It seems justifiable to conclude that vascular plants of continental habitat islands affected by climatic shifts, and oceanic islands affected by sea level drop, colonized principally in glacial periods, when immigration was facilitated by larger island areas, smaller distances to source areas, and stronger wind and ocean currents (*12*). During such periods, the islands would have acquired an "hyperequilibrial" number of species relative to modern island areas and distances. The present number of species per island, representing a nonequilibrium situation, has apparently departed little from the high level reached during glacial times. A decay in species numbers to an equilibrium consistent with modern island parameters would depend more heavily on the reduction in the area of an island following climatic change than on the changed distances. Consequently, one would expect to find a stronger correlation of the numbers of species with modern areas than modern distances. Figures 1 and 2 show this to be the case.

Very rapid readjustment of species numbers following changes in island areas (or artificial manipulation of species) is known in several groups of animals which are highly mobile and exhibit considerable amounts of interspecific competition (*13*). As a result, modern species diversity of such animal taxa is quite strongly correlated with both modern areas and distances (*1–3, 13*). The contrasting lack of rapid extinctions in the flora of the paramos or the Galápagos Islands following glacial retreat and sea level rise might be due to several factors (*14*). First, plants are long-lived relative to birds and insects and would require a longer time to readjust to a new immigration rate. Second, the number of individuals of a plant species is often higher than that of an animal species. Again, more time would be required for complete extinction of a plant species. Finally, competition between species, although an important element, is often not as taxon-directed in plants as it is in animals and would only slowly eradicate all the individuals of a particular species. The correlations of modern plant species diversity with the present areas and distances from source areas of both the Galápagos Islands and the paramos, previously considered to constitute a reasonable fit to the MacArthur and Wilson equilibrium model, probably reflect the fact that, in these cases, the modern areas and distances are often proportional to their glacial counterparts (Figs. 1 and 2).

These results show that historical factors such as geological changes in island areas and the distances of the islands from sources of propagules, as well as the relative life span, population size, vagility, and extent of interspecific competition of the island taxa involved, must all be considered in determining the applicability of the model of island biogeography to either present or past situations.

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14. Glacial areas in square kilometers: Pinta, 100; Marchena, 190; Fernandina, 735; Isabela, 6070; Genovesa, 50; Espanola, 160; San Cristobal, 960; Santa Maria, 270; Rabida and San Salvador, 910; Santa Fe, 150; Santa Cruz and Seymour, 1550; Pinzon, 30; Wenman, 3; and Culpepper, 10.
15. Several of these ideas resulted from discussions with B. Holt, A. Schoener, and J. Terborgh. I particularly thank N. Roth and J. Terborgh for help and E. Wilson and T. P. Webster for kindly reading the manuscript. The Information Systems Division, Smithsonian Institution, provided facilities and advice.

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Hyporheic Communities of Two Montana Rivers

Abstract. *Collections of stream organisms from a domestic water supply system adjacent to the Tobacco River revealed that a detritus-based community exists in subterranean waters circulating through floodplain gravels at least 4.2 meters below and 50 meters laterally from the river channel. Several stone fly species spend their entire nymphal life cycles in underground habitats of the Flathead and Tobacco rivers.*

One of the most interesting aspects of stream ecology is the manner in which aquatic organisms segregate across and within stream bed substrata in response to preferences for specific microhabitats encompassed by the lotic environment. Complex horizontal distributions of animals determined by availability of food and suitable shelter are well documented (*1*; *2*, pp. 206–216). Riverine water may circulate deep within the substrata and to some distance laterally from the stream channel in areas of extensive fluvial deposition of small rocks and gravel. Interstices in the channel substrata are often sufficiently wide to allow vertical and lateral colonization of subterranean water by surface macrobenthos (*3, 4*). Subterranean habitat of streams has been referred to as the hyporheic area, and the indigenous faunas are usually composed of many very small individuals of species also common on the surface of the stream bottom (*4, 5*). Common riverine invertebrates may be distributed as deep as 70 cm vertically within substrata (*3, 4*) and to 60 cm laterally in shore groundwaters (*2*, p. 407). We report here the hyporheic habitats of two rubble-bottom rivers in northwestern Montana; the habitats extend to at least 4.2 m in depth and up to 50 m laterally from the river channel. The hyporheic community is dominated by large stone flies, which spend all except the adult stage of their life cycles deep in subterranean waters.

