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[Article]

Spatial Variation in Brown Trout Production: The Role of Environmental Factors

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Abstract.—Spatial variation in Spanish populations of brown trout *Salmo trutta* was studied in 10 streams of contrasting environmental and biological characteristics based on data compiled over 7 years (1992–1998). Three of the streams had soft water (mean alkalinity as $CaCO_3 = 19.3$ mg/L) supplied by granite catchments at elevations around 1,250 m above sea level and had a low abundance of macroinvertebrates (mean density = 598 individuals/m^2; mean biomass = 0.63 g/m^2). The remaining streams had hard water (mean alkalinity = 253.6 mg/L) flowing over limestone at 850–1,400-m elevations and possessed a greater benthic faunal abundance (mean density = 2,433 individuals/m^2; mean biomass = 2.76 g/m^2). Mean brown trout population characters varied significantly throughout the study area (density = 1,567–5,594 fish/ha; biomass = 56.6–240.2 kg/ha; annual production = 47.0–182.0 kg/ha, and the ratio of annual production to mean biomass = 1.01–1.56). A stepwise multiple regression analysis revealed a significant relationship between brown trout production and chemical features indicative of high water productivity, which accounted for 61% of the variance explained by the model. A broader spatial analysis, based on a review of the available European work, corroborated that annual brown trout production in streams flowing over limestone bedrock was greater (mean = 121.6 kg/ha; range = 30.0–253.3 kg/ha) than that in streams flowing over siliceous bedrock (mean = 76.6 kg/ha; range = 3.5–234.0 kg/ha). Data from brown trout populations throughout Europe showed a significant positive correlation between production and alkalinity according to the model $\log_{10}(\text{production}) = 1.41 + 0.31 \cdot \log_{10}(\text{alkalinity})$, which explained 53% of the variance. Our findings support previous evidence on the influence of water fertility on salmonid production and expand knowledge of the factors that influence brown trout production within the native range of the species.

Introduction

The dynamic measure of production rate has long been recognized as an excellent indicator of the quantitative performance of a fish population in a particular environment because it integrates biomass, recruitment, growth, and mortality (Le Cren 1972; Waters 1999). Production studies are a useful tool for the management of recreational fisheries because they serve to estimate the annual yield that a particular river can support and to evaluate the impact of environmental changes on fish populations (Mann and Penczak 1986; Elliott 1994; Kwak and Waters 1997).

Production dynamics of brown trout *Salmo trutta* have been extensively studied owing to the species' economic and recreational importance (Elliott 1994). Only some studies have examined brown trout production in a variety of streams for extended periods (e.g., Mortensen 1982; Mann et al. 1989; Elliott 1993; Waters 1999). Elliott's (1993) 25-year study of brown trout in England and Waters' (1999) 21-year study in Minnesota are remarkable for elucidating regulation mechanisms of one population in the long term. Therefore, more spatiotemporal research is needed to provide insight into the factors that regulate brown trout production. Our study is based on data collected in 10 streams over 7 years to evaluate the effects of environmental variation on production rates.

Contrasting production rates over regions have been associated with environmental factors (e.g., stream physiography, chemistry, temperature regime, discharge regime) that usually operate in a density-independent way, and density-dependent factors that operate both within (e.g., intraspecific competition) and outside (e.g., fish community structure) the population (Elliott 1994; Milner et al. 2003). Density-dependent mechanisms seem to regulate trout populations in highly productive waters but not in mountain streams,

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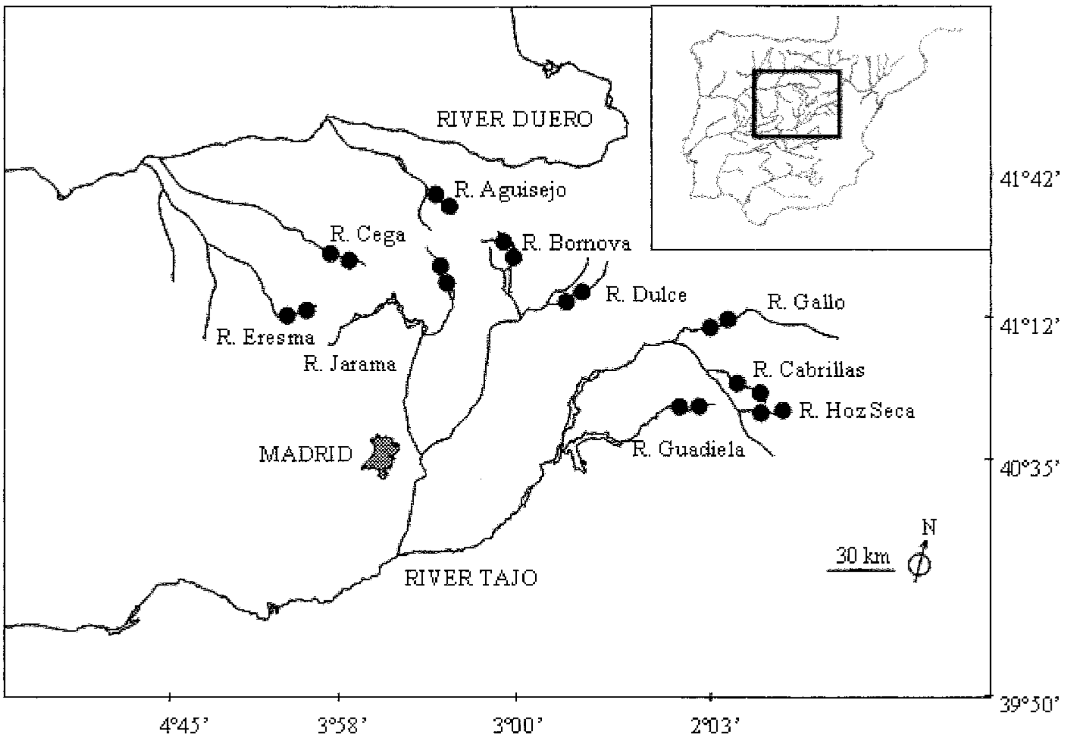

FIGURE 1.—Locations of the 20 sampling sites (dots) in 10 Spanish streams surveyed for brown trout population characteristics in December 1992 and every third month thereafter (March, June, September, and December) through December 1998 (R. = River).

where the density of fish is insufficient for them to operate (Elliott 1987; Gibson 1988; Jonsson et al. 1998). In headwater areas, salmonid production generally seems to be regulated by abiotic factors, such as water chemistry and physical habitat (e.g., Cooper and Scherer 1967; Mann and Penczak 1986; Scarnecchia and Bergersen 1987; Kwak and Waters 1997). Biotic communities of headwater reaches are often heterotrophic and depend on allochthonous detritus as an energy source (Randall et al. 1995). Fish production, which is limited by nutrients and thus is regulated from the bottom up rather than from the top down, has been shown to be positively correlated to production at lower trophic levels or to nutrient content, an indicator of water productivity (Meyer and Poepperl 2004).

