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Ecology of the Alluvial Aquifers of the Flathead River, Montana

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I. INTRODUCTION

Stanford and Gauvin (1974) reported the presence of abundant insect larvae deep in the alluvia of the Tobacco River, a small gravel bed river in northwestern Montana. The insects were entrained in an infiltration gallery that provided potable water from the alluvial aquifer to the town of Eureka, Montana. The collection system was located ca. 150 m from the river and 3 m below the floodplain surface. The most abundant forms were stone flies (Plecoptera) of the genera *Isocapnia* and *Paraperla*. However, many other taxa, traditionally thought of as river macrobenthos, were also present,

either actively or passively entering the collection system from the interstitial aquifer of the river. The discovery, coupled with the wide range in western North America of adult *Isocapnia* and *Paraperla*, led the authors to propose that the deep penetration of benthos into the saturated alluvia of gravel bed rivers was likely a widespread phenomenon that had significant ramifications for river ecology.

A decade later Stanford and Ward (1988) confirmed the occurrence of the same Plecoptera, along with over 70 other invertebrate taxa, in the shallow alluvial aquifer of the much larger Flathead River in the Kalispell Valley (Fig. 1); Plecoptera larvae were pumped from drilled wells on the valley bottom up to 3 km from the river channel. Others working on interstitial fauna of gravel bed streams and rivers in Europe (Bretschko and Klemens, 1986; Danielopol, 1976; see also Chapters 12 and 13), Canada (Coleman and Hynes, 1970; Pugsley and Hynes, 1986; Williams and Hynes, 1974), and elsewhere in the United States (Boulton et al., 1991, 1992; Palmer, 1990; Pennak and Ward, 1986; Ward and Voelz, 1990; see also Chapter 15) also demonstrated speciose interstitial assemblages, but at the scale of meters or less. Based on our work summarized below and research on the Rhône River in France (Marmonier et al., 1992; Dole-Olivier et al., this volume), it is clear that a diverse and abundant interstitial fauna may inhabit the alluvium of entire floodplains kilometers from the river channel. Our long-term studies in the Flathead catchment now emphasize the four-dimensional nature of the riverine and floodplain landscapes (Ward, 1989) and the processes and implications related to water and materials exchange between floodplain alluvial aquifers and the river (Stanford and Ward, 1993).

The purpose of this chapter is to summarize the data and interpretations linking the groundwaters and surface waters in the Flathead catchment. Much of the work remains unpublished, and some original data are included herein.

II. BIOPHYSICAL SETTING OF THE CATCHMENT ECOSYSTEM

The Flathead River–Lake Catchment encompasses 22,241 km² in western Montana and British Columbia (Canada) (Fig. 1). The altitudinal gradient ranges from 750 m above sea level (a.s.l.) at confluence with the Clark Fork of the Columbia River to 882 m a.s.l. at Flathead Lake and over 4000 m a.s.l. on the Continental Divide. The geology is complex. Rock ages and composition vary from the very old and nutrient-poor Belt Series of the Precambrian age in Glacier National Park (drainage area between the Continental Divide and the North and Middle Forks; Fig. 1) to much younger limestones and other Mesozoic strata in the headwater reaches of the North, Middle, and South Forks. All of these formations were modified and molded into the present landscape by the cordilleran orogeny and subsequent erosion

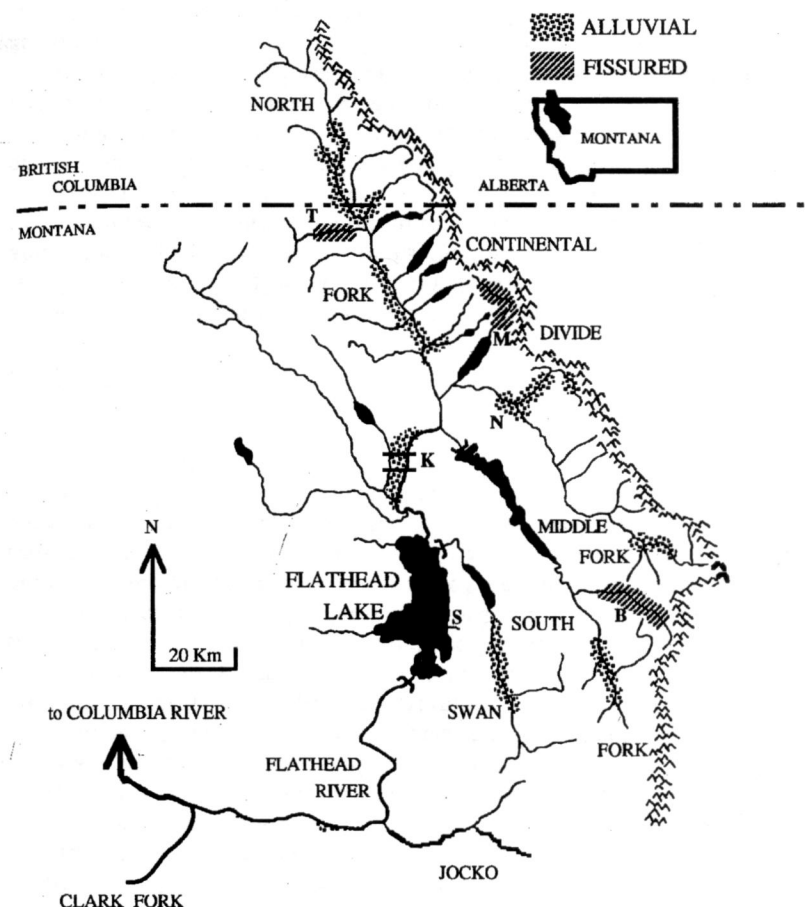


FIGURE 1. Flathead River catchment in Montana and British Columbia, Canada, showing alluvial floodplains (stippled), including the primary study sites at Nyack (N, a montane floodplain) and Kalispell Valley (K, a piedmont valley floodplain). Well transects at the Kalispell Valley site are shown as bold lines. Lakeshore alluvia containing groundwater biota occur at site S (Flathead Lake Biological Station). Cave streams in fissured bedrock substrata were studied at site T (Trail Creek) and were reported at sites M (McDonald Creek) and B (Spotted Bear River) [after Stanford and Ward (1993)].

by Pleistocene glaciation and fluvial outwash processes (Locke, 1990; Ross, 1963).

