EPHEMEROPTERA OF REGULATED MOUNTAIN STREAMS IN SPAIN AND COLORADO

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ABSTRACT

A comparative analysis of the Ephemeroptera was conducted using data from 16 regulated mountain streams at 8 locations throughout Spain and 8 in the Colorado Cordillera. An additional 16 unregulated stream reaches served as reference stations. Faunal richness was reduced by stream regulation, taxonomic composition was altered, and population densities were changed. Baetids increased in abundance, whereas heptageniids declined below deep-release dams. Ephemerellids exhibited species specific responses to regulation. European and North American congeners were identified that exhibited similar responses to regulation. Climatic differences (e.g., absence of winter ice in Spanish streams) account for the differential effects of regulation on Iberian and Cordilleran mayfly faunas.

INTRODUCTION

Regulated streams, lotic reaches below dams, are characterized by markedly different environmental conditions than free-flowing streams (Ward and Stanford 1979a, Lillehammer and Saltveit 1984, Petts 1984, Craig and Kemper 1987) with corresponding differences in zoobenthic communities (Ward and Stanford 1979b, Ward 1982, Armitage 1984). Stream regulation directly alters downstream temperature patterns, flow regimes, and seston dynamics, which in turn modify other habitat conditions (e.g., substratum, aquatic flora).

The purpose of this paper is to examine the responses of lotic Ephemeroptera to stream regulation based on studies conducted on mountain streams in Spain and the Colorado Cordillera. Comparisons are made of taxonomic composition, diversity, and abundance of the mayfly faunas at regulated and unregulated locations.

METHODS AND STUDY SITES

The Ephemeroptera fauna was examined using nymphal data from 16 regulated streams at 8 sites in Spain and 8 in Colorado (Fig. 1). Each study site consisted of a regulated sampling station in the tailwaters below a dam and an unregulated (reference) station above the reservoir or on a tributary.

Brief site descriptions are given in Table 1. Precise sampling methods and more detailed site descriptions have been presented elsewhere (Spain: García de Jalón 1980, García de Jalón and González Tinago 1986a, 1986b, García de Jalón *et al.* 1988, Casado *et al.* 1989; Colorado: Ward 1976, Ward and Short 1978, Zimmermann and Ward 1984, Ward *et al.* 1986). All samples were collected from rubble riffles in high-gradient streams characterized by good water quality; none of the sites received point sources of pollution or exhibited oxygen problems. Trout occurred in all streams except the Rio Guadalhorce in the south of Spain.

RESULTS

Thirty-six mayfly species were identified from the Spanish streams, twenty-six from Colorado. Species richness was typically reduced at regulated stations (Fig. 2), irrespective of differences in release depth, reservoir function, or elevation.

The density response to regulation, however, varied greatly between sites (Fig. 3) and between species (Table 2). With abundant species it was often possible to identify Spanish and Colorado congeners that exhibited similar responses. Species in category I (Table 2) may attain extremely high densities in tailwaters under certain conditions (e.g., an annual mean of 11,563 *B. tricaudatus* m^{-2} at Site C4).

Baetidae, Heptageniidae, and Ephemerellidae collectively constituted the majority of the mayfly fauna at most reference stations (Figs. 4 and 5). Baetids were an important component of the fauna at all sampling stations. Baetids increased in relative abundance below deep-release dams, but decreased below surface-release dams. *Baetis* was the most diverse and abundant mayfly genus in both Spain and Colorado. Heptageniids were an important component of the mayfly fauna at reference stations. Although reduced or eliminated below deep-release dams (Fig. 4), heptageniids greatly increased in relative abundance in the tailwaters of the Rio Cinca (Fig. 5). Ephemerellids were well represented at most reference stations. Although exhibiting a general decrease below deep-release dams in Colorado, this family exhibited similar mean relative abundance values at reference and regulated stations in Spain. Ephemerellids decreased in relative abundance in tailwaters below surface release dams, except in S. St. Vrain Creek, a high elevation (3153 m a.s.l.) site in Colorado (Fig. 5), where *Ephemerella infrequens* was much more abundant downstream.

