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Ecology of the Agüera: a review of fourteen years of research in a Basque stream.

Arturo Elosegi, Ana Basaguren* & Jesús Pozo**

Abstract

We review the main results of fourteen years of research in the Agüera stream (northern Spain) from an ecosystem perspective. Physico-chemical characteristics show large spatial variations in the Agüera hydrographic net because of differences in geology and soil uses across the basin. Temporal variations are important at different scales, from diel to inter annual, making difficult to characterise water chemistry. Floods can occur at any time of the year, although they tend to be less frequent in summer. As a result of differences in rainfall patterns, the physical habitat for stream biota seems quite unpredictable, and the period free of flood-disturbances rather variable from year to year. In general, the biota shows small seasonal and large interannual differences in biomass. During long dry periods periphytic algae can be very abundant in mid reaches, and play a key role in nutrient retention. As a result, the Agüera shows an important capacity of self-purification. Biological traits suggest that the invertebrates have adapted to a low-seasonality environment with frequent, unpredictable floods. The timing of floods is important also in functional aspects like the efficiency of the ecosystem to process inputs of leaf-litter, the main food source in most headwater reaches.

These results stress the importance of sustained interdisciplinar research in one stream, of the ecosystemic perspective, and of looking at different spatial and temporal scales in the conceptual framework of the drainage basin.

• Key words: Stream ecology, water quality, stream metabolism, organic matter, breakdown, invertebrates, periphyton.

Laburpena

Lan honetan Agüera ibaian hamalau urtez eta ikuspuntu ekosistemikotik egindako ikerketen emaitza nagusiak laburtu ditugu. Agüeraren sare hidrografikoan uren ezaugarri fisiko-kimikoek aldaketa espazial handiak azaltzen dituzte, arroan barrena geologia eta lurraren erabilpenak asko aldatzen direlako. Aldaketa garrantzitsuak gertatzen dira denboran zehar, hainbat eskalatan, egunean zeharrekotik hasita urtetik urtera gertatzen direnetara, eta aldaketok uraren ezaugarri kimikoak karakterizatzea zail egiten dute. Uholdeak noiznahi gertatzen ahal dira, baina udan ez dira hain ohikoak. Euriteen gorabeheren ondorioz, ibaiko biotaren habitat fisikoak nahiko igertezina dirudi, eta uholderik gabeko tartea urtetik urtera asko aldatzen da. Orokorrean, bizidunen biomasak urtean zehar aldaketa txikiak jasaten

* *University of the Basque Country. Laboratory of Ecology, Faculty of Sciences.*
P.O. Box 644. • 48080 Bilbao, Spain.

ditu, baina aldaketa handiagoak urtetik urtera. Agorraldi luzetan alga perifitikoak oso ugariak izan daitezke ibaiaren erdi aldean, eta orduan eragin gakoa dute mantenugaiak atxekitzen. Horren ondorioz, Agüerak auto-arazketarako gaitasun aparta du. Ezaugarri biologikoek iradokitzen dutenez, ornogabeak urtesasoien arabera gutxi aldatzen den, baina uholde igertezinak dituen ingurunera moldatu dira. Uholdeak garrantzitsuak dira, era berean, ibaiaren ezaugarri funtzionaletan, hala nola, ekosistemak orbela (iturburuetako bazka nagusia) prozesatzeko duen efizientzian.

Emaitza hauek nabarmentzen dute ibai bat modu jarraiean eta hainbat disziplinetatik ikertzearen garrantzia, ikuspuntu ekosistemikoarena, eta eskala espazial zein denboral desberdinei erreparatzearena, beti ere drainatze-arroaren eskemaren baitatik.

• **Gako-hitzak:** Ibai-ekologia, ur-kalitate, ibai-metabolismo, materia organiko, deskonposizio, ornogabe, perifiton.

Resumen

Revisamos los principales resultados de catorce años de investigación en el río Agüera (norte de España) desde una perspectiva ecosistémica. Las características físico-químicas muestran grandes variaciones espaciales en la red hidrográfica del Agüera, debido a diferencias en la geología y usos del suelo a lo largo de la cuenca. Las variaciones temporales son importantes a diferentes escalas, desde la nictemeral hasta la interanual, dificultando la caracterización del quimismo de las aguas. Las riadas pueden ocurrir en cualquier momento del año, aunque tienden a ser menos frecuentes en verano. A consecuencia de las diferencias en el patrón de lluvias, el hábitat de la biota fluvial parece bastante impredecible, y el periodo libre de crecidas variable de año en año. En general, la biota muestra diferencias estacionales reducidas e importantes diferencias interanuales en biomasa. Durante periodos largos de sequía las algas perifíticas pueden ser muy abundantes en tramos medios, y desempeñar un papel clave en la retención de nutrientes. En consecuencia, el Agüera muestra una importante capacidad de autodepuración. Los caracteres biológicos sugieren que los invertebrados están adaptados a un ambiente de escasa estacionalidad pero donde ocurren riadas impredecibles. El tiempo de ocurrencia de las riadas es también importante en aspectos funcionales como la eficiencia del ecosistema para procesar entradas de hojarasca, la principal fuente de alimento en la mayor parte de tramos de cabecera.

Estos resultados recalcan la importancia de la investigación multidisciplinar y sostenida en un río, de la perspectiva ecosistémica, y de la observación a diferentes escalas espaciales y temporales, dentro del esquema conceptual de la cuenca de drenaje.

• **Palabras clave:** Ecología fluvial, calidad del agua, metabolismo de las aguas corrientes, materia orgánica, descomposición, invertebrados, perifiton.

Introduction

Rivers and streams are key ecosystems for man, as they offer important resources like water, energy, fish, transportation, fertile soils, or firewood, but also potential hazards like floods. Therefore, as human population and technological capacity rised through historical times, rivers and streams have been increasingly managed, often for mutually exclusive purposes. As a result, rivers all over the world have been dredged, straightened, polluted, dammed, and water has been withdrawn, fish stocks overexploited, and many plant and animal species threatened with extinction, to the point that almost no natural river or stream remains in Central and Western Europe, and many are severely impacted by human activities (L'VOVICH & WHITE, 1990). Thus, many of the resources aforementioned are no longer available, and there are frequent conflicts between uses, like water supply for drinking, industry and irrigation, or angling and hydropower generation.

At least in the so-called First World countries, awareness of the importance of a healthy environment has grown steadily during the last decades, and with it, the necessity of improving degraded ecosystems to a state in which they can fulfill more of the societal needs has become evident. Thus, ecosystem restoration (to revert to a "natural" state) and rehabilitation (getting closer to but without reaching a "natural" state) have become hot issues in environmental management (BRADSHAW, 1983; KAUFFMAN *et al*., 1997; FISRWG, 1998). For instance, the European Water Framework Directive (WFD, 2000/60/EC) recently adapted, sets out a policy and strategy for protection and restoration of aquatic ecosystems to at least good status by 2015, as well as protection of waters of high status. High and good status are the combination of physico-chemical characteristics of the water, of hydromorphological aspects of the water body, and of the structure and function of biological communities linked to the water systems. This is obviously a very ambitious goal that will require extensive improvement of inland and coastal water bodies.