For the past 2 years we have been studying stone fly (Plecoptera) ecology in the Flathead River and its three forks in the area above Flathead Lake,

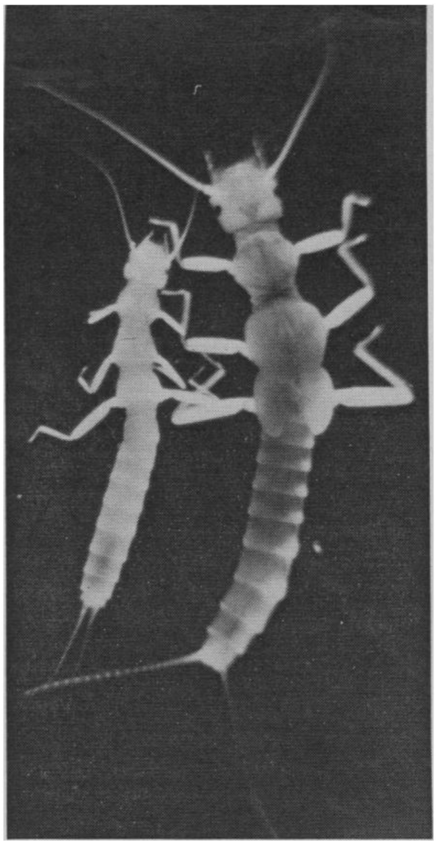

Fig. 1. Nymphs of *Paraperla frontalis* from underground habitat of the Tobacco River in northwestern Montana. Mature nymphs are up to 2 cm long, excluding antennae and cerci.

Montana. The river is a typical rhithron habitat with substrata of glacial cobbles and floodplain gravel deposited extensively. We have attempted to quantify plecopteran populations by using colonization samplers, baskets 0.028 m^3 (1 cubic foot) in volume, filled with material from the natural substrata and embedded in the river bottom (*6*). These samples, together with qualitative samples obtained by dislodging organisms into a screen downstream, accounted for distribution horizontally and to 30 cm vertically. Several species, however, were collected only as last instar nymphs preparing to emerge; earlier instars were present in less than 1 percent of all benthic samples. Adults were extremely abundant along the shoreline during and just after spring emergence, with as many as 5000 specimens accumulating weekly in small shoreline emergence traps. We hypothesized that these stone flies reside deep in riverine substrata, surfacing only to emerge and complete the life cycle.

This hypothesis was verified by the troublesome appearance of numerous stone fly naiads in a newly constructed domestic water supply for the town of Eureka, Montana. Subterranean water is obtained through three infiltration galleries located 30 to 50 m from the Tobacco River. The galleries are approximately 10 m long and were constructed much like a sand-gravel filter; perforated pipes surrounded by graded gravels (0.6 to 2.5 cm) were embedded horizontally at a depth of 6 m (20 feet) in floodplain gravel. The three galleries deliver water to two cylindrical concrete reservoirs, each of which resembles a well 2.5 m in diameter and 6.2 m deep. The reservoirs are connected to allow simultaneous operation of two large pumps. Water stands static in the pump reservoirs at 1.8 m below ground level, corresponding to the water table in the immediate area. After chlorination, water is pumped from the reservoirs to a large holding tank for gravity dispersal to domestic users. Very little stress is placed on the galleries when the system is pumped at capacity [5700 liters (1500 gallons) per minute], and the static level does not change. Only during periods of high use in late summer is the system pumped at capacity. The water delivered is of high quality and remains quite clear during periods of turbid river runoff. Subterranean water from the galleries is chemically similar to water flowing in the river channel. Daily and seasonal thermal and dissolved oxygen regimes are dampened slightly in the galleries (*7*).

Stone fly nymphs were present when the system was initially operated in August 1973; they were sufficiently abundant to greatly annoy domestic users. Concerned officials of the state health department asked us to identify the nymphs, and the consulting engineer for the water supply project requested our help in alleviating the problem. No reduction in the number of viable larvae entering the system was observed after intensive backflushing of the galleries with heavy doses of chlorine. This indicated that the hyporheal plecopterans were extensively distributed and not abnormally concentrated in the coarse gravel surrounding the perforated pipes of the galleries. By installing monofilament mesh nets over the delivery ends of the gallery pipes, we were able to prevent further movement of larvae into the system and to collect study specimens.