Oligoneuriella rhenana, from the predominantly pantropical family Oligoneuriidae, was abundant at reference stations of the Rio Duratón (51%

of mayfly fauna), Rio Tietar (54%), and Rio Guadalhorce (34%), but was rare or absent at all regulated stations (Fig. 4). Oligoneuriids were not encountered in the Colorado streams.

DISCUSSION

The greater number of mayfly species from Spain (36 versus 26 from Colorado) reflects the distribution of the Spanish streams in different physiolographic regions. In contrast, the Colorado study streams are all within the Southern Rocky Mountain Province. The inclusion of high elevation (>3000 m a.s.l.) sites in Colorado did not increase faunal richness because the mayfly species occurring at high elevations are euryzonal forms rather than specialized headwater elements (Ward 1986).

Changes in temperature and flow regimes have been ascribed major roles responsible for altered zoobenthic communities in regulated streams (Ward and Stanford (1979b). Temperature and flow exert a myriad of direct and indirect effects on Ephemeroptera (Brittain and Saltveit 1989).

Seasonal flow constancy, increased substrate stability, high water clarity, and the winter-warm conditions that characterize reaches below some deep-release dams (Ward 1982) result in dense accumulations of periphyton (Dufford *et al.* 1987), which favors certain species (e.g., *Baetis* spp., *Ephemerella infrequens, E. ignita*), but is detrimental to others such as *Drunella doddsi* and heptageniids that are adapted to clean rock surfaces. These same factors also favor the development of aquatic angiosperm beds that provide current refugia for species such as *Tricorythodes minutus* and *Ephemerella ignita* (Alba-Tercedor and Millán 1978). Ice action plays a major role in the cordilleran streams and compounds the differences in environmental conditions between reference and regulated (ice-free) stations, whereas ice is virtually absent from the Iberian streams.

Three of the regulated stations in Spain were located below hydroelectric dams. The Rio Cinca (S6) and Rio Duratón (S2) exhibited substantial decreases in mayfly densities at regulated stations (Fig. 3). The regulated Rio Cinca station lacked macrophytes and there was little periphyton on rock surfaces (Garcia de Jalón *et al.* 1988). This is the station where heptageniids were greatly enhanced. A similar flow regime in a regulated Canadian river resulted in increases in mayflies adapted to torrential conditions, including 2 heptageniids and *Drunella doddsi* (Radford and Hartland-Rowe 1971). The Rio Duratón has a channel morphology which minimizes the effects of the flow fluctuations. Macrophytes are abundant, periphyton is well developed, and heptageniids are absent from the regulated station. In the Rio Tera (S3) irrigation releases moderated the effects of the hydropower induced flow fluctuations (Casado et al. 1989). Mayfly densities were substantially higher at the regulated site (Fig. 3) where *Baetis rhodani* and *Ephemerella ignita* dominated the fauna. Species specific differences in drift behavior and susceptibility to stranding, interacting with channel morphology, also modifies the composition of mayflies in streams subject to rapid flow fluctuations (Brittain and Saltveit 1989).

The great decline in mayfly density at the regulated station on the Rio Guadalhorce (S8) is attributable to severe flow reductions by diversion. *Baetis* and two genera adapted to lentic conditions (*Cloeon* and *Caenis*) comprised the entire fauna. It is uncertain why mayflies also declined severely in the Rio Tietar (S7), but faunal composition suggests periodic dewatering.

Temperature is of great importance in the evolutionary ecology of stream insects (Ward and Stanford 1982). All major components of the temperature regime (e.g., annual and diel ranges, summer maximum, winter minimum, degree days) are modified by stream regulation. Many aquatic insects rely on a wide range of thermal information to cue various life cycle events; such species are typically eliminated from regulated streams, within which little thermal information is available. Only *Baetis* were able to tolerate the extremely narrow temperatures at regulated stations at C5 (2-8°C annual range) and C6 (3-11°C), both of which exhibited increased flow constancy. These sites exhibited greater reductions in faunal richness (Fig. 2) and density values (Fig. 3) than any of the study locations.