The land mass is drained by a network of mostly pristine streams and lakes. Streams generally begin as spring brooks emerging from fissured aquifers in the bedrock or from alluvia usually associated with the glacial history (see Fig. 6 in Chapter 1). The annual hydrologic pattern of surface flow is distinctively maximized in May–July by spring snowmelt in the

mountain headwaters of each subcatchment. Streams, lakes, and near-surface aquifers fill to capacity or flood, depending on the intensity and duration of the snowmelt spate. Lower volume floods may occur at other times of the year, resulting from short-term, heavy precipitation created by the collision of Pacific maritime and continental air masses within the catchment. Average annual flow of the sixth-order (Strahler, 1965) Flathead River at confluence with 480-km² Flathead Lake is 340 m³/sec. Three dams regulate the flow of the mainstem river above and below Flathead Lake and the top 3 m of the lake (Fig. 1).

Glaciation undoubtedly was responsible for the initial formation of the larger alluvial reaches (Fig. 1), although local Quaternary alluvial structures in the catchment have not been studied in detail. Our primary study sites are the Kalispell Valley alluvial aquifer (K; Fig. 1), between the Whitefish (mean $Q = 20\text{ m}^3/\text{sec}$) and Flathead River channels upstream from Flathead Lake and the Nyack Valley aquifer on the Middle Fork (N; Fig. 1). The Nyack Valley is an aggraded segment that constricts into steep canyons at the upstream and downstream ends. In both cases the valleys apparently were shaped by glaciation, and postglacial fluvial outwash left an expansive deposit of cobble and gravel alluvia about 10 m thick, overlying an impermeable layer of Tertiary clay. Subsequent flooding and migration of the active river channel across the valley in response to centuries of cut and fill alluviation and, perhaps, block fault tectonics deposited 1–3 m of fine sediments on the ancient floodplain surface. Hence, the extant landscape of the Kalispell Valley is composed of the modern floodplain and channel, low terraces of the ancient floodplain, higher, lateral terraces created by glaciation (see Fig. 3), and a shallow, unconfined alluvial aquifer. Ancient river channels (paleochannels) are visible as depressions in the ancient floodplain surface, and the buried channels are remarkably evident in traces done with ground penetrating radar (G. Poole, Flathead Lake Biological Station, unpublished). The montane valley (N) differs from the piedmont valley (K) only in being smaller, and it lacks the high lateral terraces.

Rubble bottom streams also occur in karstic caves in Mesozoic limestones (B and T in Fig. 1) (J. A. Stanford, *et al.*, unpublished) and in the Belt Series substrata (M; Fig. 1) (G. Gregory, Glacier National Park, West Glacier, Montana, personal communication). The drainage patterns of the cave streams have not been documented.

The waters of the Flathead are cold, and concentrations of dissolved nutrients, such as nitrogen, phosphorus, and organic matter (DOM), in surface waters are naturally near or below detection limits; so the lakes and streams naturally do not produce much plant and animal material compared with most other waters in the United States (Ellis and Stanford, 1988; Stanford *et al.*, 1992).

An important feature of the Flathead is that many aquatic species are present, owing in part to the pristine, oligotrophic nature of the waters and

the wide variety of aquatic habitats along the altitudinal gradient (Hall *et al.*, 1992). Moreover, the Flathead exists midway in the north–south continuum of the Rocky Mountains, and three major river systems of the North America continent share adjacent headwaters in Glacier National Park (*i.e.*, the area between the North and Middle Forks and the Continental Divide; Fig. 1). these include the Saskatchewan, Missouri, and Columbia Rivers, which drain into the Arctic, Atlantic, and Pacific Oceans, respectively. Hence, many species on the fringe of their continental distribution are present, and the area is a “melting pot” of biodiversity. For example, 67% (101 species) of Plecoptera reported for the Rocky Mountains from Alaska to New Mexico have been collected in the Flathead catchment [updated from Stanford and Ward (1983)]. Native biota include species [*e.g.*, bull charr (Fraley and Shepard, 1989) and west-slope cutthroat trout (Marnell, 1988)] that are relatively rare in North America, having been eliminated from less pristine areas by humans or existing as relict populations since Pleistocene glaciation (Stanford and Prescott, 1988).

Biophysical features of the catchment are naturally interrelated; processes in one place or time may be influenced or controlled by adjacent processes. For example, the riparian plant assemblages of the alluvial floodplains appear to be closely linked to piezometric gradients associated with groundwater down- and upwelling (Stanford and Ward, 1993). Although the river–lake ecosystem is reported to be relatively pristine for similarly sized catchments in the human-dominated latitudes of the world, stream- and lake-level regulation by dams (Stanford and Hauer, 1992) and other human sources of disturbance have exerted measured influences on natural ecosystem integrity (Spencer *et al.*, 1991; Stanford and Ward, 1992). It is within this complex biophysical setting that we wish to summarize what currently is known about the groundwater ecology of the alluvial aquifers of the Flathead River.

III. METHODS

Research wells, installed with a hollow auger drilling rig (Fig. 2), consisted of slotted PVC pipe. We used an electric saw to cut 5 mm × 5 cm alternating slots in the pipe before installation. The wells were capped on the top and bottom, although bottom caps were also slotted to allow fauna that collected in the wells between sampling periods to escape. Wells were arrayed across the modern and ancient floodplains of the Kalispell Valley, including two transects (Fig. 3) that were intensively studied. Most wells penetrated at least 5 m into the saturated alluvia.

Over 200 wells were installed to determine aquifer characteristics, such as flow direction and basic ion chemistry, in comparison with those of the river. Several large wells were installed by the Montana Bureau of Mines and