To assess the ecological state of, and especially to restore an ecosystem, albeit partially, it is essential to have a clear reference endpoint (BRADSHAW, 1983; KARR & CHU, 2000). Ideally, the reference should be the state of the original ecosystem prior to being impacted by human activities. Unfortunately, many rivers across the World have been altered for so long that no relevant data exist of their original state. In this situation, one could choose a similar, unimpacted river, and manage its impacted counterpart accordingly, but even this is difficult in many European regions, given the virtual absence of natural rivers. In fact, most references to natural aquatic systems had to be removed from the WFD first drafts. Therefore, the WFD states that to assess the ecological state of a river reach, we must compare it with a similar river that is in high ecological status, a state with minimum or no impact. Even this is more easily said than done, as we should have several reference datasets for each type of river system. This implies a deep knowledge of the physical structure, water chemistry, plant, invertebrate and vertebrate populations, as well as basic functional properties of lotic ecosystems ranging from small streams to large rivers and estuaries in each ecoregion (MOOG & CHOVANEC, 2000). In many European countries most of the data necessary are sadly missing, because this research has often been considered "basic", and thus, given low financial priority.

The group of stream ecology, at the Science Faculty, University of the Basque Country, has been researching the ecology of Basque streams since 1988. Our main goal is to know the basic structure and function of streams running to the Atlantic coast of Spain. We have studied mainly the Agüera, one of the less modified streams near Bilbao, with the financial support of the University of the Basque Country, the Basque Government, the Spanish

Government, and now, the European Community. Here, we review some of our findings in the Agüera, and depict some of the main characteristics of Basque streams.

The drainage basin

The Agüera stream (Fig. 1) drains a basin of 145 km^2 in the border between Biscay and Cantabria (northern Spain). Its highest point is mount Burgueño (1044 m a.s.l.), but there are several other mountains around 1000 m high (Jorrios, Armañon, Kolitxa…). The basin is carved over Cretaceous materials: the southern part corresponds to Upper Cretaceous sandstones and mudstones of deltaic origin, the central part to thick "Urgonian" arrecifal limestones from the Middle Cretaceous, and the northern part to fluvial, lacustrine and estuarine sandstones and mudstones from the Lower Cretaceous, with some scattered patches of limestone. As a result of the Pyrenean Orogeny, the substrate has been severely folded and faulted, and some of these faults control the course of the stream, which runs North from the source to the neighbourhood of Agüera, then turns North-West, and after Trebuesto recovers the North bearing. An interesting feature is the importance of groundwater drainage in the central calcareous belt, where several important springs occur (Cruz-San Julián *et al*., 1986), as well as more diffuse groundwater discharges to the stream channel.

The climate is humid oceanic, with an annual precipitation of 1,500 mm, mainly in form of rain, regularly distributed throughout the year. The annual mean temperature is 14.3°C, and the monthly mean varies between 9.8°C in January and 18.5°C in August (data from Udalla, corresponding to the period 1990-2000).

Population density is low, settlements disperse, and the biggest villages are those of Villaverde (pop. 426), Trucíos (pop. 540) and Guriezo (pop. 1,715). The main human activities are forestry, livestock farming and agriculture. As a result, 50% of the territory is covered by tree plantations (mainly *Eucalyptus globulus* Labill and *Pinus radiata* D. Don), 29% by grassland, meadows and croplands, 10% by deciduous oak forests, and 7% by holm oak forests. Other vegetation types include scattered shrubs and herbs over limestone outcrops, and alder forests on river banks. In general, these land uses are mixed in an intricate patchwork, although there are extensive eucalyptus plantations in the lower part of the basin. During the last years eucalyptus became more abundant, while meadows and pine plantations decreased. Eucalyptus are harvested for pulpwood in a very short rotation time (ca. 12 y), usually in large clearcuts. Pine forests are harvested every 35-40 years, especially for furniture, and oak forests are scarcely harvested at all. Livestock is dominated by sheep and cattle. Most graze extensively in mountain pastures, heathland and forests, although there are some farms where livestock are kept in high densities. As an additional source of income, corn, potatoes and vegetables are grown in small land patches. The industry is virtually absent from the basin, but tourism is gaining importance, and the number of weekend houses is rising, although the number of residents has decreased in some 250 persons in the last 15 years, especially in Guriezo.

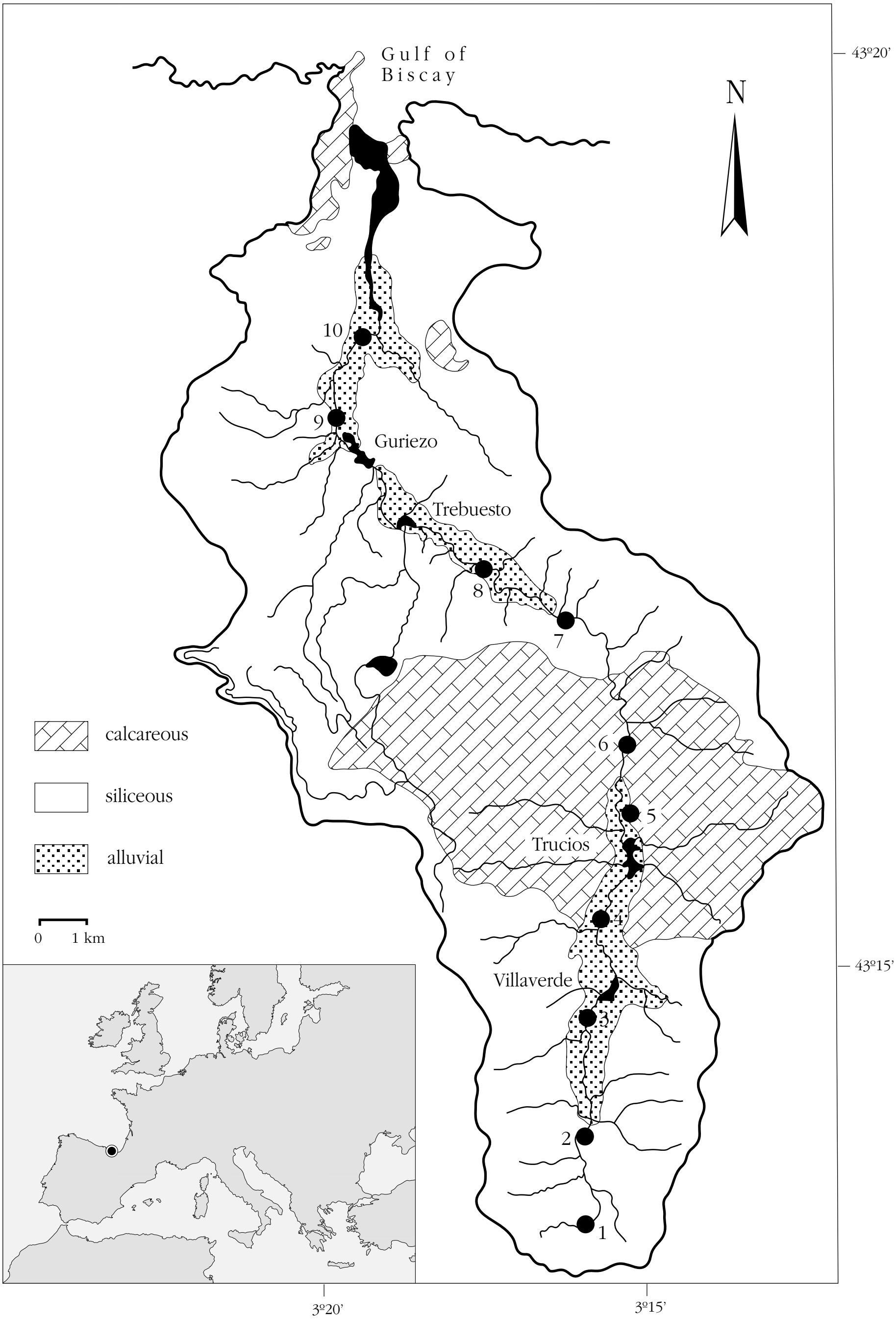


Fig. 1.- The Agüera stream basin. Geography, lithology and location of the main urban areas. The numbered black dots are some of the stations sampled in the main reach and referred in the text.