The brown trout is one of the most important freshwater angling species in Europe. However, the wild stocks of south European countries are currently threatened by habitat destruction, pollution, introduction of exotic species, overfishing, and introgression of foreign genes as a result of artificial stocking (Elvira 1995a, 1995b; Almodóvar and Nicola 1998, 1999, 2004a; Almodóvar et al. 2001, 2002; Elvira and Almodóvar 2001). Moreover, the geographical position of the Iberian Peninsula seems crucial for the conservation of brown trout's genetic diversity (Machordom et al. 2000; Suárez et al. 2001). There is, therefore, an urgent need for conservation and management plans aimed at protecting brown trout, especially considering this species' great social and economic value. Strategies must be based on an assessment of population ecology and on detailed knowledge about factors and mechanisms that control the population's dynamics.

Our primary objective was to examine whether the spatial variation in population characters among resident brown trout populations in Spain is influenced by local biotic and abiotic conditions. In particular, we hypothesized that the differences in physicochemical characteristics and invertebrate abundance of streams would ultimately affect production rates. To test this prediction, we compared population variables and production rates in 10 streams of contrasting chemical and biological character based on a data set compiled during 7 years (1992–1998). Brown trout production was expected to be lower in streams with low nutrient content than in more productive streams. We also compared our results with the available European data, expanding on the spatial scale of our analyses and the knowledge of factors influencing brown trout production geographically.

Study Site

This study was carried out in 10 streams, (Figure 1); seven were tributaries to the River Tajo (Hoz Seca,

TABLE 1.—Physical and biological characteristics of 10 streams in central Spain. Mean (SD) stream values of physical variables were calculated from measurements for each sampling site during the entire study period, 1992–1998. Mean water temperature during the growing season (GS) was estimated for March–September. Abundance of benthic macroinvertebrates was assessed in each sampling site every third month from December 1992 to December 1998.

Characteristic	Gallo	Dulce	Bornova	Hoz Seca	Cabrillas	Guadiela	Aguisejo
Physical characteristics							
Elevation (m)	970	885	1,120	1,340	1,266	1,190	1,240
Drainage area (km^2)	1,311	263	366	173	206	3,470	211
Width (m)	9.0 (1.7)	4.9 (0.6)	4.0 (2.7)	8.6 (4.3)	4.3 (1.6)	5.0 (1.6)	2.4 (0.2)
Depth (cm)	50.1 (9.9)	46.1 (8.1)	21.9 (10.1)	38.4 (13.9)	31.9 (22.8)	31.8 (17.5)	11.2 (2.5)
Annual discharge (m^3/s)	1.3 (0.3)	0.7 (0.3)	1.7 (1.7)	3.6 (2.4)	0.9 (0.4)	4.5 (2.3)	0.5 (0.3)
Annual temperature (°C)	12.0 (3.4)	13.1 (3.1)	9.6 (5.0)	10.2 (1.0)	10.2 (3.5)	10.9 (3.6)	10.1 (3.6)
GS temperature (°C)	14.1 (2.5)	15.0 (2.5)	11.3 (6.9)	11.5 (0.8)	12.1 (2.9)	13.3 (2.4)	12.0 (2.1)
Biological characteristics							
Density (individuals/m^2)	5,947 (812)	1,978 (201)	353 (118)	1,349 (128)	1,583 (160)	583 (167)	798 (352)
Dry biomass (g/m^2)	6.21 (1.03)	2.70 (0.29)	0.73 (0.27)	1.72 (0.21)	1.59 (0.20)	0.53 (0.16)	1.54 (0.42)

Cabrillas, Gallo, Dulce, Guadiela, Bornova, and Jarama), and three were tributaries to the River Duero (Cega, Eresma, and Aguisejo). The study streams were selected because they encompassed a wide range of environmental conditions within a reduced area. A complete survey of the study area enabled us to determine the percentage of representativeness of different groups of mesohabitats (Calow and Petts 1992). On the basis of this morphodynamic survey, two sampling sites with a similar habitat were selected in each river. The study reaches corresponded to first-order streams and ranged from 39°50′N to 41°42′N and from 2°03′W to 4°45′W. The brown trout is the only or the prevailing fish species present throughout the study area, and its populations comprise exclusively resident individuals. The study streams are open to recreational angling, but the sampled reaches were in preserved sections where fishing and stocking activities are forbidden. The study area predominately contains small villages with few people, and agricultural practices consist of small landholdings mainly devoted to subsistence farming and have little impact on water quality. Therefore, the streams are relatively unaffected by land use or pollution (Almodóvar and Nicola 2004b).

Mean elevation, drainage area, and flow regime varied greatly among study streams. The Rivers Jarama, Cega, and Eresma arise from granite and gneiss catchments at elevations between 1,100 and 1,300 m above sea level. The greater part of their water comes from surface drainage, and they become torrential in their upper reaches at snowmelt in spring. The remaining rivers (Hoz Seca, Cabrillas, Gallo, Dulce, Guadiela, Bornova, and Aguisejo) run through limestone bedrock at elevations from 850 to 1,400 m; their geology and mild climate produce an even flow regime throughout the year.

Methods

Environmental factors.—Physical habitat data were collected concurrently with fish sampling at each site. A number of transect lines were spaced 10 m apart at each site (based on Simonson et al. 1994). Along each transect, we measured wetted width (m) and water depth at 1-m intervals. Hydrological data consisting of daily discharge during the study period (1992–1998) were extracted from a national database held by the Spanish Ministry of Environment. The study reaches were close to a gauging station located on the same river. Reach elevations were measured directly from topographic maps.

The water temperature was measured with data loggers (Minilog Vemco, Ltd.) permanently placed in each river during the study period, and mean daily temperature was the average of the maximum and minimum readings in each 24-h period. Water samples were taken from each sampling site beginning in December 1992 and then every March, June, September, and December from 1993 to 1998; measured water variables included conductivity (μS/cm), total dissolved solids (TDS; mg/L), pH, chloride, sulfate, phosphate, alkalinity as $CaCO_3$ nitrate, nitrite, sodium, potassium, calcium, magnesium, and ammonia (all but pH mg/L). In situ measurements included conductivity and TDS (Hach Model 44600 portable conductivity/TDS meter) and pH (Hach Model 43800 portable pH meter). Alkalinity was determined by means of the sequential titration procedure (Hach Model 16900 digital titrator). Nutrient concentrations were determined by a series of chemical reactions with a Hach Model 45250 DR/2000 spectrophotometer. The ions Na^+, K^+, Ca^{2+}, and Mg^{2+} were estimated by atomic absorption spectroscopy.

