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THE HYPORHEIC ZONE CONSIDERED AS AN ECOTONE

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ABSTRACT

Physical, chemical, or biological exchanges that occur between the groundwater system and surface waters pass through the interstitial sediments underlying the river channel. This paper assesses the role these interstitial sediments can have in lotic ecosystem functioning. In addition to regulating energy and material exchange in lateral and upstream-downstream linkages, hyporheic sediments support an important biocenosis and can be an important site for evolution and colonization. The hyporheic zone is a transitional zone of boundary control between adjacent ecological systems and may be considered as an ecotone.

KEY WORDS: Hyporheos, rivers, meiofauna, ecotone.

INTRODUCTION

Interstitial alluvial sediments of lotic systems and sediments associated with riverine aquifers harbor numerous fauna (KARAMAN, 1935; HERTZOG, 1936; CHAPPUIS, 1946; MOTAS, 1958; HUSMANN, 1966). Previous studies have been descriptive and have emphasized the organisms' vertical and horizontal distribution. While the habitat has been considered as a biocenosis, little attention has been given to the role the biocenosis has in fluvial system dynamics.

This article considers the hyporheic habitat as an ecotone and emphasizes the importance of hyporheic sediments on mediating interactions between running waters and contiguous groundwaters. Similarly, WARD (1989) conceptualized the vertical dimension in lotic systems as exchanges of matter and energy between the channel and contiguous groundwater. Since interstitial alluvial sediments may extend laterally from the river channel for large distances (STANFORD & WARD 1988), they may have a large influence on neighboring regions and impact lotic function.

THE HYPORHEIC ZONE AS A SUPPORT FOR AN IMPORTANT BIOCENOSIS

Since the 1950's, European and North American researchers have reported an important biocenosis, called hyporheos, in the gravel beds of rivers and lake shores (ORGHIDAN,1955; WILLIAMS & HYNES, 1974). SCHWOERBEL (1961) defines the hyporheic zone as a practical term for a superficial groundwater habitat underlying a running water bed. Subsequent work has indicated a true hyporheal fauna confined below the water-substrate interface (HYNES, 1983). Besides an important biomass of bacteria and fungi, common fauna are protozoa, invertebrate worms, rotifera, crustacea and insect larvae, which may be distributed as deep as 70 cm vertically within the substrata (ANGELIER, 1953) and up to 60 cm laterally on the shore (HYNES, 1970).

There is a numerous and widespread fauna in the hyporheic zone. For example, O'DOHERTY (1988) and PERLMUTTER (1988) describe a community rich in species and with densities of up to 40,000 ind m^{-2} in the low order streams of the Southern Appalachian Mountains, U.S.A. A remarkable example is given by STANFORD & GAUFIN (1974). In their study the stonefly *Paraperla frontalis* is found only in subsurface samples and leaves the interstitial medium for emergence. A large variety of taxa (Sabater, unpublished data) were obtained at eighteen sites along the river Ter (Spain) from a depth of 20-50 cm with a Bou Rouch pump (BOU, 1974). Proportions of each taxon at each site are shown in figure 1.

In rivers with extensive hyporheos, standing crop biomass could easily exceed benthic epigean biomass. For example, STANFORD & GAUFIN (1974) found that the hyporheic zone extends laterally up to two km and to a depth of 10 m from the river. As expected when sampling a new habitat, new species not found in surface water are encountered in the hyporheic layers (DUMONT, 1983; SABATER 1987a, 1987b; SABATER & DE