THE STREAM CHANNELS

The source of the Agüera is located below mount Kolitxa, at 450 m a.s.l., and its mouth in Oriñon, 30 km downstream. With the tributaries, the Agüera's hydrological net include 106 km of first-order reaches, 42 km of 2nd-order and 25 km of third-order ones (measured at a scale 1:50,000). Drainage density is low (1.4 km/km^2), because of the hard substrate and abundance of underground drainage (ELÓSEGUI, 1992). It is an erosive stream, whose straight channel is often incised and disconnected from the scarce floodplains. Carved over horizontal strata, the small tributaries show a typical step/pool profile, and third-order reaches riffle/pool sequences. Boulders, cobbles and gravel are the main substrate, although there are extensive outcrops of bedrock that result in locally very small bottom roughness (DÍEZ *et al*., 2001).

Riparian forests appear along most reaches, but their cover and maturity is highly variable (ELÓSEGUI & POZO, 1998; DÍEZ *et al*., 2001). In the main axis of the Agüera stream less than 1 km (3%) is devoid of riparian forests (ELÓSEGUI, 1992).

There are 14 small dams from the source to the mouth of the Agüera, most built for mills and old iron factories that are long unused. Nevertheless, many probably are important barriers for fish. Some short reaches of the Agüera, especially around the villages, are channelized, but their total length is less than 2 km (ELÓSEGUI, 1992).

HIDROLOGY AND WATER CHEMISTRY

Because of their climate, Atlantic rivers and streams are temporally less variable than Mediterranean ones, as rainfall periods are more extended and dry periods less severe. Furthermore, interannual variability is usually lower in temperate than in Mediterranean or semi-arid environments (BLONDEL & ARONSON, 1999; MCKEE *et al*., 2000). For instance, during the study period, the rainfall in Udalla (Cantabria) ranged from 957 mm in 1991 to 1,933 mm in 1996, and annual discharge of the Agüera ranged from 62.3 Hm^3 in 1990 to 142.0 Hm^3 in 1998, a relatively low variation.

Nevertheless, although the climate in Biscay and Gipuscoa is mild and typically oceanic, the small distance from the mountains to the sea make rainfall patterns highly variable in space, streams are steep and torrential, and severe floods historically have occurred at any time of the year (ASEGINOLAZA, 2000). The frequency and size of floods are key factors for stream biota and function (TOWNSEND & HILDREW, 1994), but the critical threshold for a flood to be considered a disturbance depend on the organisms considered (STOCK & WARD, 1989; MARKS *et al*., 2000). ELÓSEGUI (1992) showed that in the Agüera stream floods below 20 m^3/s produced only partial scouring of periphyton, whereas floods over 30 m^3/s reduced drastically periphytic biomass and could then be considered catastrophic disturbances for algae. Fig. 2 shows the hydrographs of years 1998 and 2000 at the mouth of the Agüera. The patterns are quite contrasting: 6 floods over 30 m^3/s occurred in 1998, rea-

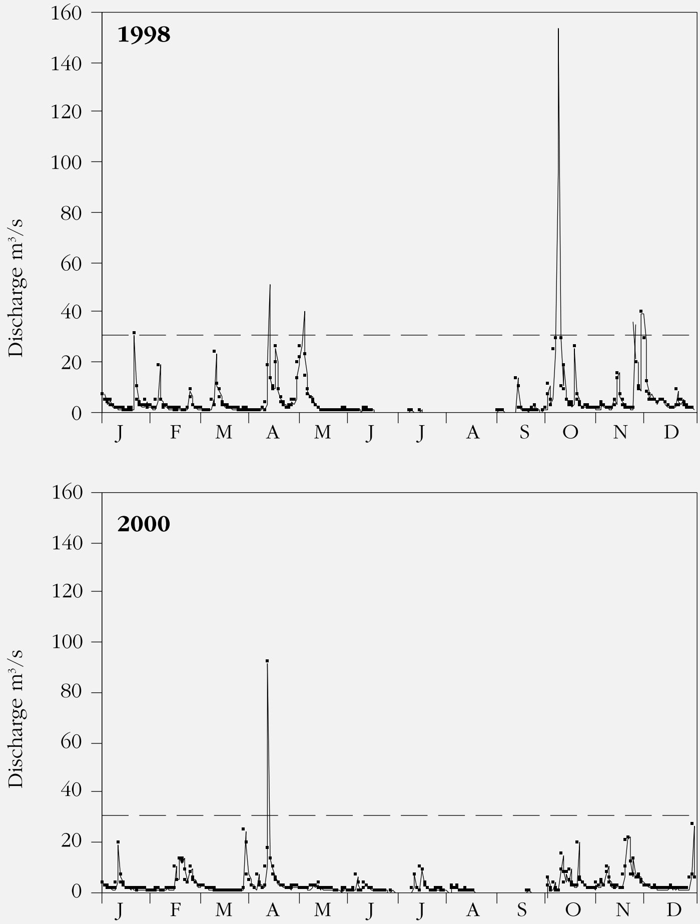


Fig. 2.- Hydrograph of a wet and a dry year at the mouth of the Agüera. The dotted lines mark the threshold for catastrophic scouring of benthic algae.

ching a peak of 153 m^3/s, whereas in 2000 only one flood greater than 30 m^3/s was registered. Therefore, the disturbance frequency and time available for development of the communities can change greatly from year to year. From 1988 to the present, the length of the flood-free periods has been very different: it lasted a whole year from 4th April 1988 to 5th April 1989, a period in which there were important restrictions to drinking water supply in Bilbao; in contrast, in year 2000 the period of hydrological stability was restricted to 5 months from May to September.

Hydrological variability in the Agüera affects physico-chemical characteristics of the water, which can differ greatly from dry to wet years (ELÓSEGUI & POZO 1992, ELÓSEGUI &

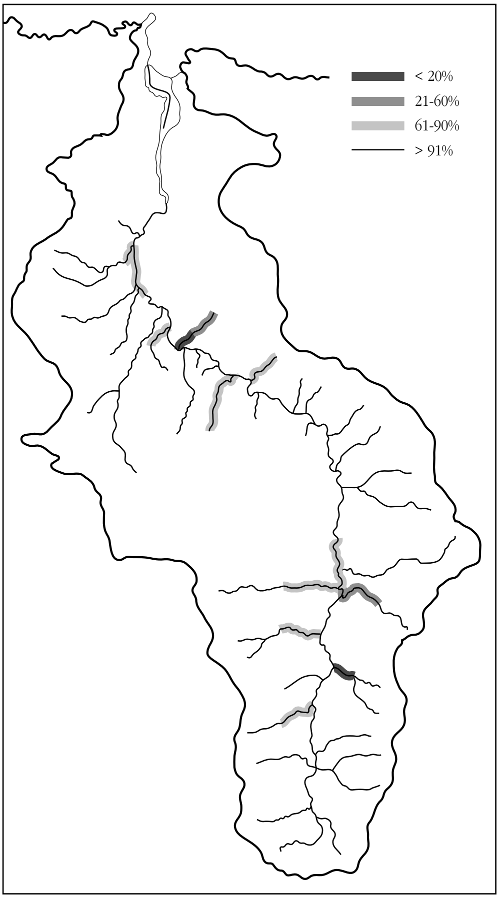


Fig. 3.- Oxygen saturation through the Agüera basin in summer (10th July 1990). Note that despite the general good oxygen levels, some small tributaries suffered severe hypoxia.

Pozo, 1994a). Different sources of variability (both spatial and temporal) overlap, giving a rather complex pattern of changes for the variables studied (Elósegui & Pozo, 1994a; Elósegui *et al.*, 1997).

