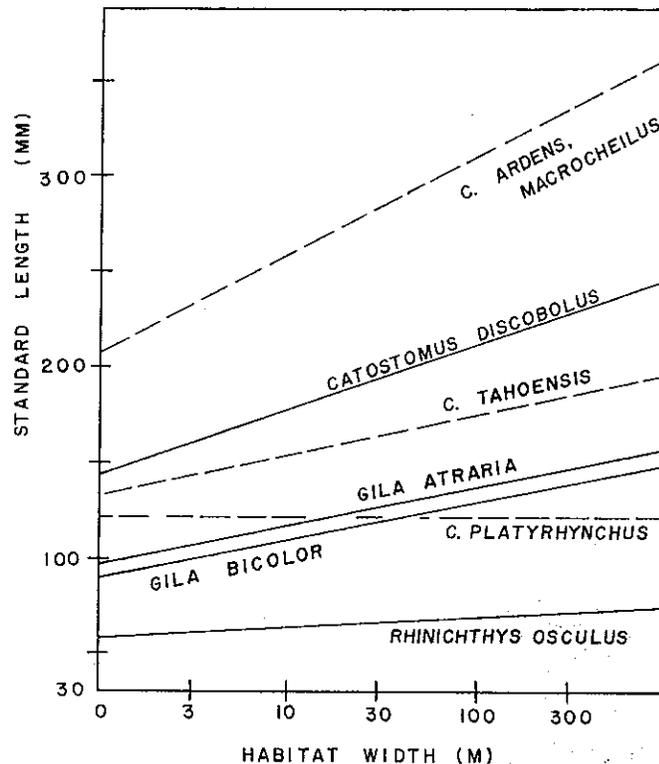


FIGURE 8. Regression of maximum adult size (in each sample) against habitat width. Solid lines are significant; dashed lines not significant (Table 2).

mature later, at lengths of more than 150 mm. *Gila atraria* may live as long as 11 years and grow to more than 400 mm in SL in one of its largest habitats, Bear Lake, Utah and Idaho (Sigler and Miller 1963).

The smallest minnow in North America is a close relative of *Gila*; it lives in shallow waters in the Bonneville Basin. *Iotichthys phlegethontis* matures at about 25 to 30 mm SL and rarely grows larger than 50 mm SL. It is not variable in size and not widespread. *Ptychocheilus*, which includes the largest minnows in North America, inhabits coastal streams from central California to British Columbia and the Columbia and Colorado drainages. *Ptychocheilus* formerly

Table 2. Relationship Between Maximum Adult Size per Sample and Habitat Width in Several groups of Intermountain Fishes

	K (Samples)	Average Maximum Size	Min-max. of Maximum Adult Size	Correlation (R) Between Maximum Size and Log Width	Intercept (SE)	Slope (SL) on Log Width (SE)	Significance
<u>Rhinichthys osculus</u>	192	63	35-107	.28	60(2)	5.3(2.5)	.03
<u>Gila bicolor</u>	121	110	35-319	.36	90(6)	21(5)	.00
<u>Gila atraria</u>	41	117	62-215	.39	97(9)	20(8)	.01
<u>Ptychocheilus</u>							
<u>oregonensis</u>	13	201	123-400				
<u>lucius</u>	6	448	376-730				
<u>Catostomus discobolus</u>	60	183	80-400	.32	145(17)	34(13)	.01
<u>Catostomus</u>							
<u>platyrhynchus</u>	52	120	69-178	.00	122(7)	0(8)	.97
<u>Catostomus tahoensis</u>	30	145	84-260	.30	132(17)	22(24)	.11
<u>Catostomus ardens</u>	15	261	149-485	.19	208(80)	54(78)	.50
and <u>macrocheilus</u>							

only adults are analyzed; measurements are in mm standard length.

<u>Tuclius</u>	6	448	376-730	.32	145(17)	34(13)	.01
<u>Catostomus discobolus</u>	60	183	80-400				
<u>Catostomus</u>							
<u>platyrhynchus</u>	52	120	69-178	.00	122(7)	0(8)	.97
<u>Catostomus tahoensis</u>	30	145	84-260	.30	132(17)	22(24)	.11
<u>Catostomus ardens</u>	15	261	149-485	.19	208(80)	54(78)	.50
and <u>macrocheilus</u>							

^aOnly adults are analyzed; measurements are in mm standard length.

inhabited the Great Basin but not in Recent time. It is excluded from small waters by ecological requirements related to size.