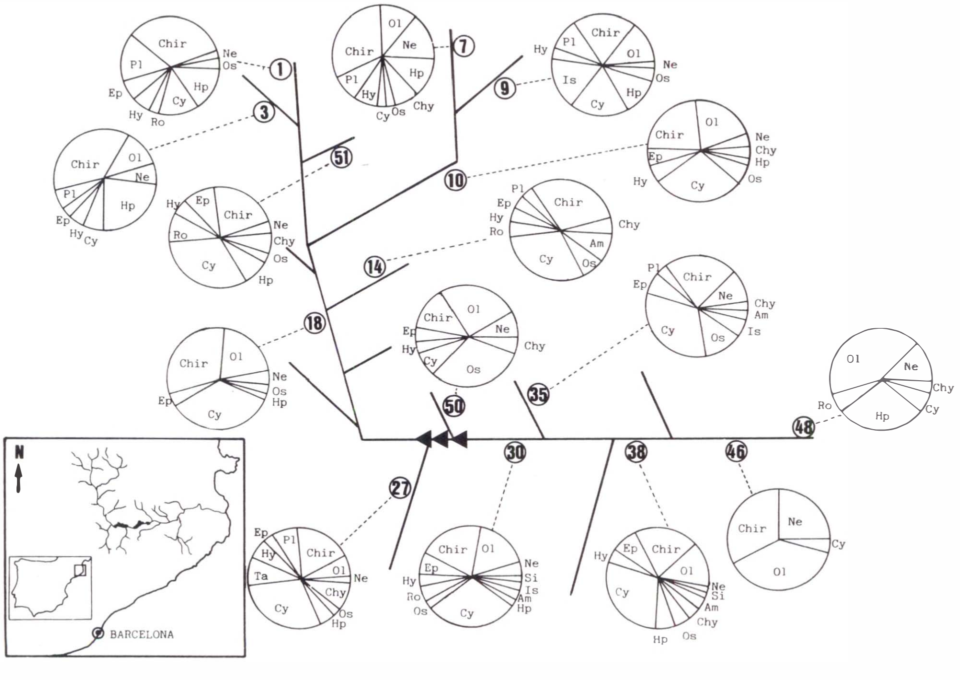

FIGURE 1. Different proportions of each taxon of meiofauna found along the Ter river (location in inset). Chir, Chironomidae larvae; Pl, Plecoptera larvae; Ep, Ephemeroptera larvae; Ro, Rotifera; Ne, Nematoda; Ol, Oligochaeta; Ta, Tardigrada; Cy, Cyclopoida; Hp, Harpacticoida; Chy, Chydoridae; Os, Ostracoda; Is, Isopoda; Am, Amphipoda; Sy, Syncarida; Hy, Hydracarina.

MANUEL, 1989).

A mixed community of stygobiont and epigean river species colonize the hyporheic zone temporarily or permanently (CHAPPUIS, 1950; WILLIAMS & HYNES, 1974; DANIELOPOL, 1976, 1984, 1989; DOLE, 1983; PENNAK & WARD, 1986). Hypogean (subterranean) taxa, called stygobionts, are abundant in the hyporheic zone. These organisms have developed specific morphological specializations and requirements (see MARGALEF, 1976; HOLSINGER, 1988). An important reference on stygofauna is BOTOSANEANU (1986).

Surface animals may enter the interstitial medium to find food or refuge from physical (SLACK, 1955) or biological adversities. STANFORD & WARD (1988) observed overlap between epigean and stygobiont taxa in several wells located in the hyporheic zone. CREUZE des CHATELLIERS & MARMONNIER (1990) found that physical perturbations caused high numbers of Cladocera and Ostracoda to enter interstitial layers. VILA (1989) considered that the large number of Cladocera species found in the surface sediments of several Indiana streams could, in part, be explained by retreat to deeper sediments after an increase in discharge.

THE ROLE OF THE HYPORHEIC HABITAT IN PROVIDING A PATHWAY FOR ACTIVE COLONIZATION

Surface flow and groundwater have a dynamic and seasonally variable influence on the hyporheic habitat due to hydrologic disturbances such as spates and droughts, that alter the physical structure of hyporheic sediments. A disturbance can affect energy flows into and out of the sediments. For example, high discharge could restructure sediments and either deplete or recharge sediments with detritus. Consequently, community structure and faunal distribution in the hyporheic zone are dynamic and vary between sites and seasonally within a site depending upon the disturbance regime (DOLE, 1983, 1985; WILLIAMS, 1984). Sampling regimes must be structured accordingly and such dynamics complicate extrapolations of the results of studies that only consider a single point in time or space.

Biota may navigate through the interstitial waters by following several factors or combination of factors; thermal or ion concentration gradients (STANFORD & WARD, 1988); food quality or quantity (e.g. detritus); or by following a preferred prey species. Organisms can also transform their environment, e.g. pelletization of sediment that affects water circulation (DANIELOPOL, 1984).