Eurythermal species with a high degree of life cycle flexibility are the most abundant mayflies in most regulated streams (Brittain and Saltveit 1989, Rader and Ward 1989). Bivoltine and multivoltine species have an advantage over univoltine mayflies in regulated streams, as do those with a long period of egg development and asynchronous nymphal development.

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Table 1. Summary data for the study sites shown on Figure 1. Elevation is for the reference stations.

Stream/ Reservoir	Map Code	Elev. m a.s.l.	Stream Order	Reservoir Function	Release Depth
Lozoya/ Pinilla	S1	1100	4	Storage	Deep
Duratón/ Burgomillodo	S2	800	3	Hydro.	Deep
Tera/ Cernadilla	S3	900	4	Hydro. & Irrig.	Deep
Duero/ La Cuerda del Pozo	S4	1100	4	Irrig.	Deep
Pisuerga/ Requejada	S5	1200	4	Irrig.	Deep
Cinca/ Piñeta-Laspuña	S6	590	4	Hydro.	Shallow
Tietar/ Rosarito	S7	350	4	Irrig.	Deep
Guadalhorce/ Conde de Guadalhorce	S8	380	4	Irrig.	Deep
Joe Wright/ Chambers	C1	3045	3	Irrig.	Deep
S. Platte/ Cheesman	C2	1860	6	Storage	Deep
Trout/ Manitou	C3	2454	3	Storage	Shallow
Colorado/ Granby	C4	2420	6	Storage	Deep
Blue/ Dillon	C5	2748	5	Storage	Deep
Fryingpan/ Ruedi	C6	2367	5	Storage	Deep
S. St. Vrain/ Brainard	C7	3153	3	Storage	Shallow
N. St. Vrain/ Buttonrock	C8	1951	3	Storage	Deep

Table 2. Examples of ecologically equivalent congeners based on population responses to stream regulation.

Spain	Colorado
I. Common at both reference and regulated stations:	
Baetis fuscatus, B. rhodani	*Baetis bicaudatus, B. tricaudatus*
Ephemerella ignita	*Ephemerella infrequens*
II. Common only at reference stations:	
Baetis gr. *lutheri*	*Baetis insignificans*
Serratella albai	*Serratella tibialis*
Rhithrogena gr. *hybrida*	*Rhithrogena hageni*
Epeorus torrentium[a]	*Epeorus albertae, E. longimanus*
Oligoneuriella rhenana	- - - - -
- - - - -	*Drunella doddsi*
III. Common only at regulated stations:	
Cloeon dipterum, C. simile	- - - - -
- - - - -	*Tricorythodes minutus*[b]

[a]numbers increased below a hydropower dam
[b]85% of all mayflies below a surface-release dam