At each site, benthic macroinvertebrates were sampled in riffles every March, June, September, and

TABLE 1.—Extended.

Characteristic	Eresma	Cega	Jarama
Physical characteristics			
Elevation (m)	1,290	1,250	1,213
Drainage area (km^2)	124	133	11,597
Width (m)	6.3 (1.0)	5.8 (0.6)	5.9 (2.1)
Depth (cm)	21.8 (4.5)	29.0 (6.5)	28.6 (9.4)
Annual discharge (m^3/s)	3.2 (2.3)	4.1 (1.8)	5.0 (5.9)
Annual temperature (°C)	6.5 (4.0)	6.8 (4.2)	8.6 (4.4)
GS temperature (°C)	8.0 (3.9)	8.1 (3.7)	10.1 (3.6)
Biological characteristics			
Density (individuals/m^2)	682 (139)	737 (188)	502 (72)
Dry biomass (g/m^2)	0.78 (0.19)	0.48 (0.07)	0.59 (0.11)

December from December 1992 to December 1998. On each occasion, we used a Neil cylinder core-type sampler with a 250-μm-mesh net to collect three samples (Edmondson and Winberg 1971). Samples were preserved in 10% formalin for later sorting, identification, and counting in the laboratory. Identified specimens were dried in an oven at 60°C for 24 h and weighed to determine biomass.

Brown trout populations.—Electrofishing took place at 20 localities every March, June, September, and December from December 1992 to December 1998 by means of a 220-W DC generator. The sampling sites were 80–100 m long and 2–14 m wide and encompassed an area of 240–775 m^2. Brown trout were anesthetized with MS-222 (tricaine methanesulfonate; Sigma-Aldrich Co.), and their fork lengths (mm) and weights (g) were measured. The fish were placed in holding boxes to recover and then were returned to the stream. Brown trout density (fish/ha) and its variance were estimated separately for each sampling site by applying the maximum likelihood method (Zippin 1956) and the corresponding solution as proposed by Seber (1982) for three removals assuming constant capture effort. The biomass (kg/ha) was estimated as the product of mean individual weight and population density. Annual production (kg/ha) and its variance were calculated according to the increment summation method outlined by Newman and Martin (1983). The ratio of annual production to mean biomass (P/B) was then calculated. Population and production variables and associated variances were computed by means of Pop/Pro Modular Statistical Software (Kwak 1992).

Data analysis.—We compared population and production variables via multifactor analyses of variance (ANOVA) and verified assumptions of normality of distributions (Shapiro–Wilk W) and homogeneity of variances (Levene's test). Brown trout density, biomass, and production and benthic density and biomass were $\log_{10}$ transformed to fulfill the normality assumption. The significance level α for all statistical tests was set at 0.05.

Differences in water quality variables between streams were explored via principal components analysis (PCA) with a correlation matrix because of the large number of variables and the fact that some of them were intercorrelated. The data were standardized before the analysis was done. The between-streams PCA reduced the number of explanatory variables by defining independent synthetic variables (linear combinations of chemical water characteristics) that best reflected between-river variations in water quality patterns. To better define the differences among the resulting groups within each obtained factor, we compared the coordinates of groups by use of one-way ANOVA (Capen 1981).

Pairwise correlations (Pearson's product-moment correlation coefficient) and simple regression analyses were used to explore the relationships between environmental variables and brown trout density, biomass, production, and P/B ratio. Forward stepwise multiple regression analyses employed brown trout density, biomass, production, and P/B ratio as dependent variables; the independent variables were the resulting factors from water quality PCA as well as elevation, mean daily water temperature during the growing season, and density and biomass of macroinvertebrates.

To address the probable differences between European and North American annual brown trout production (kg/ha) models based on alkalinity (mg/L), we used ANOVA to compare production estimates observed in our study with expected values of the model developed for U.S. salmonid populations by Kwak and Waters (1997): Annual production = 40.66 + 0.48(alkalinity). Statistical analyses were performed by means of the STATISTICA 6.1 computer package (StatSoft, Inc.).

Results

Environmental Factors

Abiotic and biotic features were significantly different among the study streams (Table 1). The streams exhibited seasonal variations in water discharge and temperature that were typical for the Mediterranean climate. However, the Rivers Jarama, Cega, and Eresma were colder and more variable in flow regime than the other streams (Figures 2, 3). Peak flows in these streams occurred from winter to spring (mean = about 6 m^3/s), and flows approaching base flow were observed during summer (mean = about 0.5

TABLE 2.—Mean (SD) values (mg/L, except as noted) of water quality variables for 10 streams in central Spain where brown trout populations were examined. Samples were collected from each sampling site every third month from December 1992 to December 1998 (TDS = total dissolved solids).

Variable	Gallo	Dulce	Bornova	Hoz Seca	Cabrillas	Guadiela	Aguisejo
Conductivity (μS/cm)	963.9 (16.7)	602.4 (15.7)	155.7 (42.9)	598.1 (35.8)	606.1 (22.6)	690.9 (20.1)	307.5 (14.8)
TDS	480.9 (8.1)	302.6 (8.0)	126.0 (13.8)	301.0 (18.4)	303.9 (11.1)	269.0 (9.2)	211.1 (18.2)
pH	8.1 (0.0)	7.7 (0.0)	7.9 (0.1)	8.2 (0.2)	7.8 (0.1)	8.1 (0.3)	7.9 (0.0)
Chloride	85.1 (2.0)	16.7 (1.2)	4.8 (0.3)	3.4 (0.6)	16.1 (1.1)	16.0 (0.7)	3.1 (0.1)
Sulfate	126.4 (3.3)	57.0 (6.7)	12.1 (0.6)	43.4 (2.6)	194.7 (15.7)	171.4 (9.9)	15.6 (0.8)
Phosphate	0.33 (0.02)	0.13 (0.03)	0.08 (0.01)	0.04 (0.01)	0.18 (0.05)	0.05 (0.01)	0.26 (0.03)
Alkalinity	302.6 (6.6)	303.3 (1.8)	72.2 (1.1)	265.0 (12.8)	281.7 (13.7)	252.5 (4.5)	297.7 (8.6)
Nitrate	9.9 (0.4)	12.0 (0.4)	1.0 (0.2)	1.1 (0.1)	3.1 (0.3)	2.3 (0.1)	0.1 (0.0)
Nitrite	0.107 (0.007)	0.022 (0.003)	0.018 (0.003)	0.020 (0.003)	0.030 (0.008)	0.018 (0.002)	0.036 (0.003)
Sodium	52.5 (1.8)	7.7 (0.5)	2.8 (0.19)	21.4 (2.2)	9.6 (0.4)	10.6 (0.5)	1.5 (0.1)
Potassium	4.1 (0.1)	1.7 (0.1)	1.2 (0.1)	1.2 (0.1)	1.8 (0.1)	1.4 (0.1)	1.3 (0.1)
Calcium	119.5 (4.3)	92.2 (4.4)	22.0 (0.9)	73.3 (4.7)	128.3 (9.3)	120.5 (8.3)	72.1 (4.1)
Magnesium	25.4 (0.9)	24.6 (0.5)	4.7 (0.1)	18.7 (0.8)	27.7 (0.9)	31.4 (0.9)	17.0 (0.6)
Ammonia	0.099 (0.008)	0.046 (0.007)	0.054 (0.005)	0.005 (0.003)	0.010 (0.005)	0.055 (0.005)	0.046 (0.004)