The hyporheic zone can be a mixing ground important in evolution, large scale migratory patterns and survival in a habitat without large predators. RUFFO (1961) considered that the interaction of groundwaters and water in the hyporheic zone could allow for the migration of organisms between different aquatic systems on an evolutionary time scale (Fig. 2). So, although not presently connected, modern faunal assemblages may have been shaped from interactions permitted by this "interstitial highway" (WARD, 1989). ROUCH & DANIELOPOL (1987) suggested that some surface species inhabiting interstitial waters are already preadapted morphologically and

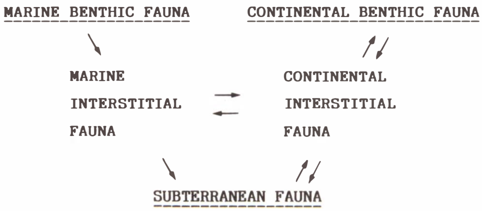

FIGURE 2. Scheme showing pathways on an evolutionary time scale for the migration of organisms between groundwaters, hyporheic zone, and surface waters.

physiologically to colonize groundwater habitats. For example, SKET (1985) pointed out that several crustacean species are able to tolerate low oxygen conditions. DANIELOPOL (1989) mentioned other examples.

The study of phylogenetically related species may give an insight into the origin and evolution of the stygobionts as well as the degree of adaptation to the subsurface environment. MARGALEF (1983) suggested that many hyporheal species found refuge from cold weather in meridional basins during the Pleistocene glaciations. These basins were later centers of dispersion and recolonization.

IMPORTANCE OF THE HYPORHEIC ZONE IN AFFECTING PROCESSES OCCURRING IN THE RIVER CHANNEL

The hyporheic zone can have a dynamic flow regime. At high discharge, water moves from the river channel into the hyporheic zone, whereas at low discharge groundwater is discharged from the hyporheic zone into the river. Groundwater outflow contributes to the basal flow in most river channels (HYNES, 1983). There is evidence that the thickness of the hyporheic zone is related to the amount and extent of discharge and recharge areas in the river channel (GODBOUT & HYNES, 1982). Larger areas of discharge and recharge occur in coarse sediments than in sandy sediments (MESTROV & LATTINGER-PENKO, 1981).

Changes in the geomorphology along the longitudinal river profile result in a pattern of alternate areas of upwelling and recharge. Further understanding of species distribution and processes such as nutrient dynamics will require more detailed knowledge of matter flux and hydrodynamics at each hydrologically distinct stream section. For example, preliminary mass transport calculations indicate that nutrient discharge from the hyporheic zone may be crucial for the enhancement of phytobenthos production (STANFORD & WARD, 1988). The nutrient flux in upwelling zones may potentially result in biological "hot spots" (increased production, high species number), paralleling those reported in the upwelling areas of marine systems. In streams, however, site specific variables such as strong lateral or upstream inputs may prove to be overriding factors.

The hyporheic zone may also be a nutrient sink. HILL (1981) reported a fifty percent reduction in nitrate attributed to bacterial denitrification in deep sediments. Hyporheic metabolism may contribute significantly to total metabolism and could impact surface recharge nutrient dynamics. However, few studies have considered its importance (GRIMM & FISHER, 1984).

Conversely, nutrient uptake in surface waters may impact recharge waters. For example, GRIMM *et al.* (1981) attributed nitrate uptake in desert stream reaches to algal activity. There has been little work on the role of potamoplankton on nutrient or carbon dynamics, especially in the lower reaches of large rivers. Transfer of floodplain bacterial inputs into ciliate biomass (CARLOUGH & MEYER, 1989) would increase carbon spiraling distance as animals drift downstream. As in lakes, there may also be tight coupling between the "leaking" of nutrients from zooplankton and phytoplankton excretion and uptake as the "slugs" move downstream. Recent channelization and reduced floodplain interaction due to human activities in lower reaches may have reduced the role of the hyporheic zone in mediating interchange between surface and groundwater and increased the importance of water column processes.