In general, spatial differences are large in the Agüera stream and reflect the geology and land-use of the sub-basins drained by each reach, plus the sewage inputs from villages. Thus, four zones can be differentiated in the main axis of the stream (Pozo *et al.*, 1994b): from the headwaters to Villaverde, there is a zone of soft waters with low nutrient concentrations; from Villaverde to Trucíos the stream runs through the calcareous belt in the middle of the basin, and its conductivity, as well as its nutrient content, increase; downstream from Trucíos there is a long reach without nutrient inputs where the stream recovers very high water quality; and finally, when running through Trebuesto and Guriezo, urban sewage causes an increase in nutrient contents. This pattern gets more complex when we look at the tributaries, as they show a more diverse array of conditions. For instance, an extensive survey of 60 reaches showed that oxygen levels were very low in some tributaries running near dairy farms (Fig. 3). Similarly, the phosphorus concentration of some tributaries was 10 times higher than the highest detected in the main axis (Elósegui *et al.*, 1997). Although those tributaries were small and had overall little influence on oxygen and pollution levels in the main stream, they could be ecologically important as they could act as barriers for dispersal of many organisms.

To discern which factors were responsible for the physico-chemical characteristics of the water through the basin, we measured 26 environmental variables in the sub-basin drained by each of 60 reaches studied. These included physiographical variables (size, perimeter and differential elevation of the basin, length of the drainage net, drainage density, Gravelius's

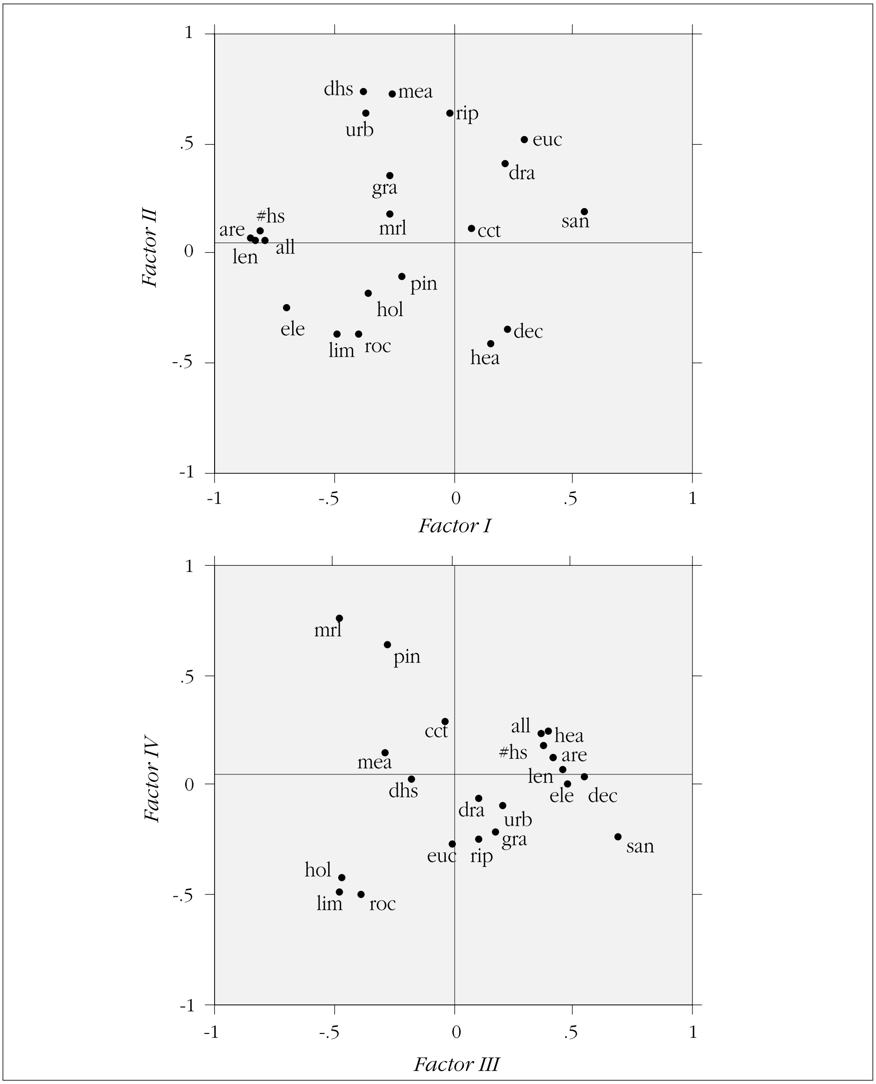


*Fig. 4.- Results of PCA with the main morphometric variables measured for 60 sub-basins in the Agüera system. (*are = *area drained;* len = *length of drainage net; ;* dra = *drainage density;* gra = *Gravelius's index of compactness;* #hs = *number of houses;* dhs = *density of houses;* urb = *% of basin covered by urban areas;* all = *% of basin covered by alluvium;* mrl = *% of basin covered by marls;* lim = *% of basin covered by limestone;* san = *% of basin covered by sandstone;* euc = *% of basin covered by eucalyptus;* pin = *% of basin covered by pine;* rip = *% of basin covered by riparian forests;* dec = *% of basin covered by other deciduous forests;* hol = *% of basin covered by holm oak;* cct = *% of basin covered by clearcuts;* roc = *% of basin covered by bare rocks;* hea = *% of basin covered by heathland;* mea = *% of basin covered by meadows and croplands.*

index of compactness), percentage cover of the main geology types, percentage cover of main soil uses, and number of houses. A Principal Component Analysis was performed with these variables. The first four axes accounted for 20.7, 14.8, 13.9 and 10.9% of the total variance, respectively. Factorial axis I was related to the size of the sub-basin, and inversely correlated to variables like basin surface and perimeter, percentage cover of alluvial sediments and number of houses (Fig. 4). Axis II was related to humanization of landscape, as it opposed lowland sub-basins with more urban and agricultural cover to upland sub-basins covered by forests. The plane of axes III and IV showed the link existent between lithology and soil uses, and located on its lower left quadrant sub-basins in limestone areas covered by holm-oak, and on its higher left quadrant sub-basins covered by pine plantations over marls. The right half of this plane grouped siliceous basins, either small tributaries, or low reaches of the main axis where the importance of the calcareous belt decreases rapidly downstream from Trucíos. Therefore, soil uses, human settlements and geology are tightly linked in the Agüera basin. A cluster analysis with the results from this PCA yielded five classes of sub-basins (Table 1). Class 1 was characterised by small and steep siliceous basins, with scarce alluvial materials, and covered by forests or heathland; class 2 grouped basins with high percentage or marls, and covered by pine plantations; class 3 grouped siliceous basins covered with eucalyptus plantations and with abundant meadows; class 4 corresponded to calcareous basins with abundant holm-oak forests; and class 5 grouped low reaches of the Agüera stream, that as a result of their bulk size had more mixed geology and vegetation. Finally, we performed stepwise regressions between PCA factorial axes and the main physico-chemical variables measured in all 60 sites, seasonally through one year. Most variables were correlated to more than one factorial axis, showing the complex interrelation between basin and water characteristics (Table 2). Variables linked to the mineral content of water were negatively correlated to axes I and III, showing the effect of lithology on them. Nutrients were correlated to axis II, because of the effect of agriculture and human settlements on eutrophication. An interesting feature was that the behaviour of nitrate was opposed to those of nitrite and phosphate. The main origin of nitrate seems to be soil leaching, whereas nitrite and phosphate are especially associated to sewage inputs (Harper, 1992). Ammonia showed no correlation with the first factorial axes.

Table 1.- Differential characteristics of the main 5 classes of sub-basins, as resulting from PCA of variables linked to physiography, vegetation and human activities.