m^3/s). The water temperature was close to 2°C in winter and 13°C in summer. The remaining seven streams were little affected by surface runoff at times of heavy rainfall, reaching maximum and minimum mean values around 1.5 m^3/s in December–January and 0.5 m^3/s in August–September. The temperature regime exhibited a mean value around 8°C in winter and 15°C in summer.

The scarce agricultural activity and low population density in the study area may explain the observed low concentrations of nitrates, nitrites, ammonia, and phosphates (Table 2). The PCA revealed two main axes accounting for 74.2% of the total variance of chemical water variables between streams. The coefficients of the two components are shown in Table 3, and the sites corresponding to the first two components are presented in Figure 4. Factors rotation was not employed because the factors were clearly marked by high loadings for some variables and low loadings for others. Vectors representing the chemical variables

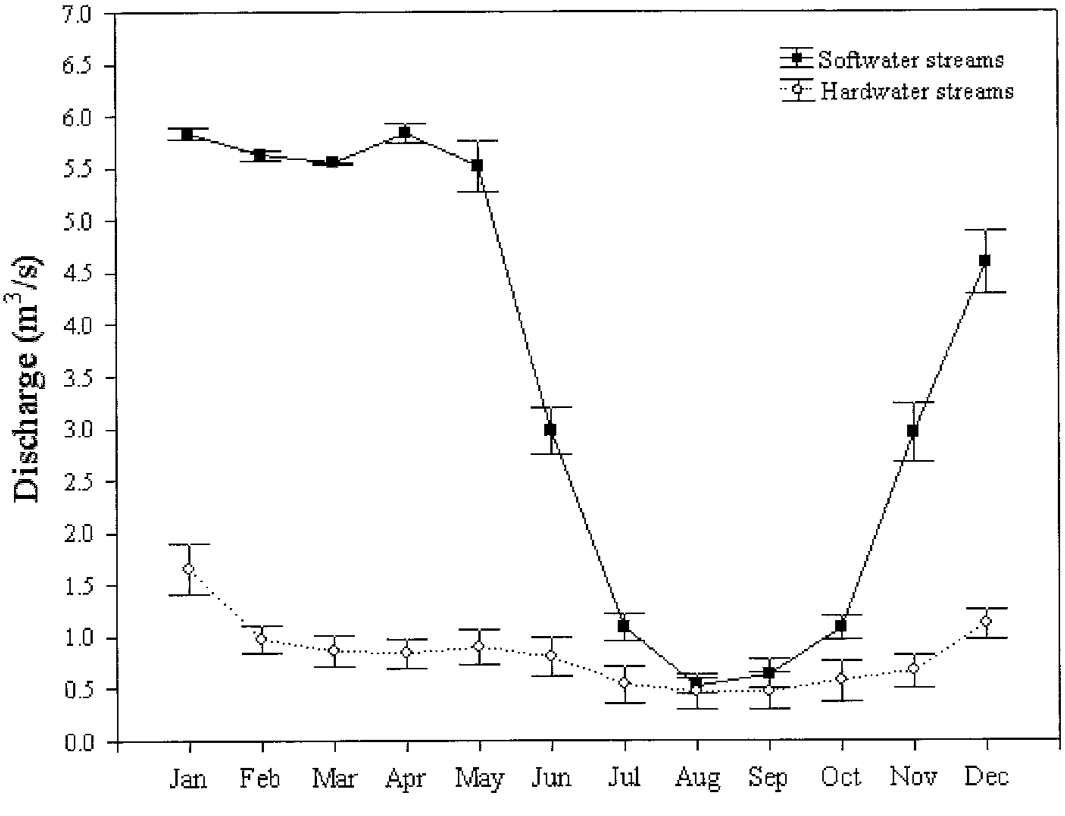

FIGURE 2.—Mean ± SD monthly discharge in soft-water (Rivers Jarama, Cega, and Eresma) and hard-water streams (Rivers Hoz Seca, Cabrillas, Gallo, Dulce, Guadiela, Bornova, and Aguisejo) in Spain during 1992–1998.

TABLE 2.—Extended.

Variable	Eresma	Cega	Jarama
Conductivity (μS/cm)	65.3 (4.1)	17.7 (1.2)	26.0 (1.1)
TDS	33.7 (1.8)	8.9 (0.8)	13.3 (0.7)
pH	7.1 (0.1)	7.1 (0.1)	7.2 (0.1)
Chloride	8.6 (0.5)	0.6 (0.2)	2.7 (0.4)
Sulfate	2.0 (0.6)	2.1 (0.7)	4.4 (0.4)
Phosphate	0.10 (0.03)	0.15 (0.05)	0.11 (0.03)
Alkalinity	27.0 (2.6)	19.2 (2.1)	11.6 (0.7)
Nitrate	1.1 (0.2)	0.9 (0.8)	0.4 (0.1)
Nitrite	0.031 (0.013)	0.036 (0.015)	0.019 (0.004)
Sodium	6.8 (1.6)	1.4 (0.4)	1.8 (0.1)
Potassium	0.6 (0.1)	0.4 (0.1)	0.7 (0.2)
Calcium	2.9 (0.3)	3.3 (0.9)	2.3 (0.2)
Magnesium	0.9 (0.1)	0.8 (0.2)	0.9 (0.2)
Ammonia	0.042 (0.007)	0.029 (0.013)	0.053 (0.006)

indicated their influence on the streams by means of their length and angle with respect to the axes.