WILLIAMS & HYNES (1974) considered the hyporheic zone as a sink for fine particulate organic matter (FPOM; e.g. $< 50\ \mu m$) from the channel. However, FPOM decomposition supports the ground water food chain and could constitute a nutrient subsidy to primary production in areas of the river channel where hyporheic waters are discharged (STANFORD & WARD, 1988). STANFORD & WARD (1988) found that the annual nitrogen load to channel water in the Flathead River is increased 75% at baseflow due to aquifer discharge. RUTHERFORD & HYNES (1987) suggested that dissolved organic carbon (DOC) fluctuations at baseflow can be explained by the stream beds capacity to remove surface water DOC. LUSH & HYNES (1978) and LOCK *et al.* (1984) observed rapid DOC uptake by substrata suggesting an active biological uptake in the hyporheic zone.

HUSMANN (1978) has stressed that well oxygenated hyporheic areas are biologically active zones that contribute to the self purification of organically polluted waters; similar processes occur in waste treatment plants. Such considerations cannot be ignored in studies related to the spiraling concept (NEWBOLD *et al.*, 1982). However, CROCKER & MEYER (1987) have stressed the important role of hyporheic sediments in generating DOC from *in situ* POM decomposition.

In general, nutrient concentrations are significantly higher in interstitial waters than in surface waters (HYNES, 1983; VALET *et al.*, 1990). Phosphate and nitrogen concentrations in the River Ter are higher in the hyporheic than in surface waters (Fig. 3). Given the importance of nutrients to productivity, a large hyporheic nutrient pool could result in an important contribution to the system metabolism. This suggests that physical and biological

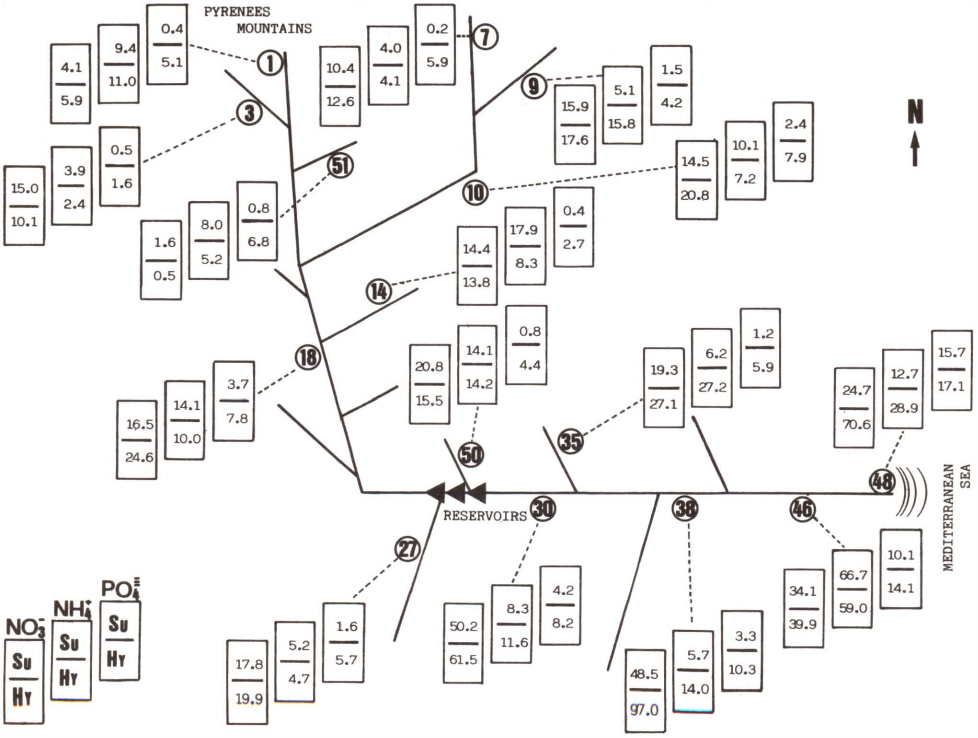

FIGURE 3. Comparison of phosphate, nitrate and ammonium concentrations between hyporheic (Hy) and surface (Su) waters along the Ter river.

processes occurring within the hyporheic zone should be included in a conceptualization of stream ecosystem function. Even preliminary research comparing nutrient levels in interstitial waters with levels entering the river channel would increase our understanding of nutrient dynamics in streams.

