VARIABILITÉ DES POPULATIONS DE SALMONIDÉS EN EAU COURANTE : ÉTUDE DE LA VARIANCE LIÉE À DIFFÉRENTES ÉCHELLES SPATIALES OU TEMPORELLES ET IMPLICATIONS POUR LES MODÈLES D'HABITAT.

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RÉSUMÉ (traduit par les éditeurs)

Les populations de truite *(Salmo trutta,* L.*)* et de saumon *(Salmo salar,* L.*)* des cours d'eau sont caractérisées par des variations spatiales et temporelles. La capacité des modèles d'habitat (modèles empiriques reliant l'abondance des poissons à des variables spatiales) à expliquer la variance totale de l'abondance reste cependant réduite aux seules composantes spatiales. Il est pourtant important de mieux connaître leur contribution à cette variance totale, d'où la nécessité d'estimer la performance potentielle maximum des modèles par rapport à leur performance actuelle. Une partition de la variance peut aider à dégager les rôles respectifs des facteurs spatiaux et temporels (synchrones) influençant l'abondance des populations en étudiant leur variation en fonction de l'appartenance géographique des échantillons.

Des modèles d'habitat (HABSCORE), récemment développés pour les cours d'eau du Pays de Galles, ont été utilisés pour expliquer la variance d'un jeu de données recueilli sur 10 ans. Les facteurs spatiaux expliquent entre 46 et 62 % de la variance totale pour les cours d'eau du bassin de la Conwy. Cela montre les limites maximums de la performance de modèles construits à cette échelle. A l'exception d'une faible performance pour les parrs de saumon, les modèles d'habitat prennent en compte de 60 à 95 % de la composante spatiale, soit 38 à 46 % de la variance totale.

La structure de la variance a été comparée à quatre niveaux différents d'analyse : entre les différents tributaires de la Conwy (1), entre 9 systèmes différents de cours d'eau (2), entre trois régions (3) et dans tout le Pays de Galles (4). La variance spatiale évolue de 22-42 % (moyennes) au niveau local (1) à 42-65 % au niveau régional (4). Parallèlement, la variance temporelle (soit, une mesure du synchronisme de la variabilité des populations) décroît de 24-39 % du niveau local (1) à 0.7-9.0 % au niveau régional (4).

Au niveau inter cours d'eau (2) et à plus large échelle, la variance temporelle de l'abondance des 0^+ est beaucoup plus faible que pour les poissons > 0^+. Certains des facteurs influençant la variabilité aux différentes échelles géographiques sont discutés brièvement.

Mots-clés : salmonidés, cours d'eau, densité de population, variance spatiale et temporelle, modèles d'habitat, synchronisme, échelle géographique.

VARIANCE STRUCTURING IN STREAM SALMONID POPULATIONS, EFFECTS OF GEOGRAPHICAL SCALE AND IMPLICATIONS FOR HABITAT MODELS.

ABSTRACT

Trout (*Salmo trutta,* L.) and salmon (*Salmo salar,* L.) populations in streams exhibit temporal and spatial variation. However, the ability of habitat models (empirical models relating fish abundance to spatial features) to explain overall variance in abundance is restricted just to the spatial component. It is therefore important to be able to quantify the contribution from the spatial component to total variance. This allows assessment of both the potential maximum performance of models as well as their actual performance in relation to the maximum. Furthermore, such variance partitioning offers insight into the relative roles of spatial and temporal (synchronous) factors in influencing population abundance and how these vary according to the geographical scale of sampling.

Habitat models (HABSCORE), recently developed for Welsh streams, were used to explain variance in a ten year data set for which temporal and spatial variance could be estimated. Spatial factors explained between 46 and 62 % of overall variance within the Conwy system. This identifies the maximum limits for the performance of such models working at this scale. With the exception of poor performance for salmon parr, the habitat models accounted for 60-95 % of the spatial component, corresponding to 38-46 % of overall variance.

In addition, variance structure was compared at four different levels of analysis : within tributaries on the Conwy, within nine different large separate river systems, within three areas and within the region of Wales. Spatial variance increased from 22-42 % (means) at within-tributary level to 42-65 % at regional level. In contrast, temporal variance (a measure of synchrony in population variability) decreased from 24-39 % within tributaries to 0.7 - 9.0 % at regional level. At within-rivers and larger scale the temporal variance displayed in 0+ abundance was consistently lower than that for >0+ fish. Some of the factors influencing variability at the different geographical scales are briefly discussed.

Key-words : salmonids, streams, population density, spatial and temporal variance, habitat models, synchrony, geographical scale.