The first factor was highly positively correlated with variables related to the nutrient content of water (conductivity, alkalinity, TDS, chloride, sulfate, K^+, Ca^{2+}, and Mg^{2+}). The second factor reflected the phosphate and nitrite levels. The results indicate large differences between streams in concentrations of common ions. Visual inspection of the plots of the first and second components differentiated two groups of streams with regard to water productivity. The first factor separated a first group comprising hard-water streams (the Rivers Hoz Seca, Cabrillas, Dulce, Guadiela, Gallo, Bornova, and Aguisejo) with a high or intermediate salt content and a second group consisting of soft-water streams (the Rivers Cega, Eresma, and Jarama) with low salt levels (Figure 4). Differences between the coordinates of the hard-water and soft-water streams of the PC1 were statistically significant (ANOVA: $F_{1,8} = 16.97$, $P < 0.01$). The second axis discriminated among streams with slight urban or agricultural pollution (the Rivers Gallo and Aguisejo) and more polluted streams; the coordinates of the two groups differed significantly ($F_{1,8} = 9.60$, $P < 0.05$).

The bottom fauna in hard-water streams with a higher mineral content (mean density = 2,433 individuals/m^2, SD = 227; mean biomass = 2.76 g/m^2, SD = 0.27) and in soft-water streams with low ionic and carbonate content (mean density = 598 individuals/m^2, SD = 68; mean biomass = 0.63 g/m^2, SD = 0.07) differed significantly in terms of density (ANOVA: $F_{1,248} = 139.37$, $P < 0.001$) and biomass ($F_{1,248} = 111.33$, $P < 0.001$; Table 1). This was particularly evident in the Rivers Gallo and Dulce, which also had a

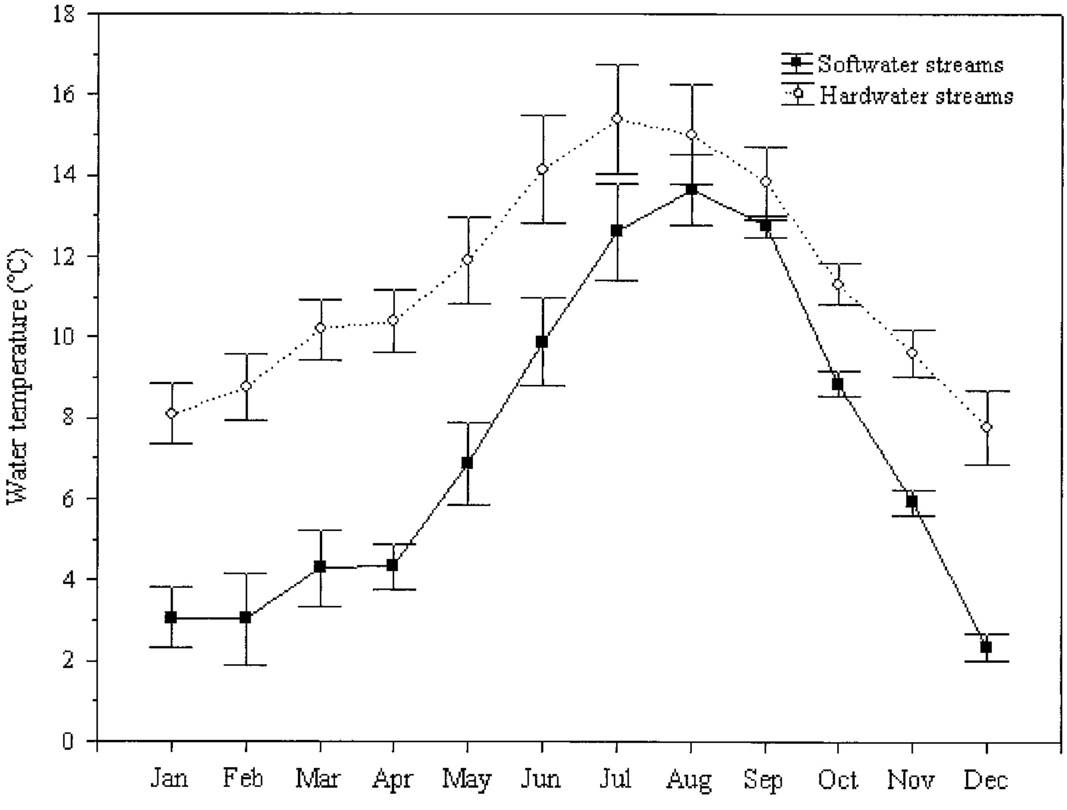

FIGURE 3.—Mean ± SD monthly water temperatures in soft-water (Rivers Jarama, Cega, and Eresma) and hard-water streams (Rivers Hoz Seca, Cabrillas, Gallo, Dulce, Guadiela, Bornova, and Aguisejo) in Spain during 1992–1998.

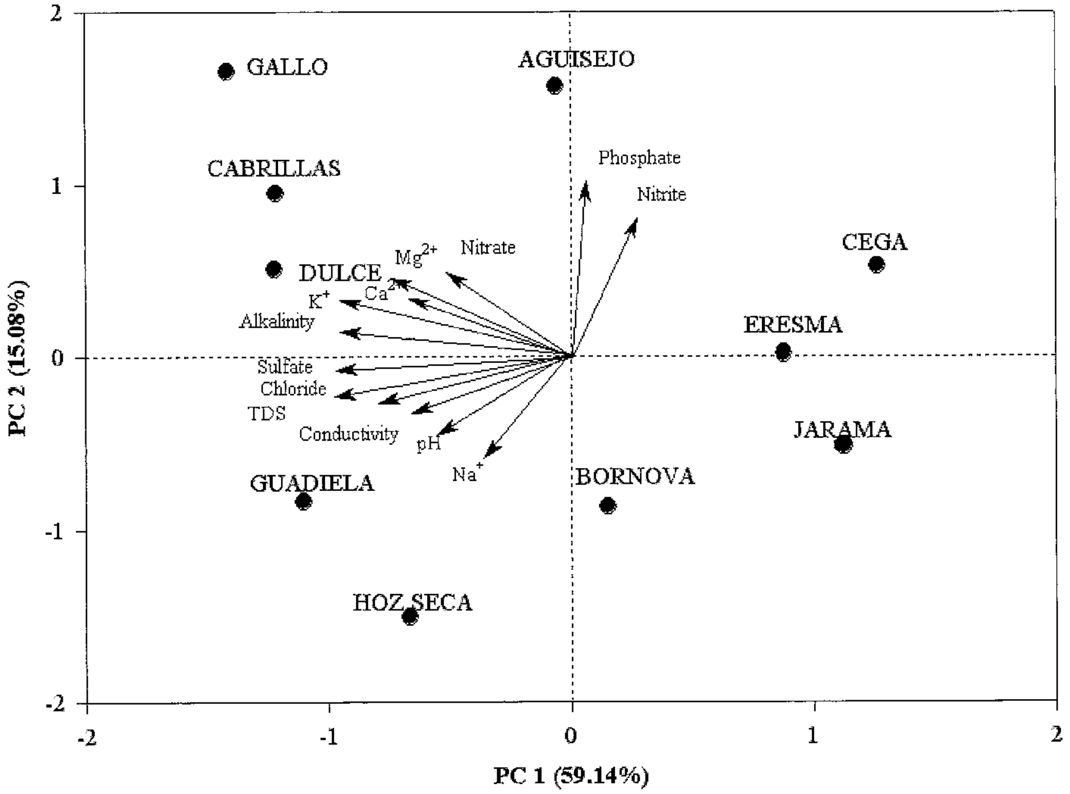

FIGURE 4.—Plot of the factor scores for water quality variables (all measured in mg/L except conductivity [μS/cm] and pH; TDS = total dissolved solids) on the first two principal components for 10 Spanish streams in which brown trout population characteristics were surveyed. Arrows show the influence of significant variables in the two axes. Alkalinity was measured as $CaCO_3$.

comparatively more stable discharge and higher temperatures, allowing the occurrence of macrophytes that provide cover for many groups of macroinvertebrates.