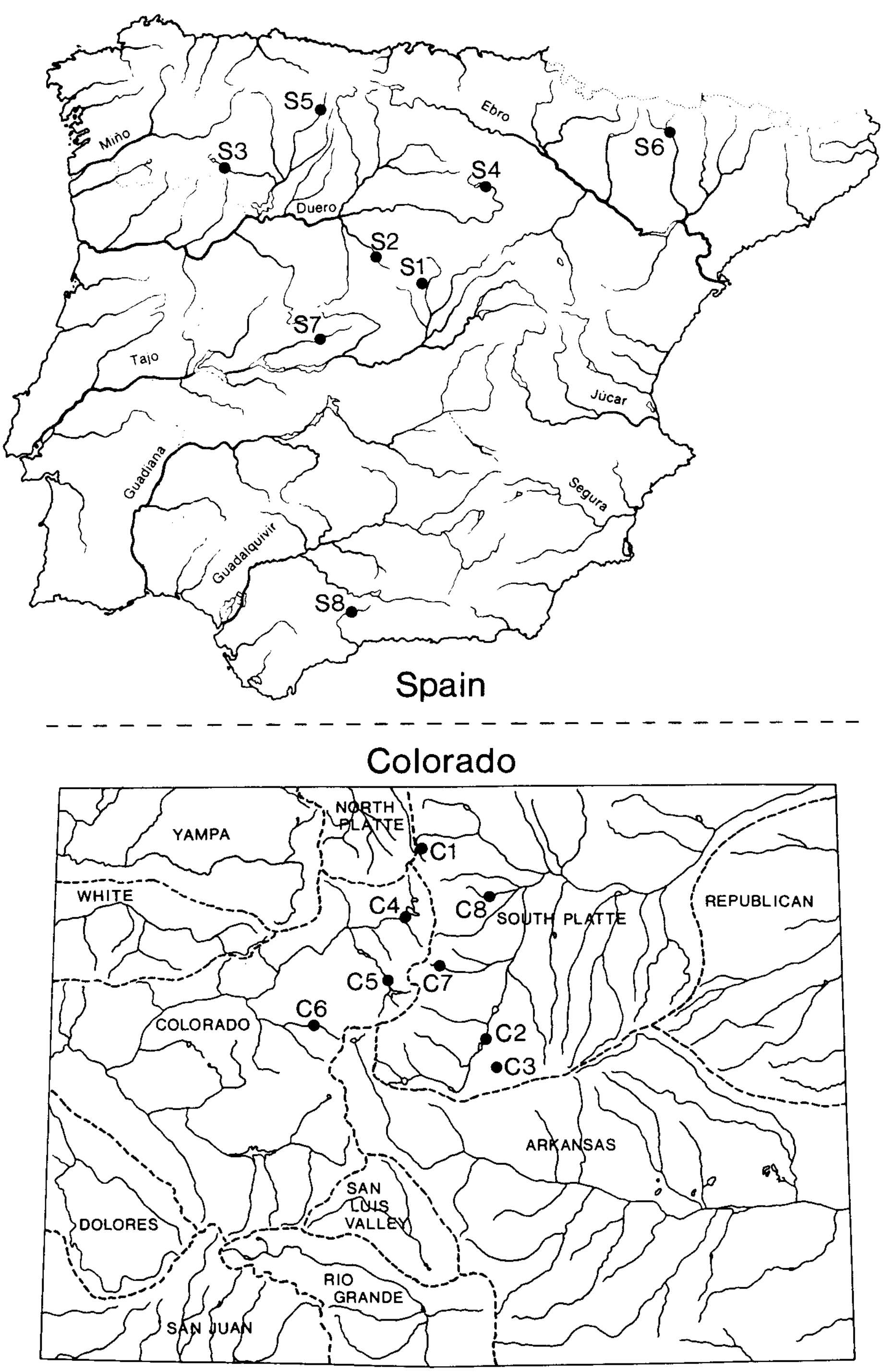

Fig. 1. Maps of Spain and Colorado showing locations of study sites.