Class	High	Low
1	sandstone, heathland, deciduous forest	houses, holm oak, alluvial, marls, meadows
2	marl, pine	sandstone
3	eucalyptus, riparian forest, drainage density, meadows, sandstone	pine, heathland
4	limestone, holm oak, rocks	sandstone
5	alluvial, channel length, surface, houses, urban	

Regression	r^2	n	p
pH = 7.96 - 0.095 FI	0.168	59	< 0.05
Alkalinity = 1.22 - 0.023 FI - 0.32 FIII	0.423	59	< 0.05
Conductivity = 204.1 - 22.8 FI - 32.3 FIII	0.439	59	< 0.05
Calcium = 31.1 - 4.94 FI - 6.59 FIII	0.411	59	< 0.05
Nitrate = 498 - 52.4 FI - 44.7 FII	0.250	59	< 0.05
Nitrite = 10.5 - 4.12 FI + 2.82 FII	0.229	59	< 0.05
Ammonia	n.s.	59	-
Phosphate = 53.4 + 22.6 FII	0.095	59	< 0.05

Table 2.- Results of stepwise regressions between physico-chemical variables of the water and factorial axes resulting from PCA of variables linked to physiography, vegetation and human activities. Factor I is related to size of sub-basin, factor II to human activities, factor III and factor IV to geology and vegetation.

In a study of the effect of the three main villages in the basin, GONZÁLEZ *et al.* (1993) reported that Villaverde, despite being the smallest, produced the largest changes in water chemistry, especially increases in nitrite and phosphate concentrations. This seems to occur because Villaverde is the first village the stream meets. GONZÁLEZ *et al.* (1994) showed that sewage contributed 40-50% of the nitrite and phosphate load carried by the Agüera in Villaverde, and 30-40% to the load in Trucíos. The contribution of sewage to the load of nitrate was much lower.

From a temporal perspective, different sources of variability overlap. In general, seasonal variability is of minor importance, and affect especially to temperature. Most other changes detected through the year are due to variations in discharge (ELÓSEGUI *et al.*, 1997), that can follow contrasting patterns from year to year. Additionally, at a shorter scale, diel variability can be very important for variables like temperature, pH and oxygen, but also for nutrients and seston (ELÓSEGUI & POZO, 1994b; POZO *et al.*, 1994a). This variability is affected in part by the metabolism of the benthic community, that can be very high especially in moderately eutrophic reaches, provided that hydrological stability is long enough (ELÓSEGUI & POZO, 1998).

Thus, ELÓSEGUI *et al.* (1997) summarised the most significant scales of observation for the main physico-chemical variables. They concluded that temperature and pH depend mainly on diurnal and seasonal variations, oxygen saturation in mid and low reaches is most affected by diurnal variability, conductivity and associated variables (Ca, K…) change especially with discharge, but in a site-dependent way, while inorganic nutrients are affected by discharge and diurnal variability, through both changes in benthic metabolism and in input rate associated to human activities. These results are important to design guidelines for stream monitoring, but are seldom taken into account in most sampling protocols. For instance, with conventional sampling schedules (e.g., sampling every other week, always during daylight) the range of variation detected for oxygen can grossly underestimate the range suffered by the benthic community, as night-time values can differ drasti-

	pH		O2 saturation (%)	
Site	**Fortnightly**	**Diel**	**Fortnightly**	**Diel**
1	6.98 - 7.99	7.44 - 7.68	93 - 115	90 - 97
5	7.37 - 9.80	7.51 - 9.17	50 - 175	29 - 185
7	7.63 - 9.52	7.87 - 9.17	94 - 155	77 - 148

Table 3.- Ranges of variation in pH and oxygen saturation at three reaches of the Agüera stream, as determined from fortnightly diurnal sampling through one year, and from one diel cycle, with measurements taken hourly for 24 h.

cally from day-time ones, at least in some reaches (Table 3). Day-time sampling is especially inappropriate to detect events of hypoxia, that typically occur during the night hours (ELÓSEGUI & POZO, 1994b).

BENTHIC COMMUNITIES

Algal biomass in the Agüera shows broad spatial variations, mainly associated to light availability, nutrients, and substrate (ELÓSEGUI & POZO, 1998). SABATER *et al.* (2000) showed that spatial differences in periphytic biomass are also large in the Oria, mainly reflecting anthropogenic disturbances. At the Agüera headwaters, biomass is low and unicellular diatoms dominate; at mid reaches where canopy cover is small, and especially downstream from the villages, periphyton is dominated by filamentous green algae like *Cladophora*, and can proliferate over 200 gm^{-2}. From a temporal perspective, periphyton can be abundant through the year, provided that discharge is low. Floods are the main disturbances, as once a certain threshold is crossed, periphytic biomass decreases to very low values, in such a way that the average as well as maximum biomass of periphyton can greatly differ from year to year, depending on rainfall patterns (Fig. 5). Accrual of periphytic biomass is fastest at unshaded reaches with high nutrient concentrations. Therefore, in cases of constant low discharge, and high nutrient and light availability periphytic metabolism can be very high. Data of metabolism based on diel changes of oxygen saturation (ELÓSEGUI & POZO, 1998) show that below Trucíos algae can produce over 8 g O_2 m^{-2} d^{-1}, although estimates of year-round production are still lacking. As occurs in Switzerland streams (UEHLINGER & NAEGELI, 1998), in the Agüera floods affect more to primary production than to community respiration (ELÓSEGUI & POZO, 1998). Although we have not measured the interactions between grazers and algae, it is likely that long dry periods are detrimental to periphyton, as floods can suppress grazers, releasing algae (BIGGS, 1996; MARKS *et al.*, 2000).

Invertebrate communities are most diverse in mid- and low-reaches of the Agüera, and in general, the number of taxa shared by two reaches decreases with distance (Fig. 6). Site 9, below Guriezo, shows the lowest affinity with nearby reaches. The BMWP' index (ALBA-TERCEDOR & SÁNCHEZ-ORTEGA, 1988) of biologic quality based on invertebrates indicates that