TABLE 3.—Factor loadings (unrotated) for the first two principal components (PCs) from principal components analysis of variation in physicochemical variables of 10 streams in central Spain where brown trout populations were studied during 1992–1998. Loadings in bold italics were significant ($P < 0.05$). Variables are measured in milligrams per liter except for conductivity and pH; TDS = total dissolved solids.

Variable	PC1	PC2
Conductivity (μS/cm)	***−0.986***	−0.095
TDS	***−0.975***	0.009
pH	***−0.772***	−0.219
Chloride	***−0.761***	0.098
Sulfate	***−0.813***	0.054
Phosphate	0.058	***0.956***
Alkalinity	***−0.910***	0.232
Nitrate	***−0.622***	0.258
Nitrite	0.285	***0.809***
Sodium	***−0.627***	−0.542
Potassium	***−0.912***	0.171
Calcium	***−0.972***	0.154
Magnesium	***−0.974***	0.083
Ammonia	0.314	−0.009
Variance explained (%)	59.14	15.08

Brown Trout Populations

Brown trout population variables (density, biomass, production, and P/B ratio) were compared by use of ANOVA tests. No significant differences were found between localities within each river ($P > 0.05$), and thus mean values were considered in the comparative analyses. Similarly, populations seemed to only experience the natural interannual variability in numbers, which did not significantly change among most rivers ($P > 0.05$). Only the River Dulce showed interannual differences in brown trout density ($F_{5,42} = 11.89$, $P < 0.001$); however, post hoc tests only evidenced significant differences between 2 years (Scheffé's test: $P < 0.05$). We concluded that there were no interannual differences in population characters, and mean values corresponding to the 7 years were therefore used (Table 4). Brown trout density was significantly different between streams ($F_{9,240} = 10.15$, $P < 0.001$). Density ranged from 1,567 to 5,876 fish/ha and averaged 2,862 fish/ha.

Mean brown trout biomass for the 10 streams also showed significant variation ($F_{9,240} = 8.92$, $P < 0.001$). Total biomass varied from 56.6 to 240.2 kg/ha and averaged 87.4 kg/ha. Mean annual production showed significant differences between streams ($F_{9,50}$

TABLE 4.—Estimated means (SDs) of brown trout abundance, biomass, annual production, and the production–biomass ratio (P/B) of 10 streams in central Spain during 1992–1998.

River	Density (fish/ha; $N = 50$)	Biomass (kg/ha; $N = 50$)	Annual production (kg/ha; $N = 12$)	P/B ($N = 12$)
		Hard-water streams		
Gallo	3,074 (584)	238.9 (44.1)	182.2 (95.7)	1.06 (0.10)
Dulce	5,866 (1,071)	240.2 (27.2)	156.8 (83.9)	1.02 (0.15)
Bornova	5,594 (1,207)	109.5 (29.8)	148.5 (36.4)	1.40 (0.01)
Hoz Seca	1,567 (288)	102.4 (43.5)	122.9 (52.5)	1.56 (0.10)
Cabrillas	2,379 (1,499)	103.1 (53.6)	119.6 (29.1)	1.44 (0.19)
Guadiela	2,907 (1,963)	90.0 (35.8)	113.7 (17.0)	1.39 (0.44)
Aguisejo	2,184 (1,012)	73.7 (30.9)	92.3 (9.9)	1.29 (0.08)
		Soft-water streams		
Eresma	4,317 (2,111)	96.6 (35.9)	89.1 (22.1)	1.01 (0.17)
Cega	1,957 (1,027)	61.7 (43.4)	47.9 (9.3)	1.10 (0.32)
Jarama	2,156 (1,319)	56.6 (36.1)	47.3 (18.6)	1.09 (0.31)

$= 5.79$, $P < 0.001$). Annual production varied from 47 to 182 kg/ha and averaged 96.5 kg/ha (Table 4). The P/B ratio was also significantly different between streams ($F_{9,50} = 2.70$, $P < 0.05$), ranging from 1.01 to 1.56 and averaging 1.16.

Relationships between Environmental Factors and Brown Trout Population Variables

Density did not differ between soft-water and hard-water streams (ANOVA: $P > 0.05$), whereas significantly higher values of biomass ($F_{1,248} = 21.22$, $P < 0.001$) were noted for hard-water streams (mean = 109.7 kg/ha) compared with soft-water ones (mean, 71.4 kg/ha). Annual production was also related to the water nutrient concentration ($F_{1,58} = 24.0$, $P < 0.001$), showing significantly higher values in hard-water streams (mean = 133.9 kg/ha) compared with soft-water ones (mean = 67.4 kg/ha). The P/B ratio did not show significant differences between hard- and soft-water streams (ANOVA: $P > 0.05$).

Mean density and P/B ratio were not significantly correlated with physicochemical and benthic abundance variables (Table 5). In contrast, mean biomass was positively correlated with water temperature, conductivity, TDS, chloride, nitrate, sodium, potassium, and both benthic density and biomass, as well as negatively correlated with elevation. Mean production was correlated with the same variables as biomass and also with pH, alkalinity, calcium, and magnesium (Table 5).

The stepwise multiple-regression analyses revealed a significant relationship between brown trout production and chemical features indicative of high water productivity (PC1, nutrient content), which accounted for 61% of the variance explained by the model. Therefore, brown trout production tended to be higher in fertile streams containing high inorganic nutrient levels. The biomass of benthic macroinvertebrates was the variable with the greatest effect on brown trout biomass, accounting for 69% of the variance explained by the regression model. Variance in brown trout biomass related to stream elevation was only 15%. Thus, the biomass increased when benthos abundance increased and decreased with increasing elevation (Table 6).