INTRODUCTION

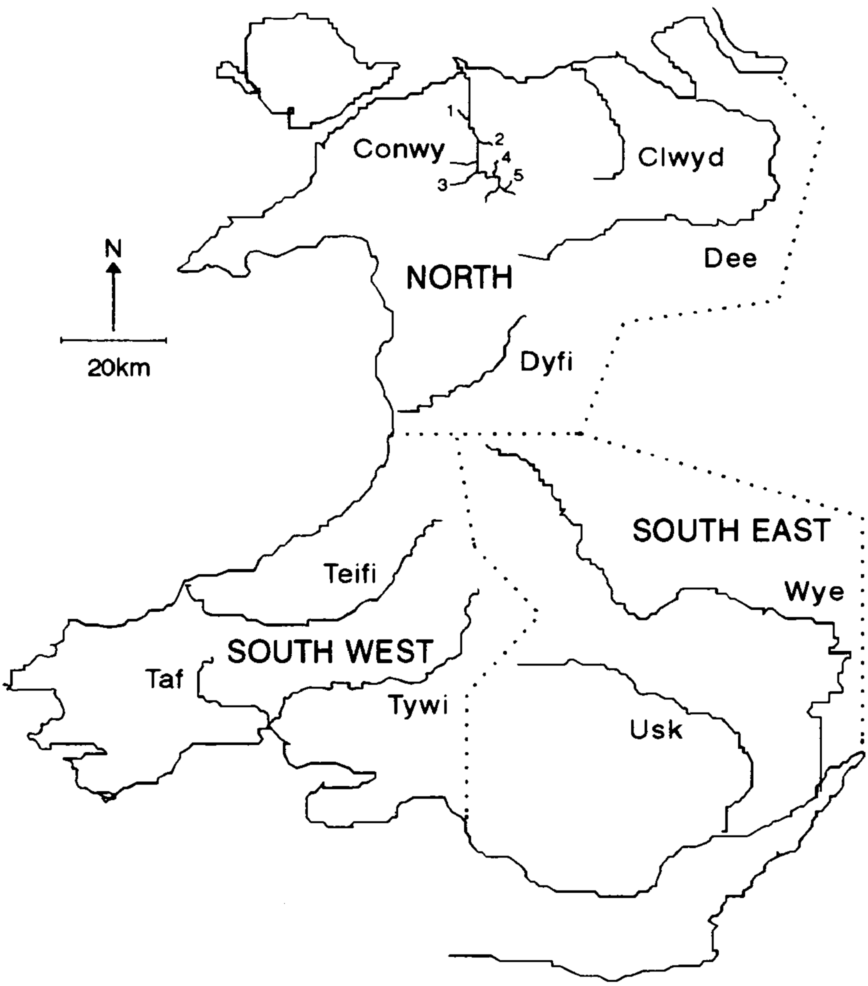
The distribution and abundance of juvenile salmonids are often used to assess environmental impacts or to monitor the outcome of fishery management strategies. For this purpose it is necessary to know the extent of temporal and spatial variability of stream populations and to have an understanding of their underlying causes. Stream habitat is commonly regarded as a significant source of spatial variance in salmonid abundance and there have been numerous attempts to explain spatial variation in terms of local site habitat features and catchment characteristics, mainly in North America (see review by FAUSCH *et al.*, 1988) but also in Europe (e.g. HERMANSEN and KROG, 1984 ; MILNER *et al.*, 1985 ; ZALEWSKI *et al.*, 1985).

Habitat models offer potentially valuable management tools (MILNER *et al.*, 1985), but only if they explain a significant proportion of spatial variability over a wide range of stream types, and if the spatial component of overall variance is significant in relation to other sources of variation. This paper summaries a study of population density variance in Atlantic salmon (*Salmo salar* L.), sea trout and brown trout (migratory and non-migratory forms of *S. trutta* L.) in the river Conwy, North Wales, surveyed over a ten-year period. Habitat models (HABSCORE) recently developed for Welsh streams were applied to these data to examine what proportion of spatial variance they were able to explain. A second set of shorter duration, but covering eight additional rivers throughout Wales allowed variance structure to be examined at different scales, from tributary up to regional level, in order to describe the relative roles of spatial and temporal factors at these different levels.

MATERIALS AND METHODS

Study catchments

The nine rivers in this study (Fig.1) drain upland catchments with base-poor geologies and subject to low intensity stock grazing on unimproved pasture, with more intensive agriculture in some lower valleys. Plantation forestry is common and acidification of some headwater streams occurs. Rainfall is typically high (>2000mm in upper catchments) and the flow regimes are spatey, with high flows occurring in autumn and winter.