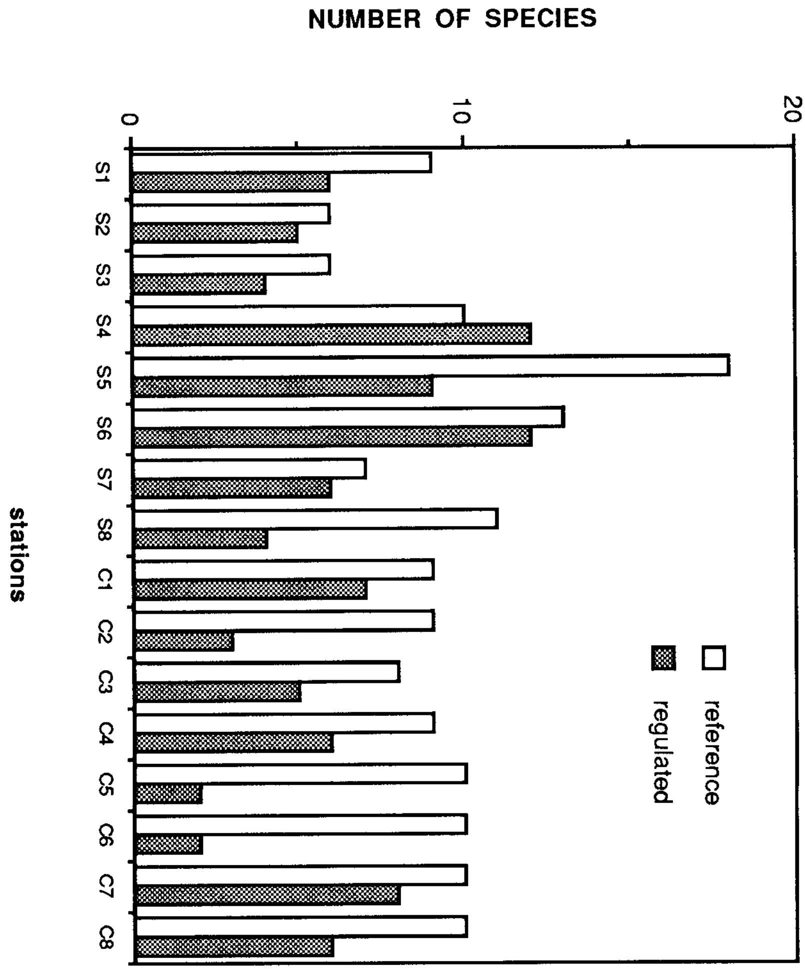

Fig. 2. Number of mayfly species of reference and regulated stations at each site.

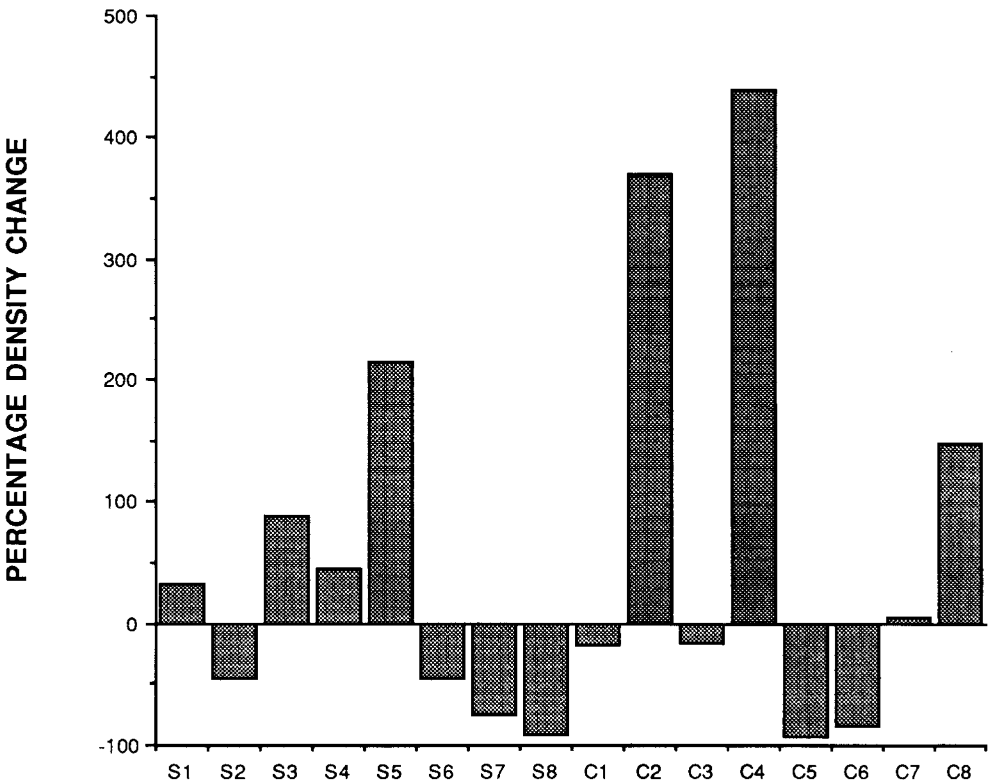

Fig. 3. Percent change in mean densities of total Ephemeroptera at regulated stations, at each site.