Because of the correlation between temperature and elevation, northern fishes (trout, whitefish, and sculpins) are the primary inhabitants of mountain headwaters in the cold desert. Trout and sculpins are small macrovores in desert streams. Trout are active mid-water swimmers; sculpins are negatively buoyant, benthic predators. Trout show size modifications in different habitat sizes (about 150 to 750 mm SL); sculpins remain small, like Rhinichthys, which are also negatively buoyant benthic fishes. Whitefish (Prosopium) are medium-sized, neutrally buoyant predators on small invertebrates. They appear to have a modest size response. Rhinichthys cataractae, like Prosopium williamsoni, inhabits lower montane, high-gradient streams. Rhinichthys cataractae is also a predator on small invertebrates; it is negatively buoyant and restricted in size.

A cross comparison of Salmo, Prosopium, Cottus, and Rhinichthys cataractae reveals an important principle concerning body size in freshwater fishes (Table 3). Benthic forms (Rhinichthys and Cottus) are smaller and less opportunistic in growth than their less benthic ecological counterparts, probably because their reduced mobility reduces their ration and increases their vulnerability to predation.

Most mountain suckers (Catostomus, subgenus Pantosteus, Tables 2 and 3) occupy the middle reaches of northern desert streams, where temperature, gradient, current, and substrate are intermediate; they are negatively buoyant benthic microvores. Most species are small and show little response to habitat size (see platyrhynchus, Table 2). Catostomus (Pantosteus) discobolus, and columbianus, however, inhabitants of the Colorado and Snake rivers (and some nearby systems), show a definite size response (see discobolus, Table 2). Southern populations (C. plebeius, Mexico) are small-bodied inhabitants of higher (cool) headwaters. Species of the subgenus Catostomus are large, benthic microvores with large swimbladders and show only a suggested size response, but the sample sizes

TABLE 3. Examples of the Relationship Between Buoyancy and Size Response^a

Group	Food and Feeding	Buoyancy and Habit	Size and Size Response
<u>Salmo</u>	Macrovore; large jaws	Neutrally buoyant; midwater	Potentially large or small; opportunistic
<u>Cottus</u>	Macrovore; large jaws	Negatively buoyant; benthic	Small; limited variability
<u>Prosopium</u>	Small invertebrates; small mouth	Neutrally buoyant; midwater	Medium and large; limited variability
<u>Rhinichthys</u>	Small invertebrates; small mouth	Negatively buoyant, benthic	Small; limited variability
<u>Catostomus (ss)</u>	Microvore; benthic	Semineutrally buoyant; semibenthic	Medium to large; limited variability
<u>Pantosteus</u>	Microvore; benthic	Negatively buoyant; benthic	Small to medium; large spp variable

^abenthic fishes tend to be smaller than their less benthic ecological counterparts and their less benthic relatives.

are inadequate. Other fishes of the intermountain desert (except endemics of large lakes) are small. They inhabit small waters or are benthic.

The fossil record offers an interesting comparison. Many of the above genera (Prosopium and other salmonids, Ptychocheilus, Catostomus) grew much larger in Pliocene Lake Idaho (Smith 1975) than anywhere in North America today or in the Pleistocene. Benthic species such as sculpins were only slightly larger. Pleistocene Lake Bonneville (Smith et al. 1968), though large, does not appear to have had larger fishes than modern intermountain lakes, but the reasons are not known.

In summary there is a tendency for fish that occupy large habitats to respond ecophenotypically with extended growth and large size. Conversely, in small habitats these species may mature early and fail to reach large size. Benthic fishes, cyprinodontoids, and some minnows are invariably small. The explanation of this phenomenon requires consideration of reproductive life history.

Life history

It is significant that the tendency for large-volume habitats to produce large fishes may be as pronounced in the intermountain desert as it is in mesic climates. This suggests that productivity and ration do not govern the phenomenon but that life-history adaptations to length of the growing season and mortality schedules may be the primary determinants. Specifically, irrespective of ration and temperature, size seems to be determined by the effect of mortality schedules on early versus late breeding. Whether ration is abundant or minimal, low adult mortality will lead to selection for iteroparity and large size, as illustrated by Gila, Ptychocheilus, and suckers in the Colorado River. In habitats of all sizes selection will favor reproduction by one-year-olds if seasonal reduction in habitat repeatedly causes heavy mortality after a season of substantial growth. This is illustrated by stream fishes in the desert portions of the Great Basin.

Medium to large; limited variability
Small to medium; large spp variable

Semineutrally buoyant; semibenthic
Negatively buoyant; benthic

Microvore; benthic
Microvore; benthic

Catostomus (ss)

Pantosteus

^aBenthic fishes tend to be smaller than their less benthic ecological counterparts and their less benthic relatives.

If adult mortality is variable because of unpredictable variation in the severity of seasonal fluctuations, individuals that invest in early reproduction will leave more descendants after destructively dry years; those that grow larger and produce more offspring later will leave more descendants in a series of wet years. In a postpluvial transition period such as the present both genotypes could be present. This is a possible explanation of some of the growth and reproductive plasticity among and perhaps within the populations discussed.