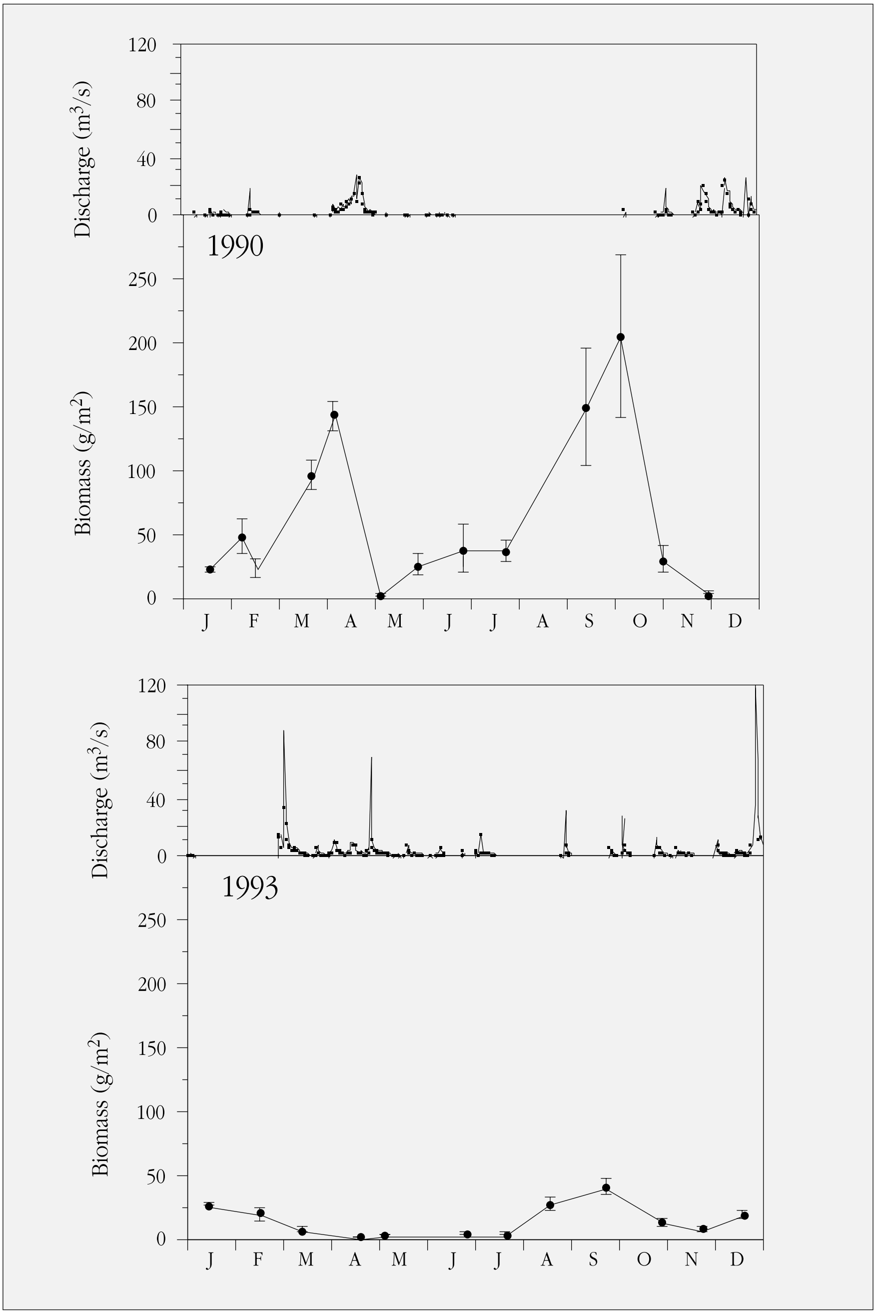
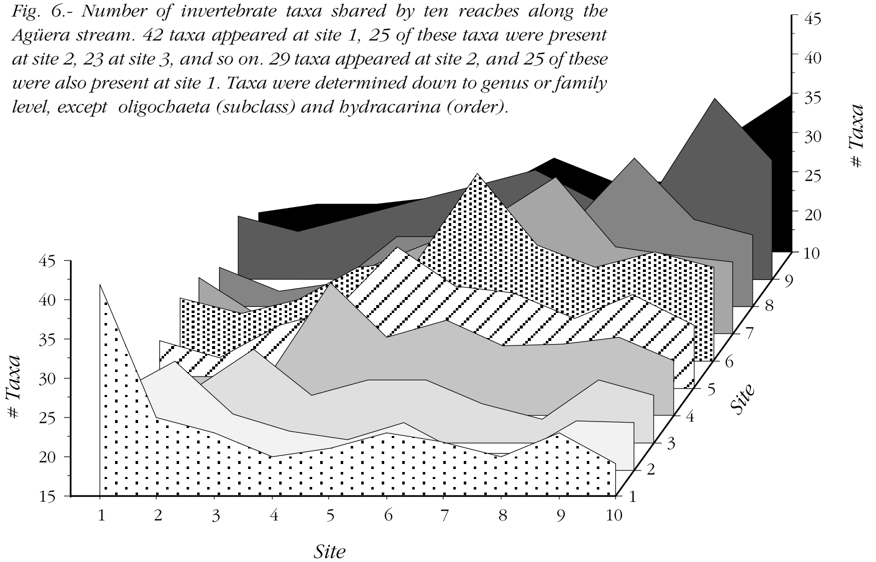


Fig. 5.- Contrasting patterns of periphytic biomass below Trucíos. 1990 was a dry year with very high algal biomass, and 1993 a wetter year, with low algal biomass. Vertical bars are standard errors. Data from ELÓSEGUI & POZO *(1998), and* LÓPEZ DE LUZURIAGA *(1995).*

Fig. 6.- Number of invertebrate taxa shared by ten reaches along the Agüera stream. 42 taxa appeared at site 1, 25 of these taxa were present at site 2, 23 at site 3, and so on. 29 taxa appeared at site 2, and 25 of these were also present at site 1. Taxa were determined down to genus or family level, except oligochaeta (subclass) and hydracarina (order).



water is of good quality in the main axis of this stream (Table 4), although the values are not very high for Atlantic streams. Impoverishment of pollution-sensitive taxa was only detected below Guriezo, and even there it was not serious. Seasonal differences in the BMWP'value (ALBA-TERCEDOR & SÁNCHEZ-ORTEGA, 1988) were related not to differences in water quality, that remained high (Elósegui, 1992), but to disturbances caused by floods, that produced a drastic decrease in invertebrate abundance (RIAÑO *et al.,* 1993). Microbiological analyses indicated that stream water was of very high quality except below Villaverde, Trucíos and Guriezo, and that it improved rapidly downstream (ELÓSEGUI *et al.*, 1995).

Table 4.- Results of the BMWP' index of water quality, calculated from the composition of invertebrate families in autumn 1988 and spring 1989. Values over 100 indicate good water quality.

Site	Autumn	Spring	Average
1	185	154	170
2	120	153	136
3	118	131	124
4	117	148	132
5	136	146	141
6	156	134	145
7	140	179	160
8	137	-	137
9	126	94	110
10	123	-	123

As occurs with periphyton, invertebrate communities show important interannual variations. For instance, we sampled invertebrates at site 7 (clean waters, between Trucíos and Trebuesto) in December 1991 and December 1992. The constancy (% of taxa present in both data) was 62.3 %, similar to the 66.7% found between May 1990 and December 1991. Most discrepancies between data occurred because of rare taxa. Nevertheless, these results warn of the caution needed to interpret data from a single sampling season.

In terms of numbers, benthic communities are dominated by collector and generalist invertebrates, scrapers, filterers and shredders being less abundant (RIAÑO *et al.*, 1993; functional feeding groups classified following MERRIT & CUMMINS, 1978). Among collectors, oligochaeta, mayflies (heptagenids, caenids, baetids) and elmid beetles abound, whereas chironomids dominate the generalist group. Filterers (simulids and hydropsichids) are abundant below the villages. The most abundant shredders are the crustacean *Echinogammarus*, the stoneflies *Leuctra* and *Nemoura* and sericostomid caddisflies. Their numbers at forested headwaters can be up to 25% of total invertebrate densities (RIAÑO, 1998). The main scrapers are the snails *Potamopyrgus* and *Ancylus*, the mayfly *Ephemerella* and helodids. In terms of biomass, shredders dominate the community at the headwaters, and are replaced by filterers and generalists when the stream runs through the villages (POZO *et al.*, 1994b; BASAGUREN *et al.*, 1996). In the reach between Trucíos and Trebuesto collectors dominate again, followed by scrapers.

According to VANNOTE *et al.* (1980), the relative dominance of functional feeding groups changes in a predictable way, as the importance of allochthonous food from the riparian forests decreases downstream, whereas autochthonous primary production increases. In the Agüera stream, human activities modified the longitudinal gradient, and thus, spatial changes in the structure of benthic communities are more complex than those theoretically predicted. Furthermore, the trophic structure of macroinvertebrate communities changes during the year, in a complex way that depends in part on the resistance and resilience of different taxa to floods (BASAGUREN & RIAÑO, 1994; BASAGUREN *et al.*, 1996). The biological cycles of most shredders are not synchronised with the period of leaf shedding, probably reflecting that leaf litter is not a limiting resource, but that its availability is unpredictable as a result of floods. For instance, biomass of *Echinogammarus* was high from spring to fall, and *Sericostoma selysii*, one of the most abundant shredders at the headwaters, had highest biomass in summer, a period of low food abundance (BASAGUREN *et al.*, 1996). In general, life cycles of invertebrates in the Agüera show low synchrony (RIAÑO, 1998; GONZÁLEZ, 1999; BASAGUREN *et al.*, in press), probably as a consequence of small seasonal differences in ambient conditions, plus unpredictable flood pattern (TOWNSEND & HILDREW, 1994).