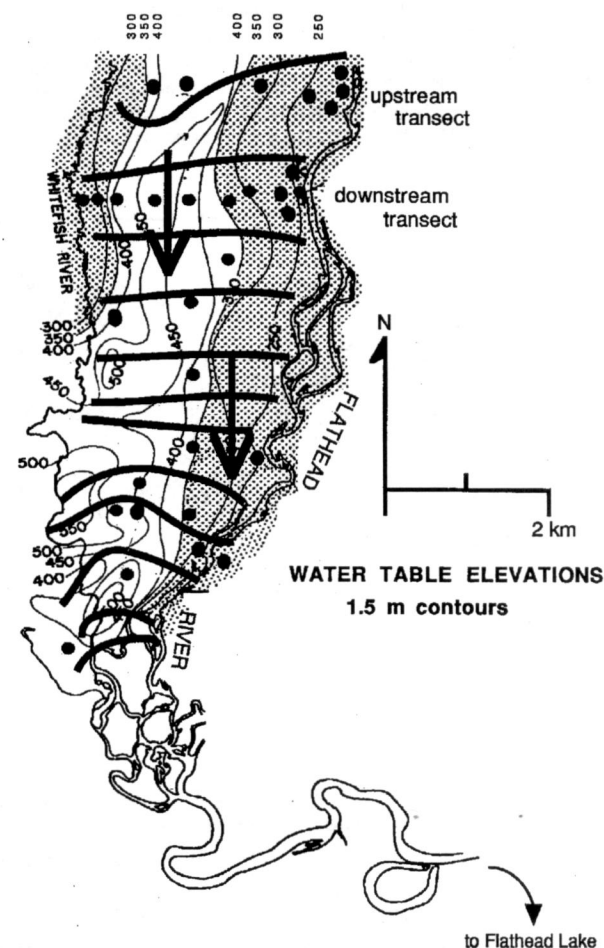


FIGURE 3 Water table elevations (1.5-m isopleths, bold contours) obtained from time series measures of depth to water in 271 monitoring wells installed in the Kalispell Valley alluvial aquifer. Thin contours are isopleths of specific conductance ($\mu\text{S}/\text{cm}$) of the groundwater. Arrows indicate the direction of groundwater flow (declining elevation of water table). Solid circles are wells (including two transects; see Fig. 5) used to sample groundwater biota; the stippled area indicates the portion of the aquifer in which amphibites were routinely collected [ca. corresponding to the $350 \mu\text{S}/\text{cm}$ contour; after Stanford and Ward (1988)].

FIGURE 2 (top) Hollow auger drilling rig used to install sampling wells (slotted PVC pipe) in the alluvial floodplains of the Flathead River. A finished well is shown in the foreground. (bottom) Janine Gibert (left) and Bonnie Ellis (right) remove small rocks that have been left in the well to allow colonization of epilithic biofilm.

Geology to allow pump tests for the estimation of hydraulic conductivity, transmissivity, and flow rates; others we fitted with temperature and pressure sensors and data loggers to document thermal patterns and water table dynamics. Wells plotted in Fig. 3, in particular the upstream and downstream transects, were sampled to determine the distribution of groundwater fauna. Data loggers for temperature and flow also were installed at river sites, and additional data were available from the U.S. Geological Survey.

On each sampling date, the depth to the water table was recorded, and then wells were purged using a gas-powered diaphragm pump connected to a 5-cm-diameter tube inserted into the bottom of the wells. The pump rate for most wells was ca. 40 l per minute. All water, fauna, and detritus pumped out of a specific well during the first 10 min were filtered with a 100- μ m-mesh plankton net. Pumping was continued until a clear water flow was attained, and then water samples for chemical constituents (nitrogen and phosphorus forms and DOM) and microbial determinations [acetone-extractable chlorophyll and epifluorescence (DAPI) cell counts] were taken from the pump stream. Temperatures, specific conductance values, and dissolved oxygen concentrations were recorded in each well before and after pumping. Samples for dissolved oxygen, specific conductance determinations, chemical analyses, and benthos also were collected in the river on specific sampling dates for comparison to well data. Biophysical data summarized herein were obtained from quarterly (spring, summer, fall, and winter) samplings of the wells in the two transects (Fig. 3) during the period January 1988–April 1989. Two of the wells, C and E, were sampled less frequently due to access problems. The transects were installed in an attempt to document the flux of water and materials through the aquifer and to avoid the urbanized area of the aquifer farther downstream, where groundwater effects were evident (Noble and Stanford, 1986). Wells were drilled in a grid on the Nyack Valley and sampled in a similar fashion.

IV. HYDRAULIC CONNECTIVITY OF THE ALLUVIAL AQUIFERS WITH THE RIVER

The boundaries of the Kalispell Valley alluvial aquifer are not clearly delineated, but the system is ca. 5–6 km wide at the upstream end and ca. 13 km long. The aquifer apparently is fed by the Flathead River and perhaps to a lesser extent by the much smaller Whitefish River and other small tributaries that flow into the alluvial domain of the valley from the Whitefish Range at the upstream end (Konizeski *et al.*, 1968). Additional geohydrological investigations are needed to precisely determine the extent of the aquifer and the relative importance of different sources of water. However, we demonstrated that the aquifer is hydraulically connected to the Flathead River; seasonal and daily dynamics of the water table are clearly correlated

with river flow (Fig. 4). Water flows through the aquifer from north to south and is highly interactive with the river (Fig. 3). Upwelling groundwaters are evident as spring brooks at many locations on the active and ancient floodplain; most erupt in paleochannels (Fig. 5). The aquifer has an average slope of 2°. Hydraulic conductivity and, by inference, interstitial porosity are variable because some wells and some layers within wells yielded water at higher rates than others. However, in general, hydraulic conductivity estimates (0.1–10 cm/sec) from pump tests were among the highest recorded in unconsolidated alluvia (Freeze and Cherry, 1979). Wells in or near paleochannels always produced the highest pump rates, which inferred that the paleochannels were zones of the highest porosity. The aquifer discharges into the Flathead River at or before the anastomosed zone downstream of the confluence of the Whitefish River (Fig. 3), where the aquifer terminates in contact with fine-grained paleodeltaic sediments of postglacial Flathead Lake.

More detailed geohydraulic investigations were performed at the Nyack Valley site (J. A. Stanford *et al.*, unpublished data). The valley is 3 km across at the widest point by 8 km long, and the alluvial aquifer occupies

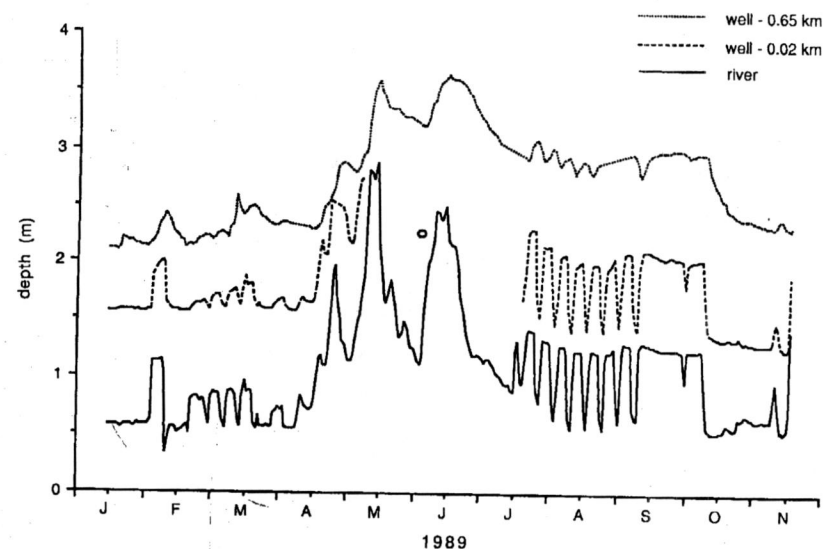


FIGURE 4 Hydrographs obtained in the Flathead River channel and in two wells located 0.02 and 0.65 km laterally (west) from a channel in the Kalispell Valley (sites Ru, A, and D in Fig. 5). Nonseasonal fluctuations were caused by discharges from a large hydroelectric dam on an upstream tributary on the South Fork (Fig. 1). Data are depths to water surface in the wells and the river channel relative to surface benchmarks as measured by hydrostatic sensors reporting on the hour to data loggers during 1989 [from Stanford and Ward (1993)].