Stone flies obtained from the Tobacco River infiltration galleries were, in fact, the same species not accounted for in benthic samples from the Flathead River. While the Flathead is a much larger river, yearly thermal re-

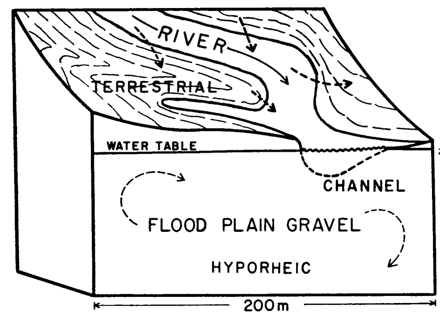

Fig. 2. Habitats utilized by stream organisms of the Flathead River. Dashed arrows indicate circulation of water from channel to hyporheic areas and vice versa. Dimensions refer to minimum floodplain width (200 m) and probable minimum vertical distribution (4.2 m) of hyporheic organisms.

gimes, substrata, and biota are remarkably similar in both rivers. Specifically, plecopteran species compositions are quite comparable.

The galleries yielded *Paraperla frontalis* (Banks) most abundantly with as many as 100 nymphs accumulating in the nets each week (see Fig. 1). Several hundred fresh specimens could be collected if we stressed one gallery by closing the other two and pumping at capacity for 30 minutes. *Isocapnia missouri* Ricker, *I. crinita* (Needham and Claassen), and *I. grandis* Banks were less common (*8*). All of these naiads were pale, almost transparent, and the eyes of younger instars were poorly developed. These characteristics and their elongated body form suggested to us that they live in the total darkness of the deep hyporheic environment, but also earned them the misnomer "maggots" from water users in Eureka. Nymphs from the galleries were surprisingly large; at nymphal maturity these stone flies are as much as 2.0 cm in length, excluding antennae and cerci.

Because of the large size of the naiads, we initially used nets with a 1000-μm mesh. However, the predominance of insect parts (such as parts of chironomids and small stone flies) in *P. frontalis* guts indicated the presence of other organisms in the underground habitat. We later used smaller (351-μm) mesh nets in an effort to capture smaller species or stages.

As expected, smaller instars of the above species were collected. Preliminary growth analysis data, based on size classes determined by measuring the length and head capsule for all naiads from each collection, indicate that *P. frontalis* spends 2 or 3 years in the hyporheic habitat before emerging. The *Isocapnia* species have at least a 2-year life cycle (*8*). Chironomids, young mayflies of the genera *Ammeletus* and *Rhithrogena*, early instar capniid stone flies, larval and adult riffle beetles, water mites, and several leeches were also taken from the galleries. Hauls made in the pump reservoir with a plankton net revealed that periphytic rhithron algae (mostly diatoms) and riverine detritus were passed through galleries abundantly. Except for *P. frontalis*, the *Isocapnia* species, and the leeches, all these organisms are common in the rhithron habitat of the Tobacco River. Obviously, a variety of potential food items either crawl or are carried passively by waters percolating downward and laterally to resident consumers living deep in the substrata. Interstices in floodplain gravel are apparently wide enough to allow fairly large invertebrates to move efficiently. While we can only demonstrate that four species, all large stone flies, are permanent residents of subterranean waters in the floodplains of the Tobacco River, it is clear that a diverse community exists deep in substrata. Many of the hyporheic residents are small benthic insects recruited from the surface of the river bottom and may move back and forth from channel to hyporheic habitats.

We have shown that the hyporheic community of the Tobacco River extends to a depth of at least 4.2 m and up to 50 m laterally from the river channel. Since no adjacent wells or infiltration galleries were available to facilitate sampling, we could not specifically determine the dimensions of hyporheic development of the larger Flathead River. Considering the tremendous emergence of *P. frontalis* and *Isocapnia* species and more extensive deposits of floodplain gravel, the hyporheic area of the Flathead probably extends several hundred meters from the channel and to considerable depth. It is likely that any stream or river with a similar hydrogeology will exhibit extensive hyporheic areas. We emphasize that deep hyporheic habitats may exist only in streams in which the channel and adjacent substrata are composed of loosely compacted floodplain gravels (*9*). The macrobenthic habitat in such streams is three-dimensional (Fig. 2). A channel habitat supports a diverse fauna in a mozaic of microhabitats which develop as a consequence of natural fluvial processes. The hyporheic area is inhabited by a more limited variety of organisms utilizing food carried by both active and passive transportation in waters moving vertically and laterally from the stream channel. For species that must emerge to reproduce, there is also a terrestrial habitat with associated ecological consequences.