A broader spatial analysis based on our data and a review of other European work (Appendix) showed that annual brown trout production in hard-water streams (mean = 121.6 kg/ha; range = 30.0–253.3 kg/ha; $N = 34$) was significantly greater than that in soft-

TABLE 5.—Correlation coefficients (Pearson r) and their probabilities ($P < 0.05$*, $P < 0.01$**, $P < 0.001$***) for comparisons of brown trout density, biomass, production, and the production–biomass ratio (P/B) vis-à-vis physicochemical and benthic macroinvertebrate abundance variables (TDS = total dissolved solids).

Variable	Density	Biomass	Production	P/B
Growing season temperature (°C)	0.18	0.70*	0.75**	−0.02
Elevation (m)	−0.60	−0.82**	−0.66*	0.49
Conductivity (μS/cm)	−0.08	0.67*	0.77**	0.15
TDS	−0.04	0.70*	0.82**	0.15
pH	−0.06	0.35	0.71*	0.55
Chloride	−0.07	0.73*	0.65*	−0.37
Sulfate	−0.12	0.26	0.46	0.28
Phosphate	−0.15	0.40	0.26	−0.41
Alkalinity	−0.14	0.53	0.66*	0.25
Nitrate	0.30	0.89***	0.69*	−0.36
Nitrite	−0.09	0.56	0.43	−0.41
Sodium	−0.11	0.66*	0.65*	−0.14
Potassium	0.08	0.76**	0.78**	−0.19
Calcium	−0.12	0.49	0.65*	0.26
Magnesium	−0.11	0.48	0.64*	0.27
Ammonia	0.32	0.51	0.38	−0.62
Benthic density (individuals/m^2)	0.04	0.83**	0.71*	−0.35
Benthic biomass (g/m^2)	−0.02	0.78**	0.65*	−0.35

TABLE 6.—Results of stepwise multiple regression analyses testing the effect of temperature, elevation, two principal components (PC1 = nutrient content of water, PC2 = water pollution), and benthic macroinvertebrate density and biomass on brown trout production and biomass in 10 streams in central Spain, 1992–1998.

Dependent variable	Independent variables	Coefficient	R^2	F	P
Annual production (kg/ha)	PC1	−36.0	0.61	12.77	<0.01
	Constant	111.05			
Biomass (kg/ha)	Benthic biomass (g/m^2)	0.57	0.84	18.17	<0.001
	Elevation (m)	$-0.05 \cdot 10^{-2}$			
	Constant	2.45			

water streams (mean = 76.6 kg/ha; range = 3.5–234.0 kg/ha; $N = 31$) (ANOVA: $F_{1,63} = 12.97$, $P < 0.001$).

Data were available for 12 pairwise correlations between mean annual production and physicochemical characteristics of streams. Of these comparisons, eight were significant: conductivity ($r = 0.69$, $P < 0.001$), alkalinity ($r = 0.74$, $P < 0.001$), pH ($r = 0.53$, $P < 0.01$), nitrate ($r = 0.63$, $P < 0.001$), chloride ($r = 0.70$, $P < 0.01$), Mg^{2+} ($r = 0.50$, $P < 0.05$), Na^+ ($r = 0.68$, $P < 0.01$), and K^+($r = 0.61$, $P < 0.01$). No significant correlations were found between production rates and ammonia, sulfate, Ca^{2+}, and phosphate. These analyses clearly showed a significant relationship ($F_{1,22} = 24.94$, $P < 0.001$; $r^2 = 0.53$) between brown trout production and water alkalinity, which is the most-often-cited determinant of salmonid production in streams, according to the model $\log_{10}(\text{production}) = 1.41 + 0.31 \cdot \log_{10}(\text{alkalinity})$. A large part of the variation in production rates among European populations resulted from differences in stream alkalinity (Figure 5). The analysis covered a wide range of alkalinity (4.3–358.0 mg/L) and annual production (18–200 kg/ha) measures. Unfortunately, some analyzed European studies did not have alkalinity data; therefore, we could not use the complete database to make the model. However, the range of annual production (3.5–253.0 kg/ha) was only slightly broader in the complete database. The observed production rates were similar (ANOVA: $P > 0.05$) to those estimated from the model of Kwak and Waters (1997). However, their model predicts annual production rates of 42.7–212.5 kg/ha, which are slightly higher than the actual rates observed in our study.

Discussion

Annual production estimates of brown trout in the streams we studied were within the range reported across native European populations: from 3.5 kg/ha in a glacial stream in Norway (Power 1973) to 253.3 kg/ha in a limestone stream in Spain (Lobón-Cerviá et al. 1986). Mean annual production rates in the Rivers Jarama, Cega, Eresma, and Aguisejo (47.3–92.3 kg/ha) were comparable to those of low-productivity streams in Denmark (Mortensen 1977) and England (Le Cren 1969; Crisp et al. 1974). Annual production rates in the Rivers Hoz Seca, Cabrillas, and Guadiela (113.7–122.9 kg/ha) were similar to those reported from streams with intermediate production rates in Denmark (Mortensen 1977), England (Le Cren 1969; Mann 1971; Mann et al. 1989), and Ireland (Kelly-Quinn and Bracken 1988). Finally, average production values in the Rivers Bornova, Dulce, and Gallo (148.5–182.2 kg/ha) were similar to those in highly productive streams in Denmark (Mortensen 1977) and Ireland (Lobón-Cerviá and Fitzmaurice 1988).

Brown trout production and biomass were positively related to the concentration of inorganic nutrients and thus to the water productivity. This, however, was not the case for brown trout density and *P/B* ratio. The marked relationship found between production estimates and the nutrient content of water seems quite a common feature of studies carried out on freshwater fish communities. Thus, Watson and Balon (1984) found that production was more a function of river fertility than water temperature in tropical streams.

Our results corroborate previous evidence on the influence of water fertility on salmonid production and are consistent with the hypothesis that abiotic factors influence and in some cases may regulate brown trout production in small upland streams. Variability in salmonid production rates in most temperate streams has been commonly attributed to differences in environmental productivity related to geological bedrock (e.g., Mann and Penczak 1986; Scarnecchia and Bergersen 1987). Moreover, our findings are also consistent with conclusions drawn previously by Neves et al. (1985) and Eggleton and Morgan (2000) for rainbow trout *Oncorhynchus mykiss*. The estimated model for total production presented by Eggleton and Morgan (2000) for Appalachian streams indicated that water chemistry measures and elevation were significantly related to rainbow trout production, explaining almost 50% of the observed variation. Further, Kwak and Waters (1997) found that 37% of brown trout production variation in Minnesota streams was explained by water alkalinity differences between streams. The same trend has been observed in the