TRANSPORT, RETENTION AND PROCESSING OF MATERIALS

Streams and rivers are systems created and maintained in a dynamic equilibrium by mechanisms of transport and retention (LEOPOLD, 1997). These processes model channel geomorphology and control the abundance and production of lotic organisms. Therefore, a part of our research focused the transport, retention and processing of nutrients and organic matter, as they travel from the riparian areas to the channel and downstream.

ELÓSEGUI *et al.* (1995) showed that mid-reaches of the Agüera are very active in retaining dissolved nutrients, especially during low flows. The benthic community seems the main responsible for nutrient retention, and thus, for the self-purification capacity of the stream. In fact, retention is most active downstream from Trucíos, a reach where algae can grow very fast, thus withdrawing nutrients from the water. Nevertheless, if the period of low discharge is long enough, periphyton can literally cover most of the stream bed, and thus stop growing (ELÓSEGUI & POZO, 1998), which would result in decreased nutrient retention. On the other hand, when floods are very frequent periphytic growth is restrained, and high discharge levels result in reduced retention (ELÓSEGUI *et al.*, 1995). Therefore, a certain frequency of floods seems necessary to maintain the self-purification capacity of the stream. Similarly, characteristics like riparian cover and streambed substrate are very important for algae (BIGGS, 1996), what opens broad opportunities to manage our river systems in order to improve their capacity to recover from organic pollution. Nevertheless, although Basque rivers can be exceptional water-purifying plants, key information to optimise this function is still missing.

As we have mentioned, most stream channels on the Agüera basin are total or partially covered by riparian forests. In these conditions of light limitation, the benthic community is expected to depend more on allochthonous organic matter, especially leaf litter from the riparian forests, than on primary production (WALLACE & WEBSTER, 1996). Thus, the type, cover and production of riparian forests have great importance on the amount, quality and seasonality of organic-matter inputs (WEBSTER & MEYER, 1997). In the Agüera basin, as occurs in large parts of the Iberian Peninsula, extensive eucalyptus plantations replaced deciduous forests and open landscapes. Eucalyptus leaves have low nutrient levels, high concentration of phenolics and essential oils, and are shed mainly in summer, whereas most native trees shed leaves in autumn (BUNN, 1988; CANHOTO & GRAÇA, 1995; ABELHO & GRAÇA, 1996). Thus, there is concern on the potential impact of eucalyptus plantations on detritus-based streams (GRAÇA, 1993).

POZO *et al.* (1997b) compared inputs of organic matter in two first-order streams, one running under mixed deciduous forests, the other under eucalyptus plantations. Inputs were 32% lower at the eucalyptus site and litter diversity was greatly reduced, with 98 % of mass corresponding to eucalyptus, a nutrient-poor species, what resulted in reduced nutrient inputs into the stream. Furthermore, timing of inputs was greatly altered: at the deciduous site most of the inputs occurred from October to December, whereas at the eucalyptus site inputs were more evenly distributed throughout the year, and peaked in summer. This differential timing is of great importance: benthic availability of coarse particulate organic matter was higher in the eucalyptus site because inputs, albeit smaller, occurred during summer, a period of low discharge when they remained in place instead of being scoured downstream (POZO *et al.*, 1997a). Similar results have been published elsewhere (MURPHY & GILLER, 2000), and stress the importance of the hydrological regime in stream organic-matter budgets.

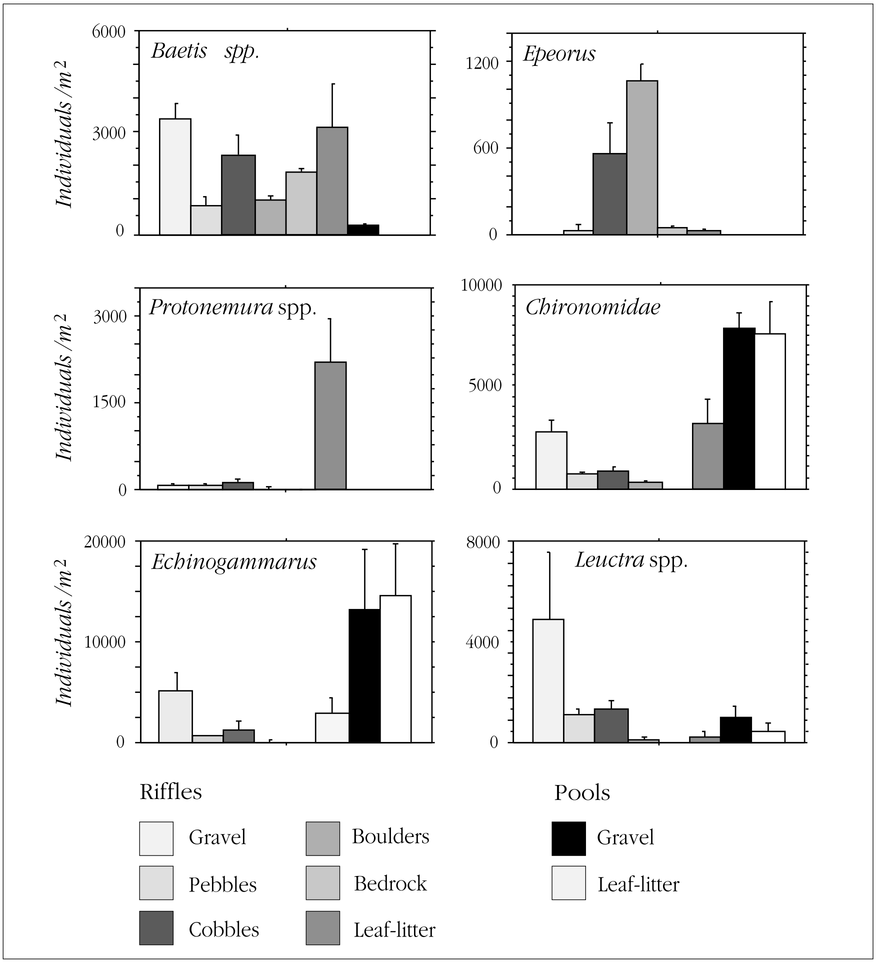
POZO *et al.* (1997a) showed that despite receiving less organic inputs and of poorer quality, eucalyptus streams processed litter with greater efficiency than deciduous forest streams, because eucalyptus inputs occurred mainly in summer and tended to be retained for longer. This clearly shows the importance of retention in stream energetics. The capacity of streams to retain leaf litter was assessed across the Agüera basin by Larrañaga (1998). He showed that retentiveness was in general great, and that during baseflow 1st-order reaches retained leaves in an average distance of 3.6 m, whereas at 3 rd-order ones retention distance averaged 16.6 m. Leaf retention distance increased with discharge, and during wet periods woody debris in the channels became one of the most important retention structures. As stated by Harmon *et al.* (1986), the abundance of wood in the form of debris dams or scattered snags has dramatic effects on stream structure and function.