In rubble-bottom rivers with extensive hyporheic areas the problem of quantifying production becomes extremely perplexing. Our observation that macrobenthic species occurring very abundantly as adults along the shoreline may be impossible to find by channel sampling indicates the possible magnitude of hyporheic production. Concerted effort and sampling ingenuity by stream limnologists will be required to adequately evaluate the function of the hyporheic community in the stream ecosystem.

Sanitary engineers should consider the possibility of encountering hyporheic organisms when they plan the construction of infiltration galleries. While the macroinvertebrates we observed are not at all a health hazard, Eureka residents certainly considered them a nuisance.

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7. Stone fly naiads taken from the galleries alive appear to be quite tolerant of low concentrations of dissolved oxygen. We have held 20 to 30 naiads in sealed 10-dram (~ 35-cm^3) vials for 10 hours at room temperature with no mortality.
8. The nymphs of these species have not yet been described taxonomically. We have associated nymphs with adults and are now certain of identifications. Our *Isocapnia* growth data are difficult to interpret because of the peculiar occurrence of dwarf males of *I. missouri* and *I. crinita*.
9. Plecopterans like or closely related to the hyporheic forms we encountered are rather uncommonly collected in North America, but the records we are familiar with strongly suggest that these stone flies reside in hyporheic habitats of other streams. W. Ricker has examined *Isocapnia* larvae from a water supply system for the small city of Banff, Alberta, Canada; source wells are located in floodplain gravel near Spray River. Numerous *I. integra* emerge from the river in the spring. Ricker also reported collecting *P. frontalis* naiads from wells 6 to 15 m deep in gravel deposits a few hundred meters from the Nanamio River, British Columbia, Canada (personal communication). A single vial containing three *Paraperla* sp. nymphs collected from a well at Chitina, Alaska, in 1934 was found by R. Baumann in the Plecoptera collection of the Smithsonian Institution, Washington, D.C. D. Potter has shown us specimens of a closely related species, *Kathroperla perdita* Banks, from a drilled well in W. T. Galliver Provincial Park, Alberta, Canada. These nymphs could have come from subterranean waters from 3 to 16 m below ground level. Adults apparently emerge from spring creeks nearby. Other collections of *Paraperla* and *Isocapnia* nymphs are rare and primarily limited to mature naiads ready to emerge. Adults, however, have been found along streams and rivers throughout the Rocky Mountains. In the few locations where these stone flies have been collected abundantly, substrate conditions were similar to those described in this report. It is likely that nymphs resided in hyporheic areas. The precise combination of substrata required for extensive hyporheic development is also comparatively uncommon. Often stream substrata are tightly compacted by deposition of fine sediments filling interstices. The result is reduced percolation of river water through the substrata, and a poorly oxygenated or even anaerobic layer may be present a few centimeters below the surface of the river bottom, precluding hyporheic colonization. However, many of the larger streams and rivers of the Pacific Northwest and Alaska are quite similar to the Tobacco and Flathead rivers, and we would expect to find well-developed hyporheic communities in them.
10. We thank A. Sheldon, G. W. Prescott, W. Ricker, R. Baumann, J. Tibbs, D. Potter, D. Carver, and W. Miller for their help.
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Comet Kohoutek: Ultraviolet Images and Spectrograms

Abstract. *Emissions of atomic oxygen (1304 angstroms), atomic carbon (1657 angstroms), and atomic hydrogen (1216 angstroms) from Comet Kohoutek were observed with ultraviolet cameras carried on a sounding rocket on 8 January 1974. Analysis of the Lyman alpha halo at 1216 angstroms gave an atomic hydrogen production rate of* 4.5×10^{29} *atoms per second.*

On 8 January 1974 at 0140 U.T. we flew a group of ultraviolet cameras and photometers on an Aerobee rocket over White Sands, New Mexico, to observe Comet Kohoutek. At the time of the observations the comet was 0.43 A.U. from the sun and twice that far from the earth; the sun-comet-earth angle was close to 90°. Among the instruments carried were three ultraviolet-sensitive electronographic cameras, of the type used in the Lunar Surface Ultraviolet Camera/Spectrograph on the Apollo 16 mission to photograph (among other things) the hydrogen corona surrounding the earth (*1*). One