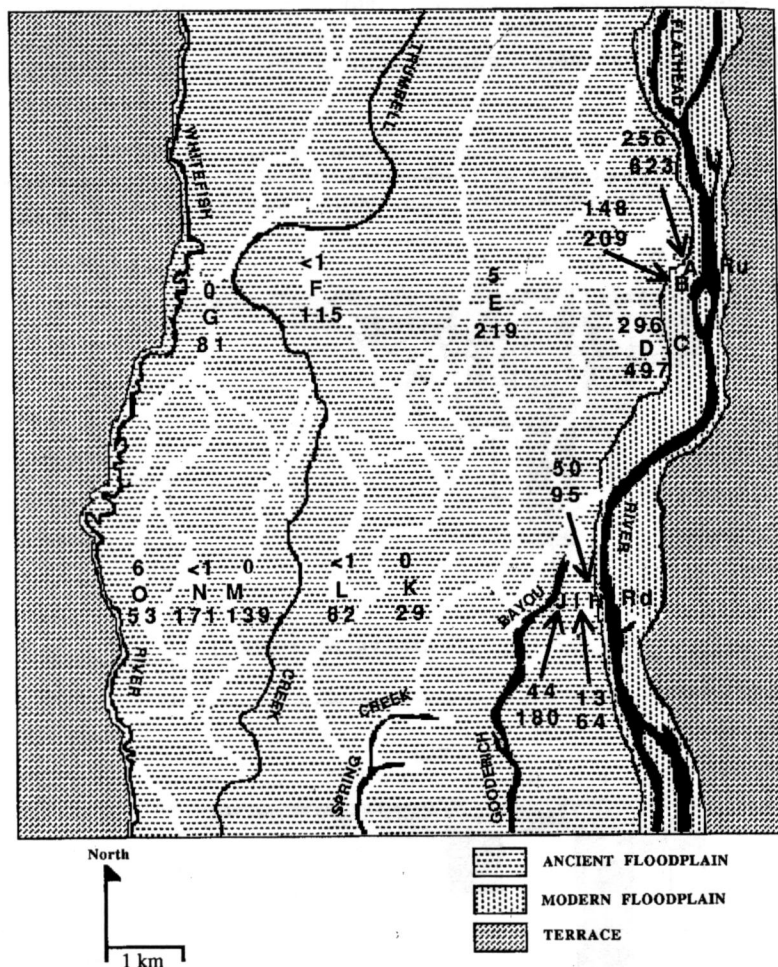


FIGURE 5 Mean abundance of amphibiites (upper numbers) and stygobites (lower numbers) in wells (letters) in two transects (see Fig. 3) across the alluvial aquifer in the Kalispell Valley (upstream transect, wells A–G from river sampling site Ru; downstream transect, wells H–O from river sampling site Rd). Paleochannels on the ancient floodplain (see text) are indicated by pathways in the stippling. Spring Creek and Gooderich Bayou are perennial spring brooks that emerge from paleochannels. No biological data were collected in well C.

the entire valley bottom. Hydrographs in wells near the valley walls were directly correlated with the river flow pattern. Maps of piezometric gradients and accretion studies showed that 30% of the river flow enters the alluvium at the upstream end of the valley. Interstitial water upwells from the middle to the end of the aquifer in relation to ponding caused by the constriction

of the valley at the downstream end. All of the interstitial flow enters the river channel directly or by spring brooks. Upwelling groundwaters create a network of spring brooks on the modern and ancient floodplain and are a primary determinant of riparian plant assemblages (Stanford and Ward, 1993).

V. TEMPERATURE AND SOLUTE DYNAMICS

Interaction between the Kalispell Valley aquifer and the Flathead River was inferred by mapping isolines of specific conductance (Fig. 3) relative to the river ($190 \mu\text{S}/\text{cm}$). Values in the aquifer were similar near the river, indicating a large hyporheic or transition zone between the river and the aquifer; values were over two times higher in wells most distant from the river, indicating a longer residence time of phreatic water.

The annual temperature amplitude in the river was $2\text{--}20^\circ\text{C}$; the river did not freeze in spite of very cold winter air temperatures (-30°C), owing to regulated flows from Hungry Horse Dam and the discharge of warm water from the aquifer into the river. The annual temperature amplitude in the aquifer was $6\text{--}11^\circ\text{C}$, and the amplitude was most pronounced in wells nearest the river. Dissolved oxygen concentrations in the wells were consistently $>50\%$ saturation ($4\text{--}10 \text{ mg}/\text{l}$). In the river dissolved oxygen was always near saturation or supersaturated (J. A. Stanford *et al.*, unpublished data).

We observed a strong tendency for dissolved constituents, especially nitrate to concentrate in the center of the aquifer (Fig. 6). Mass balance calculations suggested that 12–17% of the base flow nitrate load of the river downstream from the aquifer was derived from nitrate generation, probably due to nitrification, within the aquifer. Soluble reactive phosphorus was an order of magnitude higher in well samples than in the river, and we estimated that 4–25% of the river load during base flow was due to aquifer discharge (Stanford and Ward, 1988). High solute loads in groundwaters discharging into the oligotrophic surface waters produced mats of green algae, *Ulothrix zonata*, and diatoms that otherwise would not be present, and thereby they influenced the distribution of benthic consumers (Hauer and Stanford, 1981, 1982, 1986) and may strongly influence bioproduction in surface waters (Stanford and Ward, 1993). On the other hand, DOM values were consistently low ($<2 \text{ mg}/\text{l}$) in the aquifer, suggesting the possible carbon limitation of microbial metabolism relative to other dissolved constituents within the aquifer (Stanford and Ward, 1988).