The extreme responses to annual fluctuation in aquatic habitat, aestivation and annual reproduction with dry-season survival as eggs only, has not evolved in North American desert fishes, despite the antiquity of desert climates. In the Chaco lungfish and cyprinodonts exhibit these responses to dry seasons, even though desert climates may be less ancient in South America. It is possible that the pluvial periods have interrupted evolution of these adaptations in North American deserts. Also, because of topographic relief and its regulation of groundwater, headwaters and springs are among the more stable habitats, whereas in the Chaco headwaters are the least stable.

In limited examples adaptations to survive dry seasons in the egg stage may release cyprinodonts from the small size and early reproduction syndrome that characterizes them elsewhere. Wherever the dry season is highly predictable and the wet season favorable for rapid growth, early reproduction (more than one generation per season) may not be so successful as will larger numbers of eggs immediately before desiccation. In such conditions cyprinodonts in the Chaco may reach lengths of 75 mm SL, which is somewhat larger than they become in habitats that favor earliest reproduction.

The other major adaptation to dry seasons is migration. Avoiding desiccation by roundtrip alternation of habitats is a common adaptation of inhabitants of large river systems with headwaters in arid lands (Lowe-McConnell 1964). In intermountain desert fishes migration is not well studied, but it seems to be related to choice spawning sites rather than desiccation avoidance. Because of the relationship between

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swimming performance and body size, migration is limited to large, nonbenthic species that live in large habitats.

Emigration is a special problem. In fluctuating environments survival value could accrue to genotypes that show colonization behavior. This is the opposite of migration in that success depends on the probability of existence of an unoccupied environment more favorable for reproduction than the individual's birthplace. This probability is not insignificant in environments like the intermountain desert, where local extinctions are periodic. It may be predicted that such genotypes and behaviors will promote emigration of young fish and be accompanied by behavioral responses to evidence of relative permanence of habitat (e.g., aquatic plants) and population density.

DISCUSSION AND SUMMARY

Habitat size is the most important general factor in the control of survival, diversity, and life histories of desert fishes. Quantity of aquatic habit, however, though intuitively simple, is not easily defined or measured. A measure based on depth, though useful in certain systems (Sheldon 1968), is not reliable for many purposes because of the importance of substrate and productivity to most fishes (consider deep springs or the bathypelagic realm). Likewise, volume of water can be negatively correlated with volume of suitable habitat if the increased volume is moving through a confined channel, as in torrential rivers. A third unsatisfactory but simple measure, width of habitat, is used here as a first approximation of habitat size for desert stream fishes. Habitat width is regularly related to other measures of habitat size in streams; it fluctuates seasonally and allows comparison of seasonal variability.

Two arid regions are compared: the North American intermountain cold desert, where water originates on mountain islands and flows into lakes or temporary sinks, and the Paraguayan Chaco, where precipitation occurs during a hot, wet season and drains through

swamps and low-gradient streams, leaving fishes in a severe desert climate for about three months each year. The contrast allows elucidation of ecological and selective effects of variation in habitat size on colonization, extinction, and species richness.

The Chaco is subjected to severe annual extinction and massive annual recolonization. A comparable North American system was studied by Harrel et al. (1967). The drainage direction is from unstable dry to stable wet, and the colonization source is rich with species adapted to the productivity of the annually flooded arid lands. Species number is low where streams are small (or low) and high in large aquatic habitats. An average habitat has about 15 species, but variations of 0 to 40 occur geographically and annually.

In the intermountain desert severe extinctions also occur because of fluctuations in habitat volume. Recolonization is so restricted by barriers that many small basins are now fishless. Few samples contain more than seven species. Annual fluctuations are less severe in the intermountain desert because topographic relief ameliorates habitat volume somewhat by groundwater regulation. Recolonization is measured in geological time because of the geological barriers between drainage basins. Most of the colonization has been restricted in and among these basins over the last several million years. There is evidence of some colonization from the north (Smith 1975) and from west coastal lowlands (Bell 1974) in the Pliocene.

The Chaco and intermountain samples provide extreme examples of short- and long-term instability. The species richness at any locality in either place is a product of both scales of history. The steepness of the curves in Figures 3 and 5 reflects short-term fluctuations and adaptations (e.g., migration) to them. The striking difference in maximum species richness reflects the negative effect of long-term fluctuations and barriers to colonization in the intermountain desert.