Conwy tributaries : 1.Roe, 2.Nant y Goron, 3.Lledr, 4.Iwrch, 5.Nant y Foel.

Figure 1 : Localisation des cours d'eau étudiés au Pays de Galles.
Les affluents étudiés sont : Roe (1), Nant y Goron (2), Lledr (3), Iwrch (4), Nant y Foel (5).

Figure 1 : Location of the studied rivers in Wales.
Conwy tributaries are : Roe (1), Nant y Goron (2), Lledr (3), Iwrch (4), Nant y Foel (5).

Fish population survey

Fish were sampled annually by electrofishing 50m sites isolated by stop nets, during the period July to September. On the river Conwy twenty-eight sites on five tributaries (Fig.1) gave data for four to ten year periods, between 1982 and 1991. An additional eight rivers were sampled annually for periods of five to seven years, using the same techniques as on the Conwy. Sites were selected to be representative of the dominant stream habitats in each tributary or main river zone. Population sizes were estimated by the maximum likelihood method of CARLE and STRUB (1978).

Fish were measured (fork length, nearest 1mm) and aged by scale reading and size frequency distributions.

Habitat survey and models

Electrofished sites on the Conwy were surveyed using the HABSCORE procedure (NRA, 1991) in which transect-based measurements were made of stream habitat features. Typical site variables included width, depth, cover, flow types and substrate composition. Catchment features, taken from 1:50,000 maps and from the NRA regional water quality database, included gradient, catchment area, altitude, conductivity, distance to mouth and a flashiness index.

The HABSCORE models were produced from a data set of up to 224 sites on 11 catchments in Wales and were derived by forward, stepwise multiple regression using site and catchment features as independent variables, including a wide range of derived variables based on the joint occurrence of various physical attributes. The dependent variables were fish densities, as N/100m^2. Sites were screened carefully to avoid any subject to identifiable environmental impacts. Models were developed for four categories of salmonid: trout 0^+, trout $>0^+$, salmon 0^+ and salmon $>0^+$.

Model parameters have been reported elsewhere (MILNER *et al.*, 1993). Performance as measured by the percentage of population density (independent data set) variance (R^2, adj %) explained by the models were 72.4, 66.2, 48.3 and 26.2 % for trout 0^+, trout $>0^+$ and salmon $>0^+$ respectively.

Data analysis

The methods outlined here refer to two different exercises : a habitat modelling and catchment scale variance partitioning on the Conwy (MILNER *et al.*, 1993) and a more recent development using improved techniques in a national scale habitat modelling project (WYATT *et al.*, 1995).

Conwy data

Variance in population density was analysed by random effects two-way ANOVA (SOKAL and ROHLF, 1981), with correction for missing values using the Minitab Generalised Linear Modelling (GLM) procedure. Multiplicative models were fitted to $\log_{10}$ (n+1) - transformed data. The additive model applied to transformed data was :

$$\log_{10}((n_{ij} + 1)/A) = m + s_i + y_j + e_{ij}$$

where n_{ij} = numbers at site i in year j ; A = wetted area (100m^2) ; m = overall mean density ; s_i = effect due to site i ; y_j = effect due to year j ; e_{ij} = error, including measurement error and interaction between site i and year j.

Variance was partitioned into three components (spatial, temporal and error) at two levels of analysis : firstly between all 28 sites and secondly between sites within each of five tributaries separately. Spatial variance (V_s), temporal variance (V_t) and error variance (V_e) were approximately estimated from :

$$V_s = (MS_s - MS_e)/m$$

$$V_t = (MS_t - MS_e)/n$$

$$V_e = MS_e$$

$$\text{and} \quad V_t = V_s + V_t + V_e$$

where V_T = total variance ; MS_s = mean square (sites) ; MS_t = mean square (years) ; MS_e = error mean square ; m = number of years ; n = number of sites.

Similar models have been applied to monthly data from stream fish populations by MEADOR and MATTHEWS (1991). Temporal variance represented synchronous variation between sites at the given level of analysis, i.e. the tendency for all sites to have good or bad years simultaneously.

Habitat data were collected for 26 of 28 Conwy sites in the five tributaries during summer, 1991. Using these data, the regional HABSCORE models were applied to those sites to examine their observed densities against the values (Habitat Quality Score, HQS) expected from habitat features as predicted from the models.

The ability of HABSCORE to explain the spatial component of variance within a long term data set was assessed by comparing the spatial variance explained by HQS with the total spatial variance calculated for the 26 sites, but substituting HQS values for s_i in the model shown above.