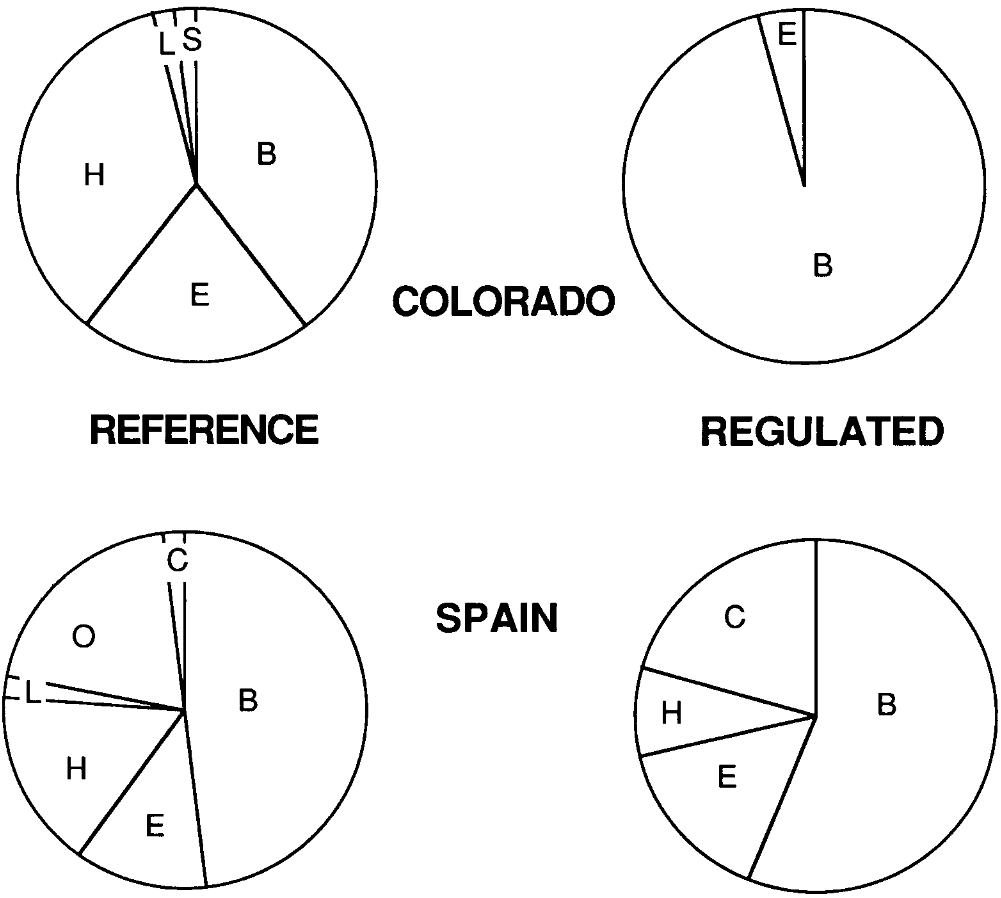

Fig. 4. Relative abundance of families as a composite of deep-release sites in Spain and Colorado. Values <1% not indicated. B-Baetidae; E-Ephemerellidae; H-Heptageniidae; L-Leptophlebiidae; S-Siphlonuridae; T-Tricorythidae; O-Oligoneuriidae; C-Caenidae.