We initially established the alternate study site at Nyack because we were concerned about contamination of the aquifer in the Kalispell Valley by human activities, especially fertilizers from farms, and the possible interactive effects of the regulation of river flow by Hungry Horse Dam. In

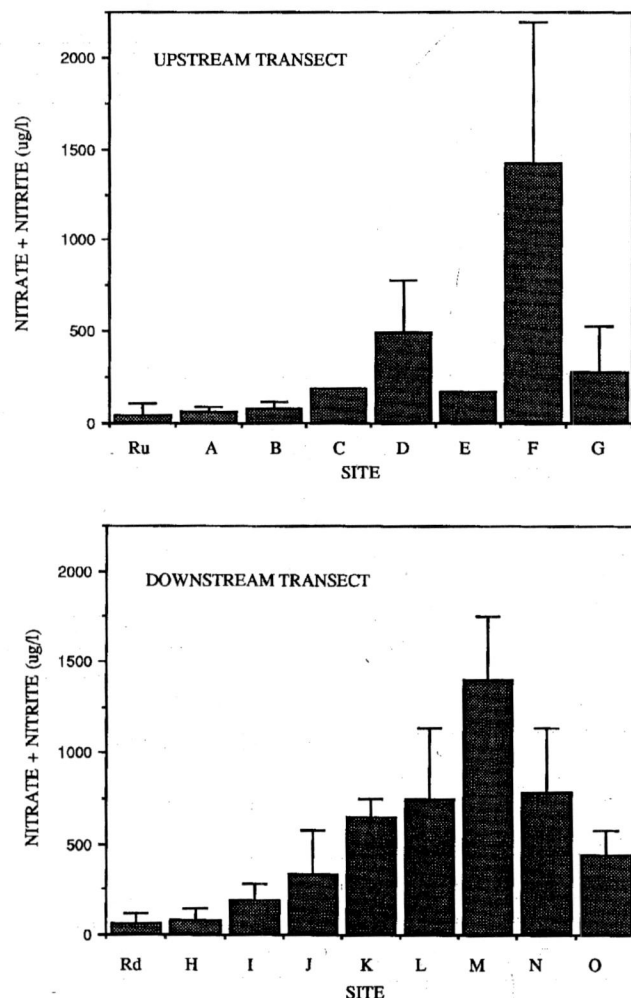


FIGURE 6 Average concentration of nitrate + nitrite ($\mu\text{g/l}$) observed in quarterly (see text) samples obtained during the period January 1988–April 1989 in the Flathead River and wells located in the transects shown in Fig. 5 (bars indicate ranges).

comparison, the Nyack Valley is virtually pristine. However, we observed no significant differences in solute or dissolved oxygen patterns. Thermal patterns were also similar, except that the river was near 0°C in midwinter and froze over at the upstream (downwelling) end for long periods (J. A. Stanford *et al.*, unpublished data). We concluded that contamination problems in the Kalispell Valley were minimal, at least on the two well

transects (Figs. 3 and 5). But, contamination of wells was highly probable (*i.e.*, highest specific conductance, lowest dissolved oxygen readings, highest DOM and nitrate concentrations, high coliform bacteria counts, and fewer groundwater biota) in a limited area of intensive housing development and individual sewage drain fields on the ancient floodplain near the town of Kalispell at the lower end of the aquifer (Noble and Stanford, 1986).

VI. DISTRIBUTION AND ABUNDANCE OF GROUNDWATER BIOTA

A. Microbial Ecology

The main objective was to determine the relative importance of free living and attached bacteria, fungi, and Protozoa in the groundwater food web of the alluvial aquifers. We also examined the entrainment of riverine algae and bacteria in the aquifers. This section is based primarily on the work of Ellis *et al.* (1995).

In the Kalispell Valley, diatoms common in the Flathead River, such as *Synedra*, *Achnanthes*, *Navicula*, *Gomphonema*, and *Cymbella* were present in well samples up to 0.35 km from the river, with autofluorescing chromatophores very visible. Green algae were found primarily in wells far from the river channel (0.65–2.55 km), whereas blue–green algae were rather ubiquitous. This strongly suggested that riverine particulate organic carbon was entrained in the aquifer. Indeed, measurable concentrations of chlorophyll *a* were detected in samples from many wells; values were consistently highest in the upstream transect (where the river is influent to the aquifer) in wells nearest the river and reached a maximum of 14 ng/l.

However, in spite of the strong hydraulic connectivity between the aquifer and the river in the Kalispell Valley (Fig. 4), the total microbial density in wells near the river was about 80% lower than that in the river, and only 2–3% of the riverine microbial density occurred in the most distant wells. In the remote wells densities averaged $ca. 9.0 \times 10^3$ cells/ml, which is at the low end of reported values for groundwater. The immediate decline of bacteria relative to the river may be due in part to a similar decline in low-molecular-weight utilizable carbon. Multiple regression analysis indicated that SRP, ammonium, nitrate + nitrite, and DOM concentrations (in that order) explained about half the variance in the free living bacteria assemblages in the aquifer.

Protozoans were detected at all river sites and in all the wells. Flagellated and nonflagellated protozoans, including amoebae and a single ciliate, were observed. Densities of all forms ranged from 0 to 213/ml. Replicate samples indicated high variances in the density estimates (*i.e.*, standard deviations averaged 26% of the mean).

In both the river and the aquifer, solitary cocci dominated densities of free living bacteria. Bacilli dominated the biomass in the river and many of

the wells. However, actinomycetes, fungi, and cocci dominated the biomass in some wells. Fungi have been found in low numbers in a few aquifers (Madsen and Ghiorse, 1993). The presence of substantial populations of fungi suggests a strong connection to the surface. Infiltration of precipitation carrying soil detritus and microbiota (perhaps including algae) may be an important process in spite of the river being by far the dominant water source for the aquifer. Moreover, most of the attached bacteria observed in water samples from the aquifer were associated with organic detrital particles. The fine mineral sediment particles flushed from the aquifer during pumping appeared to be free of any bacterial colonization. This suggested that epilithic biofilms may be important in the aquifer.