Geographical scale comparison

Variance was partitioned for the Conwy and a further eight rivers using an improved procedure based on Residual Maximum Likelihood (REML) (PATTERSON and THOMPSON, 1971), using an algorithm devised by ROBINSON *et al.* (1982) operated through Genstat 5.3 routines (PAYNE *et al.*, 1993). In a balanced design, the REML estimates of the variance components are identical to the unbiased estimates that can be produced from the ANOVA method. However, REML can also be used with unbalanced data to produce estimates of variance components that are more accurate than the approximations of the GLM-based procedures used on the Conwy data. Furthermore, for the geographical comparisons, zero data points (<5 % of sites) were omitted and data were transformed by natural logarithms. This procedure, adopted as part of a more recent habitat modelling exercise (WYATT *et al.*, 1995), alters the absolute variance values, but has very little effect on their proportional values and thus does not affect the interpretation of results in this account.

The model utilised was equivalent to a random effects two-way ANOVA :

$$\mathrm{Log_e}\,(n_{ij}/A) = m + s_i + y_j + e_{ij}$$

Using this improved procedure, variance partitioning was compared at four levels :

1. Within-tributary (Conwy only).
2. Within-river (nine rivers : Clwyd, Conwy, Dee, Dyfi, Usk, Wye, Taf, Teifi, Tywi).
3. Within-area (three areas : North, South East and South West Wales).
4. Within-region (Wales).

RESULTS

Spatial and temporal abundance variation in the Conwy

There were consistent differences in salmonid densities between and within tributaries (Fig.2). The Roe, Nant y Goron and Lledr trout populations are predominantly sea trout whereas the Iwrch and Nant y Foel contain entirely non-migratory brown trout. Most (88 %) Conwy sea trout and salmon migrate to sea at age 2 years (NRA, 1992). This is reflected in the age composition of trout populations such that $>2^+$ fish are absent or infrequent (<1.5 %) in streams supporting migratory populations (MILNER *et al.*, 1993). Because of the very low incidence of $>2^+$ fish the data following are considered in terms of late summer 0+ (fry) and $>0^+$ (parr).

For all (brown and sea) trout together, 49 % and 61 % of total variance were attributable to spatial factors for fry and parr respectively, whereas only 4 and 12 % were attributable to temporal effects (Table I). Corresponding values for salmon were 62 and 46 % for spatial and 5 and 9 % for temporal effects, respectively.

The contribution of temporal variance was greatest at within-tributary level (Table I). Synchronous variation was strong in the Roe (17-43 %), rather less in the Nant y Goron (14-31 %) and least in the Lledr (7-14 %).

HABSCORE models as predictors of variance in the Conwy

In 26 Conwy sites for which habitat data were available, the HABSCORE models explained 95, 61, 60 and 3.9 % of the spatial variance for all trout fry and parr, and salmon fry and parr respectively (Fig. 3). These values correspond to 46, 38, 38 and 2 %, respectively, of the overall variance displayed by these groups.