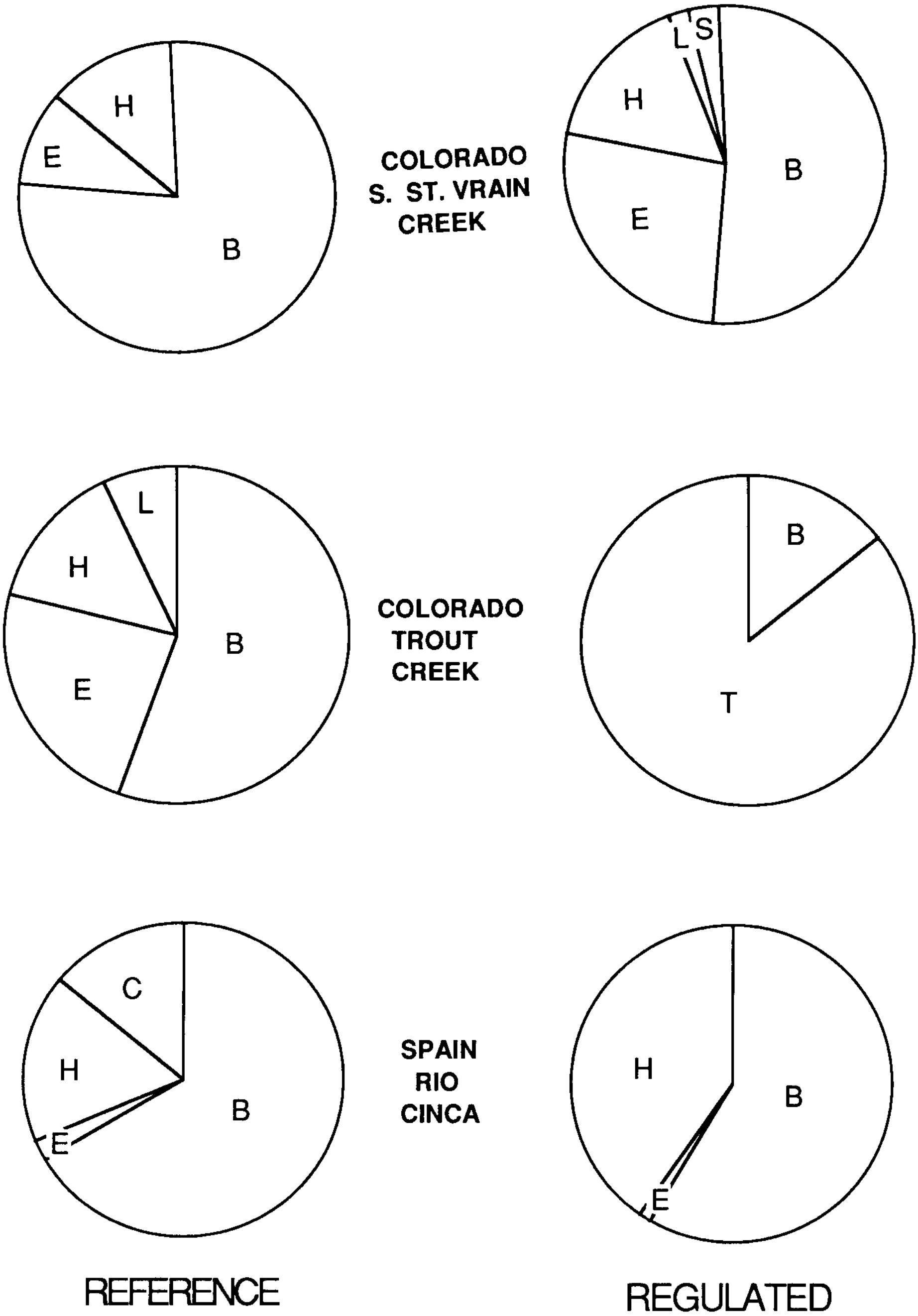

Figure 5. Relative abundance of families at surface-release sites. Values <1% not indicated. B-Baetidae; E-Ephemerellidae; H-Heptageniidae; L-Leptophlebiidae; S-Siphlonuridae; T-Tricorythidae; O-Oligoneuriidae; C-Caenidae.