The great variety of organisms inhabiting the hyporheic zone utilize food carried by both active (i.e., mediated by organisms) and passive transport in waters moving vertically and laterally from the stream channel. The vertical distribution of these animals is determined by external energy, the velocity of flow, and the diffusion of gases or matter through the alluvial sediments along the river (MARGALEF, 1983). Distinct vertical and horizontal faunal distribution patterns may even be strongly correlated with environmental gradients (FENCHEL, 1978; WILLIAMS, 1989). Even though standing crop biomass in the hyporheic zone may or may not exceed benthic biomass in surface sediments, the impact of the interstitial organisms on ecosystem processes could be substantial. For example, meiofauna were estimated to account for approximately one half the carbon assimilation in Mirror Lake (STRAYER & LIKENS, 1986).

THE HYPORHEIC ZONE WITHIN A BOUNDARY PERSPECTIVE

The hyporheic zone has the following features (DANIELOPOL, 1982; HYNES, 1983; BOTOSANEANU, 1986):

Darkness. It is functionally a sink for organic matter. By affecting water turnover rate the hyporheos can impact energy and matter transport through the hyporheic zone. It is an open functional system since it mediates physical, chemical and biological exchange between the ground water system and the surrounding surface environment; it is trophically impoverished and energy is mainly, or exclusively, allocthonous; physical variations in factors such as temperature and water flow are dampened and lag behind those occurring in neighboring surface habitats; there are gradients or discontinuous patches in physical parameters such as granulometry, conductivity or water salinity.

The widespread distribution and mobility of the hyporheic fauna coupled with the spatial and temporal independence of major external inputs of physical and chemical parameters from the sediments suggests that a precise definition and demarcation of the borders of the hyporheic zone is difficult, if not impossible (WILLIAMS, 1984; STANFORD & WARD, 1988; DANIELOPOL, 1989; TRISKA *et al*., 1989). It it therefore difficult to define ecologically a distinct hyporheic zone.

We propose that the hyporheic zone be viewed in a functional process framework as a significant component of the riverine landscape. Using ideas presented in NAIMAN *et al*. (1988), we believe that the hyporheic zone can be envisioned as a zone of transition between adjacent ecological systems. The hyporheic zone provides an example of boundary control on the function of the lotic ecosystem, since it can modify the direction, character and magnitude of materials and information exchanged between surface and subterranean zones along the river. Knowledge of the degree and strength of surface and groundwater interaction with the hyporheic zone would help us to understand processes such as nutrient loading and the regulation of matter and exchange in lateral and upstream-downstream linkages.

THE HYPORHEIC ZONE CONSIDERED AS AN ECOTONE

As a transitional zone, the hyporheic zone possesses specific physical, chemical and biological properties defined by space and time scales that can regulate the flow of energy and matter between different resource patches. The functional properties are as follows: 1) It can support high faunal densities and provide a critical habitat for some species. 2) It may be a refuge in which riverine zoobenthos escape environmental disturbances (e.g., spates, drought). 3) It contains a mixed assemblage of aquatic epigean fauna and other fauna from surrounding systems. 4) It contains a genetic pool for evolution. 5) It extends spatially allowing for species migration. 6) It is an important area for energy and material flux (e.g., nutrient cycling and decomposition). 7) It contains high concentrations of biologically important resources (e.g., nutrients, carbon). 8) It influences and is impacted by the hydrologic regime in the surrounding surface and groundwater areas. 9) It tends to dampen the amplitude of physical parameters. 10) It possesses the ability to resist change or a resilience to disturbance.

Finally, groundwater studies have two main aims of fundamental biological importance. First, interstitial biotopes provide evolutionary pathways linking groundwaters and adjacent surface freshwaters and marine environments (DELAMARE-EBOUTTEVILLE, 1957; PENNAK, 1968; HUSMANN, 1971). Attributes of the hyporheic zone are of considerable interest in investigating questions regarding the ecology, evolution and zoogeography of hyporheic fauna and questions concerning functional processes. Second, hypogean forms may be important as indicators of groundwater quality (DANIELOPOL, 1980).

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