In environments characterized by low nutrient concentrations, organisms attached to solid surfaces have an advantage in nutrient uptake in relation to free living forms, owing to continuous delivery of nutrients by water movement and because of nutrient release and feedback (looping) between bacteria and primary consumers (Protozoa and very small metazoans) that compose biofilms. In an effort to understand the epilithic microbial community of the Kalispell Valley aquifer, artificial ceramic tiles and rocks obtained from the drilling of the wells were suspended in wells with high flow rates and high oxygen concentrations for 38 days (Fig. 2). They were then removed, and [^3H]thymidine incorporation into DNA was determined. Results from all incubations ($n = 11$) indicated that production was significantly greater on the natural substrata than on artificial tiles ($p < 0.01$, ANOVA). Protozoan densities were also higher on rocks than on tiles, with values ranging from 99 to 6399/cm ^{2} on rock substrates versus 2.6 to 79/cm ^{2} on tiles. Although it is difficult to compare bacterial numbers per unit surface area with those per unit volume of water, it is evident that extensive growths occurred on rock substratum in comparison with densities in the interstitial waters (Table I). The same pattern also appeared to be true for protozoan densities: 99 to 6399/cm ^{2} on the rock substratum versus 0 to 213/ml in interstitial waters.

The incubation time selected was arbitrary, and we surmise that the populations were early stages in the colonization of the experimental substratum. Very small size classes of bacteria dominated the rock substratum, as well as groundwater and the river. But large bacteria were more common on rocks than in the interstitial waters, suggesting that biofilms provide more optimal environmental conditions. High numbers of fungi and Protozoa on the rocks also have important implications. Fungi and actinomycetes may be very active in the aerobic heterotrophic metabolism of the groundwater microbial assemblage. Even when they are present in low numbers, their contribution to total subsurface metabolic activity may be significant (Madsen and Ghiorse, 1993). The predominant form of nutrition for free living Protozoa is the ingestion of bacterial prey (Fenchel, 1987), and predation by Protozoa has been shown to accelerate the cycling of carbon and other nutrients (Stout, 1980; Fenchel, 1987).

TABLE I Bacterial Abundance and Biomass in the Interstitial Water and on Natural Substratum Incubated in Wells (see Fig. 5) in the Kalispell and Nyack Alluvial Aquifers (see Fig. 1)

Well	Distance from river (km)	Density		Volume	
		Water (number/ml)	Rocks (number/cm ^{2})	Water ($\mu\text{m}^3/\text{ml}$)	Rocks ($\mu\text{m}^3/\text{cm}^2$)
Kalispell Valley					
	0.65	$6.19 \pm 0.34 \times 10^4$	$7.49 \pm 1.11 \times 10^6$	$3.18 \pm 0.23 \times 10^3$	$7.59 \pm 0.62 \times 10^5$
	1.96	$7.51 \pm 0.34 \times 10^4$	$3.24 \pm 0.50 \times 10^6$	$5.12 \pm 0.22 \times 10^3$	$2.86 \pm 0.56 \times 10^5$
	0.03	$1.11 \pm 0.04 \times 10^5$	$3.94 \pm 0.55 \times 10^6$	$5.56 \pm 0.28 \times 10^3$	$2.66 \pm 0.30 \times 10^5$
Nyack Valley	0.35	$2.50 \pm 0.18 \times 10^4$	$1.22 \pm 0.22 \times 10^6$	$1.38 \pm 0.14 \times 10^3$	$1.08 \pm 0.27 \times 10^5$
	0.28	$3.80 \pm 0.15 \times 10^4$	$2.01 \pm 0.29 \times 10^6$	$1.91 \pm 0.08 \times 10^3$	$2.04 \pm 0.18 \times 10^5$

Although the database is not as extensive, microbial dynamics appeared to be similar at the Nyack site, in that the densities and biomass of bacteria were higher and more variable in the river than in the wells and that the numbers and biomass declined with distance from the river channel. Protozoa were detected in wells 0.28 and 0.3 km from the river. Abundance ranged from 0 to 2.0/ml in the river and from 0 to 2.4/ml in the aquifer. Although flagellates were observed, the majority had no flagella and were probably cysts. No ciliates or amoebae were detected. Chlorophyll-containing algal cells were present in a well 0.28 km from the river.

We concluded that a rich, but perhaps carbon-limited, microbial biofilm is the primary base of the food web in both aquifers. The existence of a microbial loop, which tightens the efficiency of nutrient utilization, seems highly likely and probably explains how a diverse metazoan biocenosis can exist in these aquifers.

B. Invertebrate Ecology

To date we have found over 80 taxa of groundwater animals (*i.e.*, stygophiles and stygobites; Table II) in the two alluvial aquifers of the Flathead River. Most of these were members of the very speciose benthos (200+ species) that occasionally showed up in samples from wells near the river or other groundwater collections within a few meters of water flowing in the river channel (*i.e.*, occasional hyporheos). However, 10 crustacean (Ward *et al.*, 1994), 14 insect, and several other species (J. A. Stanford *et al.*, unpublished data) were routinely collected in wells far from the river channel (stygophiles and stygobites; Table II). Of these, a copepod species new to science has been described (Reid *et al.*, 1991), and perhaps as many as 10 other crustacean and 2 insect species remain to be described. The Acarina and Oligochaeta also require further taxonomic resolution. Nematodes, segmented worms, and other unknown organisms with DAPI-stained DNA were observed in epilithic biofilms in wells and in the river and were classified as permanent hyporheos; nematode densities ranged from 0 to 7.9/ml in wells and from 0 to 2.0/ml in river samples (Ellis *et al.*, 1995).

A unique aspect of the groundwater fauna of the Flathead River is the presence of amphibitic Plecoptera (Table II). At least six species, some with multiple morphs, are involved. These insects are large bodied (2–3.5 cm in length as mature nymphs) and reside deep in the alluvia as larvae, moving to the river or spring brooks during the spring to emerge as flying adults. They mate and produce eggs, which are deposited into the river, where presumably they are entrained in the aquifer before hatching or from which the first instar larvae immediately migrate into the interstitial environment (Stanford and Gauvin, 1974; Stanford and Ward, 1988). We now think that the larvae follow thermal gradients to sites of epigeal ecdysis during the emergence process, because the wells across the valley floor

TABLE II Types, Common Species, and Total Numbers of Species of Epigeal and Hypogean Invertebrates Found to Date in the Flathead River, Based on the Typology of Gibert *et al.* (Chapter 1)