Once leaf litter enters the stream, it is used by heterotrophs, who break it down in a complex process. During the first days, litter losses soluble material by leaching, and is readily colonised by fungi and bacteria. These microbes condition leaves making them more palatable for detritivorous animals (Gessner, 1997). Once leaves have been conditioned, they are fragmented and ingested by shredder invertebrates, whose action results in increased surface-to-volume ratio of litter, and thus, promotes further microbial colonisation. Small fragments so produced are ingested by collector and filterer invertebrates. As a result of all these processes, a part of the organic inputs is metabolised to CO_2, and another part is lost downstream, in form of dead organic matter, either dissolved or particulate (Webster & Meyer, 1997). Decomposition is thus a key process and the basis of food webs in headwater streams surrounded by forests (Graça *et al.*, 2002). As we have seen, eucalyptus plantations modify the amount, diversity, quality and timing of litter inputs into streams, and thus we have studied in detail the breakdown of these inputs.

Pozo (1993) reported that at headwater reaches alder leaves decomposed much faster than eucalyptus, whereas at mid reaches differences were not significant. In these mid reaches dissolved nutrient availability was greater, and the nutrient content of leaves increased, presumably as a result of microbial activity. Basaguren & Pozo (1994) showed that at the headwaters invertebrate densities where higher on alder than on eucalyptus leaves, whereas at the mid reaches there were no differences. In the lowest reach shredders were practically absent from the benthic community, although leaf litter decayed very fast. Thus, they hipothesized that shredder invertebrates were responsible of litter breakdown at the headwaters, whereas microbial activity was more important at lower reaches. Molinero *et al.* (1996) compared the breakdown of three nutrient-poor leaf species (oak, chestnut and eucalyptus) in four headwater reaches (two surrounded by deciduous forest and two by eucalyptus plantations), and in a mid-reach with mixed vegetation and higher nutrient status. They found no influence of riparian vegetation on litter breakdown rates, and although availability of dissolved nutrients at the mid reach resulted in increased N and P contents of all leaf species, only breakdown rate of eucalyptus was increased. González *et al.* (1998) concluded that leaching and microbial decomposition of these three species at a deciduous headwater stream were similar, but that eucalyptus litter needed a longer conditioning before being used by invertebrates. Pozo *et al.* (1998) showed that in this mid-reach, fungi colonised eucalyptus leaves more than alder leaves. Fungal colonisation of eucalyptus lagged 2 weeks behind that of alder, probably reflecting its higher content of inhibitory compounds (CHAUVET *et al.*, 1997). GRAÇA *et al.* (2002) recently summarised the information available for the Agüera and several Portuguese streams, and showed some further evidence of the low quality of eucalyptus leaves.

The amount of woody debris in the Agüera system is in general low, and ranges from 0.4 to 220 m^3 per hectare of streambed (ELOSEGI *et al.*, 1999; DÍEZ *et al.*, 2001). This low volume of wood results from centuries of forest clearing and removal of fallen logs, and is typical of many rivers and streams in developed countries (ELOSEGI & JOHNSON, in press). Woody debris is especially scarce in reaches surrounded by young forests, either eucalyptus plantations or frequently coppiced alder forests. In an attempt to evaluate the impact of wood depletion in Basque streams, we experimentally removed all woody debris from

Fig. 7.- Densities of selected invertebrate taxa on microhabitats at the headwaters of the Agüera stream on 14th July 1997.



two 70 m long headwater reaches, and compared them to two unimpacted controls (DÍEZ *et al.*, 2000). The removal of wood destabilised stream beds: experimental reaches lost over 53 m^3 of sediment each, and their surface cover of fine sediments was greatly reduced, as well as their capacity to retain leaf litter. Thus, wood removal produced important changes in the abundance of different micro-habitats, that could have important effects on the benthic community, given the marked preference of many invertebrates for a certain type and size of substrate (Fig. 7). Recovery of more natural amounts of woody debris should be one of the priorities in restoration of physical habitats of Basque streams, as is elsewhere (HILDEBRAND *et al.*, 1997; GERHARD & REICH, 2000). Recently, it has been shown that although very slow to break down, wood can be metabolically important because it is not easily scoured by floods (DÍEZ *et al.*, 2002).

IMPLICATIONS FOR CONSERVATION AND RESTORATION OF BASQUE STREAMS

As depicted in the research already published, the Agüera stream is in relatively good health, and at least some reaches could be used as reference for restoration of degraded streams nearby. Furthermore, years of sustained research in the same system allowed us to detect quite extreme conditions (e.g., the exceptionally dry winter of 1989-1990), as well as the impact of infrequent natural or human disturbances (e.g., huge eucalyptus clearcuts upstream from Trebuesto in 1999-2000). This long-term approach to ecological research is essential to correctly understand the function of nature (ILTER, 2000).

From this perspective, the Agüera is a stream where geology, topography, climate and human activities interact to produce broad spatial differences in a relatively small area. Temporal variability is also important, but at some scales more than at some others. Seasonal variations are relatively small as a result of the mild climate, but floods can occur at any time of the year, affecting both the physico-chemical characteristics of the water and the benthic communities, and making the Agüera stream an unpredictable environment. Harshness, variability, heterogeneity and predictability are key factors of the habitat, that provides the templet for ecological strategies in such a way that organisms adapt their life hitories to optimise their reproductive sucess (SOUTHWOOD, 1977; TOWNSEND *et al.*, 1997). In general, invertebrates adapt by adjusting the number of generations per year and the timing of reproduction to the local conditions (GILLER & MALMQVIST, 1998). Unpredictable habitats generally favour characters that increase life cycle plasticity, mainly prolonged hatching and emergence periods, and a wide range of larval periods at one time, whereas predictable disturbances (like summer drough) favour specific adaptations like drough-resistant eggs (GILLER & MALMQVIST, 1998). Invertebrates in the Agüera show indeterminate, asynchronous life cycles, probably as a consequence of low seasonality and high unpredictability (RIAÑO, 1998; GONZÁLEZ, 1999; BASAGUREN *et al.*, 2002). Furthermore, both the environment and the communities can change broadly from year to year, making dangerous to use data from any single year, for instance, to assess the ecological state of the stream.

Another point worth stressing is the importance of taking in account the whole river network (including tributaries), and the whole drainage basin. Stream communities and processes depend on the relative position of particular reaches in the river network, as they are influenced by both upstream and downstream reaches. Upstream reaches are an evident source of particulate and dissolved materials, as well as drifting colonists. But even downstream reaches exert an influence. For instance, some tributaries dry up from time to time, and the main reach (and hyporheos for species with drought-resistant stages) is the source of colonists once water begins to run again through the channels. Thus, a certain sequence of colonists occurs, depending in part on the species present in the main axis, and on their developmental stage when the dry period ends (OTERMIN, 1998; OTERMIN *et al*., 2002). Therefore, the stream can be seen as a complex mosaic of patches, from the size of individual stones to whole reaches, in different stages of recovery from different disturbances, and linked to different sources of colonists, in what has been called the patch dynamics concept (TOWNSEND, 1989).

In the perspective of the whole drainage basin, geology, topography, climate, vegetation and human activities interact to control stream hydrology, channel geomorphology, water chemistry and stream function. Riparian areas play a key role on stream ecology, and therefore, their status must be assessed, and they must be carefully managed (FISRWG, 1998). Some of the functions of riparian areas depend on the composition, structure and maturity of riparian forests (DÍEZ *et al*., 2001) and thus, to manage them correctly we must go beyond coarse metrics like forest presence/absence, and assess more subtle effects of many management practices.

Finally, we would like to stress the importance of a functional, system approach to assess the ecological status of streams. Sound environmental management requires to incorporate variables like stream metabolism, litter breakdown, or nutrient spiralling, that give an integrated vision of ecosystem function, and therefore, are complementary to variables like water chemistry or community structure (BUNN & DAVIES, 2000). Presently, the information available, and especially, the number of standardised tools to measure and evaluate functional impairment of stream ecosystems is much lower than the number dealing with structural attributes. Thus, it is necessary to increase research on functional attributes of streams and rivers, and especially, to design assessment and management tools based on the best information available.

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