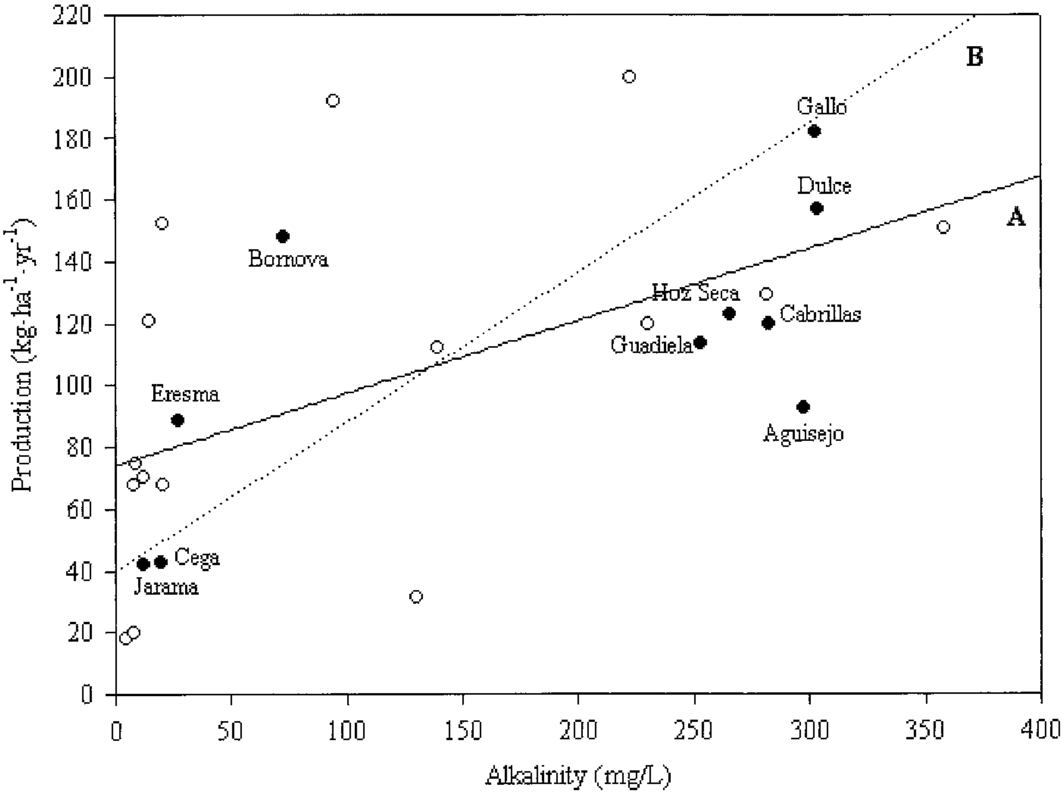

FIGURE 5.—Linear regression between mean alkalinity and mean brown trout annual production in European streams (solid line [A]). Black dots represent data from our study (10 Spanish streams); clear dots represent literature values. Data from other European streams are cited in the Appendix. The linear regression of U.S. stream data from Kwak and Waters (1997) is also included (dotted line [B]) for comparative purposes.

present work, over a broad range of alkalinities and production values.

Biomass in the streams we studied was positively related to food abundance, measured as biomass of benthic macroinvertebrates, which is indirectly related to water productivity as well. A similar relationship between trout biomass and food abundance was reported in Ontario (Murphy et al. 1981) and Oregon (Bowlby and Roff 1986) streams, and Clarke and Scruton (1999) found that benthic macroinvertebrate abundance was the variable that best defined brook trout *Salvelinus fontinalis* production in Newfoundland streams.

The observed negative relationship between elevation and brown trout biomass may indicate a response of brown trout to changes in physical and chemical factors related to elevation, such as stream depth, water temperature, or nutrient concentration, which clearly influence brown trout growth and the availability of suitable habitat for larger individuals (Nicola and Almodóvar 2002, 2004). Thus, brown trout become larger downstream, as has been widely observed in freshwater systems (e.g., Milner et al. 1978; Schlosser 1982; Anderson 1985; Clarkson and Wilson 1995).

The lack of relationship between density and nutrient content of water, food abundance, elevation, and water temperature indicates that spatial variability of brown trout density may be affected by other environmental factors, namely hydrological variability and local physical habitat, as well as biotic processes such as density-dependent mechanisms. All these factors have been demonstrated to be of major importance for predicting trout abundance elsewhere (e.g., Elliott 1994; Cattanéo et al. 2002; Armstrong et al. 2003).

In conclusion, annual production rates in brown trout headwater streams seem to depend greatly on water productivity because 60% of variation is explained by the nutrient content of water. The large geographic scale we analyzed provided deeper evidence of our conclusion that a significant proportion of the production variation is explained by some water productivity variables. Other abiotic (e.g., discharge and physical habitat) and biotic (e.g., density dependence) features often cited as limiting factors for brown trout production probably operate, as well, but at a more localized scale not considered in our study.

The observed relationships between water quality variables and fish production may assist managers in assessing the potential of streams to support an appropriate brown trout fishery. Similarly, managers might be able to evaluate the effects of human activities that produce significant changes in water quality on brown trout populations, such as acidification (Hesthagen et al. 1999) or changes in land use that affect riparian vegetation (Townsend et al. 1997).

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Appendix: European Data

TABLE A.1.—Summary of selected mean annual production estimates from the literature for European brown trout populations in hard-water (H) and soft-water (S) streams. The period of data collection (number of years, N_y) and the number of studied streams (N_s) are also indicated.

Location	Stream type	N_s	N_y	Production (kg/ha)	Reference
Norway	S	4	1–4	3.5–19.9	Power (1973)
	S	1	5	44.8	Bergheim and Hesthagen (1990)
Denmark	H	8	1–7	47.0–227.0	Mortensen (1977, 1978, 1982)
Poland	S	1	1	33.7	Mortensen and Penczak (1988)
Scotland	S	1	9	102.7	Egglishaw and Shackley (1977)
England	S, H	11	2–11	30.0–121.0	Le Cren (1969)
	H	3	3–5	59.1–85.5	Crisp et al. (1974)
	S, H	5	2–11	120.0–200.0	Mann (1971), Mann et al. (1989)
	H	1	1	138.9	Crisp and Cubby (1978)
	S	1	25	234.0	Elliott (1993)
Wales	S	1	1	85.0	Milner et al. (1978)
Ireland	S, H	4	1	31.4–152.6	Lobón-Cerviá and Fitzmaurice (1988)
	H	1	2	112.4	Kelly-Quinn and Bracken (1988)
Czech Republic	H	2	3	21.2–74.5	Libosvárský (1968)
Bulgaria	S	1	1	109.9	Jankov (1986)
Portugal	S	5	2–4	18.0–135.0	Valente (1990)
	S	1	2	70.4	Formigo and Penczak (1999)
Spain	H	3	1	78.6–253.3	Lobón-Cerviá et al. (1986)
	S	1	7	196.0	Lobón-Cerviá (2003)