Life history type	Numeric dominants	Total number of species
Stygoxene	Trichoptera	137
	<i>Archtopsycha grandis</i>	
	Plecoptera	
	<i>Taenionema pacificum</i>	
	<i>Suwallia pallidula</i>	
	<i>Isoperla fulva</i>	
	Ephemeroptera	
	<i>Ephemerella inermis</i>	
	<i>Rhithrogena</i> spp.	
	<i>Baetis tricaudatus</i>	
Stygophile Occasional hyporheos	Diptera	46
	<i>Simulium</i> spp.	
	<i>Procladius</i> sp.	
Stygophile Amphibite	Ephemeroptera	6
	<i>Ameletus</i> 2 spp.	
	<i>Paraleptophlebia</i> sp.	
	Plecoptera	
	<i>Capnia confusa</i>	
	<i>Suwallia pallidula</i>	
	<i>Sweltsa coloradensis</i>	
	<i>Hesperoperla pacifica</i>	
	Diptera	
	<i>Cricotopus</i> sp.	
Stygophile Permanent hyporheos	Plecoptera	20
	<i>Isocapnia crinita</i>	
	<i>I. grandis</i>	
	<i>I. vedderensis</i>	
	<i>I. missouri</i>	
	<i>Paraperla frontalis</i>	
	<i>Kathroperla perdita</i>	
	Copepoda	
	<i>Acanthocyclops montana</i>	
	<i>Diacyclops crassicaudus</i>	
	<i>brachycercus</i>	
	<i>D. languidoides</i>	
	Ostracoda	
	<i>Cavernocypris wardi</i>	
	Oligochaeta	
	<i>Lumbricillus</i> sp.	
	<i>Lumbriculidae</i> indet sp.	

(continues)

TABLE II (continued)

	Acarina	
	<i>Oribatei</i> indet sp.	
	<i>Halacaridae</i> spp.	
Stygobite	Amphipoda	8
Ubiquitous ^a	<i>Stygobromus</i> 2 spp. ^a	
	Isopoda	
	<i>Salmasellus steganothrix</i>	
	<i>Microcharon</i> sp.	
	Bathynellacea	
	<i>Bathynella</i> 2 spp.	
	Copepoda	
	<i>Parastenocaris</i> sp.	
	Archannelida	
	<i>Troglochaetus beranecki</i>	
Stygobite	?	?
Phreatobite		

^a Only *Stygobromus* sp. has been found in cave streams and alluvial aquifers.

sequentially become depauperate of larvae when river water penetrates the aquifer in association with the spring spate, when river temperatures are up to 4°C warmer than groundwater. Other explanations exist, including the possibility that the larvae can find surface water by following ion gradients. However, large numbers climb up the well pipes to undergo ecdysis above the water table, and water temperatures are significantly higher at the top of the wells during warm weather in the spring.

The distribution of stygobites and amphibites within the aquifer is clear. Stygobites are ubiquitous; amphibites are most common near the river (Figs. 3 and 5), although they were collected in all except three wells in the two transects (Fig. 5). By examining the distribution of the crustacean fauna using gradient and correspondence analyses, Ward *et al.* (1994) showed that crustacean stygobites attained maximum relative abundance near the center of the ancient floodplain, whereas permanent hyporheos (*e.g.*, copepods and ostracods; Table II) dominated closer to the river or in wells on the modern floodplain. Areas in the center of the aquifer (*i.e.*, about midway in the two transects across the ancient and modern floodplains) are associated with higher ion content (Fig. 3). We think that higher ion content is indicative of the longer residence time of water in the aquifer and the presence of zones of lower hydraulic conductivity and, by inference, lower porosity. Hence, faunal patterns to some extent may be attributed to variations in porosity. However, well G (Fig. 5) penetrated very porous substrata based on high pump rates (>40 l/min), yet it was characterized by high ion content, fairly abundant stygobites, and no amphibites. It is likely the high-ion waters

are phreatic and not very interactive with the river for reasons that relate to the complexity of the interstitial milieu of this aquifer. As did Marmonier *et al.* (1992) for an alluvial floodplain aquifer on the Rhône River, Ward *et al.* (1994) concluded that the distribution and abundance of the groundwater fauna on the floodplain scale are structured by hydrogeologic and geomorphic processes that are not necessarily related in any meaningful way to distance from the river owing to spatial discontinuities in the lattice-like alluvium. An analysis of the relation of paleochannels, which are known to be areas of higher hydraulic conductivity, to faunal patterns (*e.g.*, installation of wells in high-porosity sites determined by ground penetrating radar or seismic techniques) may be more revealing.

The groundwater fauna of the Nyack Valley aquifer is very similar to that of the Kalispell Valley, except that some of the occasional hyporheos are different and are found in wells near the valley wall. Phreatic waters may be more limited. Spring-brook fauna also were studied to determine affinities with the groundwater biocenosis. Although permanent hyporheos (mainly copepods) were abundant in the spring brooks, stygobites were never found and amphibites were rare. The spring-brook fauna was primarily composed of stygoxenes with temperature and substratum as primary determinants (Case, 1994).

C. Food Web Relationships

The energy base of the food web of the Flathead River alluvial aquifers appears to be the speciose microbial biofilm (bacteria and fungi) and associated microconsumers (Protozoa, nematodes, and other microscopic fauna). The productivity of this microbial loop is likely limited by the availability of short-chain DOM, because other nutrients appear to increase in concentration relative to those in the river. Although POM is entrained in the aquifer, based on the presence of algal cells with viable chromatophores and measurable concentrations of chlorophyll, the importance of detritus relative to DOM is not clear. Although others have shown that microbial metabolism in groundwaters is controlled by entrainment of POM (Chapter 7), most of the work has been done in situations in which some or most of the organic matter is derived from pollution. The pristine Flathead systems are extremely oligotrophic, and carbon limitation relative to the supply of other nutrients (N, P, and trace metals) remains at issue. Because nitrate accumulates in aquifers and oxic conditions persist in the wells, nitrification is an important process within the groundwater microbial loop. Our work is now emphasizing the assessment of N flux and the importance of the groundwater N subsidy to biofilms in surface waters.

Higher level consumers in the food web are composed of a wide variety of sizes and taxa of stygobite and stygophile consumers. Amphibitic stone flies seem to be the top consumers in the groundwater food web, at least

in the hyporheic waters. However, in phreatic waters, where large stone flies are rare, *Stygobromus* spp. likely is the top consumer.

With R. Wissmar (University of Washington, Seattle, unpublished), we analyzed the stable isotopic enrichment of ^{15}N to trace trophic relations of the groundwater food web in comparison with that of the river (Peterson and Fry, 1987). The isotopic enrichment values for river and aquifer biofilms were significantly higher in the aquifer, supporting the notion of different conversion pathways for organic compounds. Nitrogen compounds incorporated into the food web by biofilm uptake were different in the river and in the aquifer, which supports the inference of nitrification as an important biotic pathway in groundwater. As a consequence, high-level consumer groups in the aquifer showed high enrichment values; *Paraperla* and *Stygobromus* had the highest enrichment values (+8–11 ‰), supporting the notion of these genera as high or top-end consumers in the food web. However, they may not be the top consumers in the interstitial food web, because a small (5 cm) salamander, tentatively identified in the genus *Ambystoma*, was collected from well D (Fig. 5).