The geological and fossil record suggests that the interaction of intermountain pluvial habitats and isolation during the Pleistocene might have produced considerable evolutionary differentiation. Such

leaving fishes in a three months each year. n of ecological and in habitat size on species richness. vere annual extinction n. A comparable North Harrel et al. (1967). nstable dry to stable is rich with species the annually flooded low where streams are aquatic habitats. An ies, but variations of annually. rt severe extinctions ons in habitat volume. by barriers that many Few samples contain fluctuations are less rt because topographic e somewhat by ground- n is measured in ge- ological barriers between colonization has been basins over the last is evidence of some th 1975) and from west the Pliocene. n samples provide ex- long-term instability. lity in either place is cory. The steepness of flects short-term fluc- , migration) to them. um species richness re- long-term fluctuations in the intermountain record suggests that n pluvial habitats and e might have produced ifferentiation. Such

differentiation exists and has been extensively documented (Hubbs and Miller 1948; Hubbs et al. 1974; Miller 1948, 1959; Miller 1965 and references therein; Smith 1966). Quantification of the amount of differentiation in relation to the duration of isolation will prove interesting. Indirect evidence presented here suggests insufficient long-term persistence of habitat for full speciation despite apparently ideal isolating conditions.

In summary, long- and short-term fluctuations in aquatic habitat size have resulted in the low and variable species richness that characterizes deserts. Long-term fluctuations like those in the Great Basin alternately increase and depress adaptations to desert conditions and divergence of isolated populations.

Habitat size directly effects body size in fishes by ecological effects on life history. Small habitats support small fishes, even among species that are capable of larger size. Therefore it is surprising that cyprinids and catostomids in the intermountain desert are usually larger than their counterparts in the Mississippi Basin. It might be suggested that the western forms are examples of ecological release; they fill the niches occupied by large species in more diverse eastern faunas. It might also be argued that large western forms exhibit residual adaptations to Pleistocene pluvial periods. These hypotheses may be rejected by comparison of data presented here. Ptychocheilus is smaller in restricted waters; it was not smaller in the presence of diverse large salmonid, centrarchid, and ictalurid predators in the Pliocene. Gila shows significant reduction of size at maturity in small waters of the Great Basin but individuals may average four times longer in large habitats. This suggests that potential for large size is not a Pleistocene relict but is selected by ecological consequences of local habitat size.

Body size is measured as maximum adult size in each sample. The results of this study are consistent with the hypothesis that individual size is partly heritable and strongly controlled by the effects of relative juvenile and adult mortality on late versus early reproductive investment. When seasonal

fluctuations in habitat size result in heavy mortality; individuals that reproduce at small size leave more descendants than those that risk another round of mortality for another season of growth (Hirshfield and Tinkle 1975).

Reinvestment of the genotype in many small units increases the probability of survival, especially in small habitats in which large individuals might be more vulnerable to predation, oxygen depletion, or starvation. When adult mortality is low individuals leave more descendants by growing larger and producing more young over several seasons. Fish in the harsh, low-rain Colorado River (and productive, predator-rich lakes) probably show much lower adult mortality in relation to juvenile mortality. Ptychocheilus and trout are the only large native predators in the intermountain desert. Therefore survival past a threshold in the neighborhood of 200 mm in standard length places an individual in a relatively predator-free environment. All but benthic fishes in this environment are larger than their relatives elsewhere.

Benthic fishes are not free to grow substantially larger in larger habitats. The reason is probably a consequence of the relationship between individual size and home range, territory, or foraging area (Sale 1980). This phenomenon could be related to restriction of ration as a result of lower mobility in benthic species but greater vulnerability of adults to predators is as likely an explanation in streams and lakes. Similar reasons probably account for the exclusively small sizes of surface- and substrate-restricted atheriniform fishes in deserts. The failure of these benthic, surface, and edge species to grow much larger in the presence of abundant food and space indicates that, unlike many desert fishes, they are genetically limited in their pattern of growth and early reproduction. The opportunity to breed more than once a year may increase selection toward early reproduction in cyprinodonts, poeciliids, small characins, and small cichlids by negative feedback of reproductive effort on survivorship. The exceptional size of some large annual cyprinodonts in the Chaco provides support for this hypothesis; the long growing season and

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The extremely small cyprinids in the intermountain region, especially Iotichthys and Eremichthys, may be the result of rarity of small competitors for micro-crustaceans and aufwuchs. The existence of so few parallels to Notropis is probably a function of sparse terrestrial input to desert streams.

Despite the well-documented endemism in intermountain fishes, it is ecologically significant that the fauna is largely populated by representatives of the most widespread genera of freshwater fishes in North America and the Northern Hemisphere. Catostomus, Cottus, Rhinichthys, and Cyprinodon are the widest-ranging genera on the continent. Cottus, Salmo, Prosopium, and Catostomus, as well, have broad distributions in the remainder of the holarctic region. All have the capacity to succeed in the widest range of habitat sizes.

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