In addition to the importance of nutrient conversions in groundwater food webs, transport of groundwater macrofauna to surface waters may also provide an important food source for riverine consumers. The amphibitic stone flies are very abundant during emergence in the river and on the shoreline, relative to most of the benthic species (Stanford, 1975). The large volume of the groundwater system apparently allows greater production of the amphibitic stone flies, and, when they move from the groundwater into the river during the emergence process, they dominate the drift and are a major food source for fish and other top consumers in the river (Perry and Perry, 1986).

Amphibitic assemblages similar to those in the Flathead likely exist in many well-oxygenated interstitial aquifers fed by river interflow in North America and elsewhere, depending on the origin and attributes of the porous milieu (Stanford and Ward, 1993). We have found the same interstitial fauna in the Methow River in Washington, and others in western North America will likely be reported in the future.

D. Cave Streams

We know only that the stygobite *Stygobromus* spp. is present in cave streams in the Flathead catchment. Several specimens were collected with a kick net at the Trail Creek site. The stream intersects the cave about 300 m from the dry portal. Presumably the stream flows into the alluvium of Trail Creek, but additional work is needed. Hence, we conclude that *Stygobromus* is a ubiquitous genus (Table II), but we do not know if phreatobites are present in the alluvial aquifers, owing to a lack of species-specific associations with habitat types. However, this is the first report of groundwater fauna in cave systems in the Belt Series substrata of the Rocky Mountains.

VII. CONCLUSION

Shallow alluvial aquifers biophysically connected to the main channel are fundamental units of the geohydraulic continuum of the Flathead River. They are not delineated by the active river floodplain; they also include adjacent low terraces composed of ancient glacial outwash floodplains and modified by recent cut and fill alluviation mediated by flooding. Paleo-channels are evident on the ancient floodplain surface and provide clues to the complicated lattice-like structure of the alluvial aquifer. Interactions between river inflow and aquifer discharge produce biotic patterns that manifest as complex groundwater food webs and riparian plant assemblages, although detailed study of the latter remains to be performed. Over 80 taxa of stygophiles and stygobites are present in the groundwater food webs. Considerable taxonomic evaluation of the groundwater fauna also remains to be performed, and the list of stygobites will likely increase. Clearly, riverine biodiversity is in large measure influenced by the groundwater biotope. Bioproduction may be controlled by the availability of low-molecular-weight DOM, although nitrification and other microbially mediated conversions increase the solute load of the water as it fluxes from the river, through the aquifer, and back into the river. These and other process-response mechanisms also require greater elucidation. However, it is clear that the interaction zone between the river and the aquifer is expansive (*i.e.*, involving amphibitic and stygobitic forms; Figs. 3 and 5), and the flux of materials in this zone probably controls the biophysiology of the river and also may influence advective processes in Flathead Lake (*e.g.*, pelagic autotrophy in response to nutrient loads from the river).

These findings have profound ramifications for the management of river corridors in the Flathead and other gravel bed rivers, especially those that remain relatively pristine. The expansive interaction zone and the flux of water and materials between surface water and groundwater require a broader conception of the floodplain (riparian) corridor than usually is applied in river management plans. In the Kalispell Valley human activities on the ancient floodplain are beginning to subsidize the nutrient load of the aquifer and alter faunal distribution patterns. The sensitive nature of these groundwater environments requires greater appreciation in the context of pollution control. In the Flathead and elsewhere these shallow alluvial aquifers are strategic sources of potable supplies. Moreover, we are beginning to recognize important interactions between wetlands created by groundwater upwelling and wildlife. For example, for the Nyack Valley, we have observed that spring brooks are used as spawning and rearing habitats for fishes and are modified by dam building activities of the beaver (*Castor canadensis*). A variety of ungulates and their predators rely on the riparian plant communities produced by the interactions between interstitial and overland flow processes. We conclude that conservation of groundwater aquifers is important not only from the standpoint of hypogean flora and fauna that are

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Groundwater Fauna of the South Platte River System, Colorado

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I. INTRODUCTION

The groundwater fauna associated with alluvial aquifers of North American rivers has remained virtually uninvestigated. Aside from studies of the distribution of riverine animals in surficial bed sediments, most research on the hypogean fauna has been conducted during the past decade (Pennak and Ward, 1986; Stanford and Ward, 1988; Strayer, 1988; Williams, 1989; Palmer, 1990; Ward and Voelz, 1990; Boulton *et al.*, 1992). This is in marked contrast to the intensive and extensive work on the groundwater

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1994

Cover illustration: The interstitial habitat and some of the subterranean-dwelling organisms. See Chapter 8, Figure 1.

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Academic Press, Inc.
A Division of Harcourt Brace & Company
525 B Street, Suite 1900, San Diego, California 92101-4495

United Kingdom Edition published by
Academic Press Limited
24-28 Oval Road, London NW1 7DX

Library of Congress Cataloging-in-Publication Data

Groundwater ecology / edited by Janine Gibert, Dan L. Danielopol, Jack Stanford.

p. cm. -- (Aquatic ecology series)

Includes bibliographical references and index.

ISBN 0-12-282110-6 (case)

1. Groundwater ecology. 2. Groundwater. 3. Aquifers.
I. Gibert, Janine. II. Danielopol, Dan L. III. Stanford, Jack
Arthur, date. IV. Series.

QH541.5.G76G76 1994

574.5' 2632--dc20

94-17095
CIP

PRINTED IN THE UNITED STATES OF AMERICA

94 95 96 97 98 99 MM 9 8 7 6 5 4 3 2 1

In honor of Professor René Ginot

This book brings together numerous studies of groundwater ecology by researchers from all over the world. For many years Professor Ginot has contributed to and encouraged this kind of research at the University Claude Bernard (Lyon 1) in France where he created the Groundwater Hydrobiology and Ecology Laboratory in 1960. He was the guiding spirit for many of the researchers who have written chapters in this book.

An international specialist in hypogean Amphipod Crustaceans, he is the author of (among numerous volumes and papers) a remarkable monograph on *Niphargus* and of a book (in collaboration) called *Introduction to Underground Biology and Ecology* which has been responsible for awakening many a vocation.

This book gives us the opportunity to thank him for all he has done for groundwater research, and we should like to present it as a mark of our gratitude and affection.

Janine Gibert