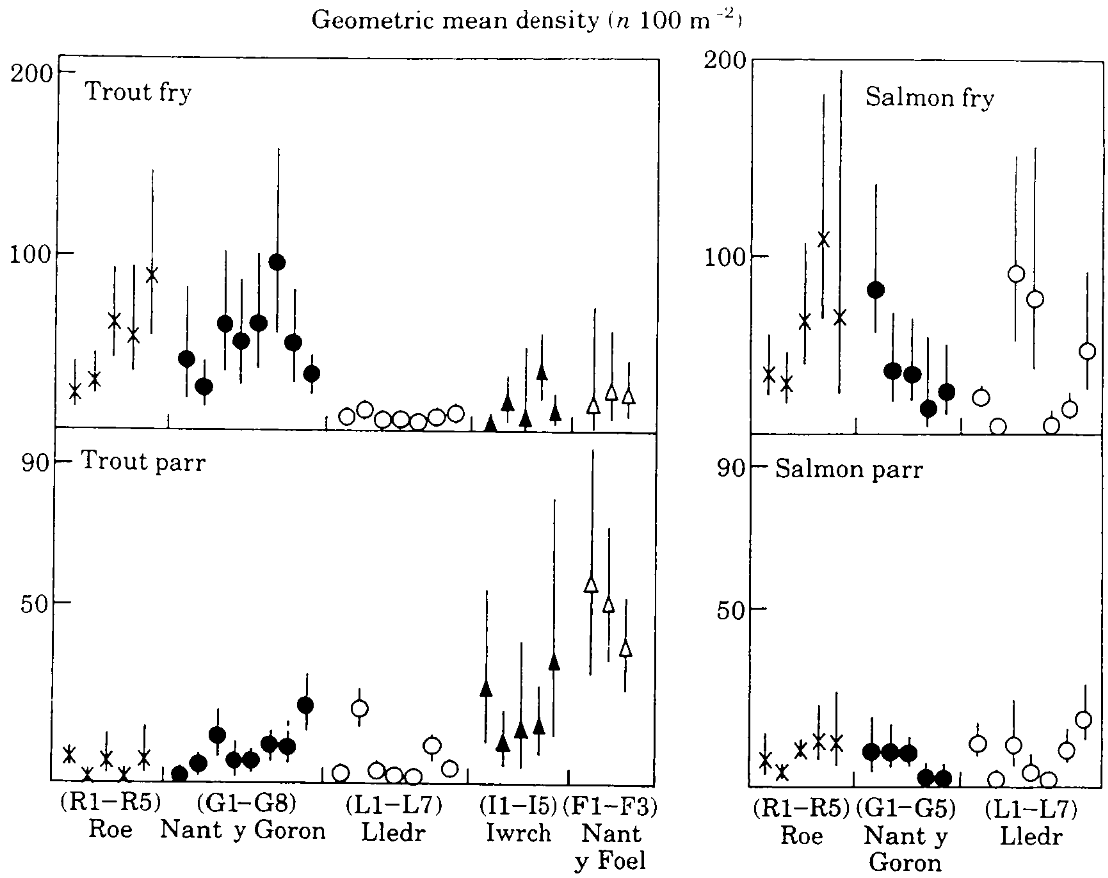


Figure 2 : Variation de densité des salmonidés intra et inter cours d'eau (5), affluents de la rivière Conwy. Moyenne géométrique à long terme (4-10 ans) à 95 %. Voir MILNER *et al.* (1993) pour la localisation précise des sites.

Figure 2 : Variation in salmonid density within and between five Conwy tributaries. Long term (4-10 years) geometric means with 95 % confidence limits. See MILNER *et al.* (1993) for site locations.

Geographical scale effects of variance partitioning

When data for nine rivers (including the Conwy) were combined (Table II), temporal variance percentage decreased from 24-39 % (mean values for the four species/age groups) at within-tributary level to 0.7 - 9.0 % at Regional level, reflecting changes in absolute variance (Fig.4). Most of the decrease occurred on moving up from within-tributary to within-river level. At within-river and higher scales, absolute temporal variance (Fig.4) was consistently lower in fry compared with parr, but this pattern was reversed at within-tributary level.

In contrast, the proportion of spatial variance (Table II) was least at within-tributary level (mean value 22-42 %) and greatest (42-65 %) at regional level, trends which reflected changes in absolute variance.

DISCUSSION

These results demonstrate the relative importance of spatial and temporal factors in explaining abundance of salmonids at individual sites and at different geographical scales. The increase in the influence of temporal factors at within-tributary level was particularly marked, indicating that local temporal factors are major determinants of abundance at that

Tableau I : Partition de la variance des populations dans la rivière Conwy et ses tributaires. Densités en $\log_{10}$ (n+1).

Table I : Population variance partitioning within the River Conwy and tributaries, $\log_{10}$ (n + 1) densities.

Spatial Scale	Species /age	Spatial Variance Sites	%	Temporal Variance Years	%	Total Variance
CONWY OVERALL						
	trout fry	28	48.7	10	3.7	0.23401
	trout parr	28	61.2	10	12.3	0.17145
	salmon fry	17	62.5	10	4.6	0.30865
	salmon parr	17	45.6	10	9.1	0.13837
WITHIN-TRIBUTARY						
(1) ROE						
	trout fry	5	40.6	10	41.2	0.08656
	trout parr	5	29.9	10	42.8	0.13906
	salmon fry	5	22.2	10	36.0	0.11629
	salmon parr	5	27.2	10	17.3	0.07158
(2) NANT Y GORON						
	trout fry	8	18.9	10	28.7	0.10100
	trout parr	8	42.0	10	22.2	0.12908
	salmon fry	5	42.0	10	13.7	0.44050
	salmon parr	5	34.2	10	30.6	0.14713
(3) LLEDR						
	trout fry	7	11.6	7	13.9	0.09461
	trout parr	7	68.6	7	7.2	0.12973
	salmon fry	7	64.6	7	10.1	0.30054
	salmon parr	7	62.4	7	9.1	0.18177
(4) IWRCH						
	trout fry	5	31.6	7	41.2	0.33254
	trout parr	5	13.7	7	58.3	0.07595
(5) NANT Y FOEL						
	trout fry	3	0*	8	66.5	0.27645
	trout parr	3	6.6*	8	29.0*	0.03973

*variances not significantly different (P<0.05, two way ANOVA), all other values signifiant (P<0.05).

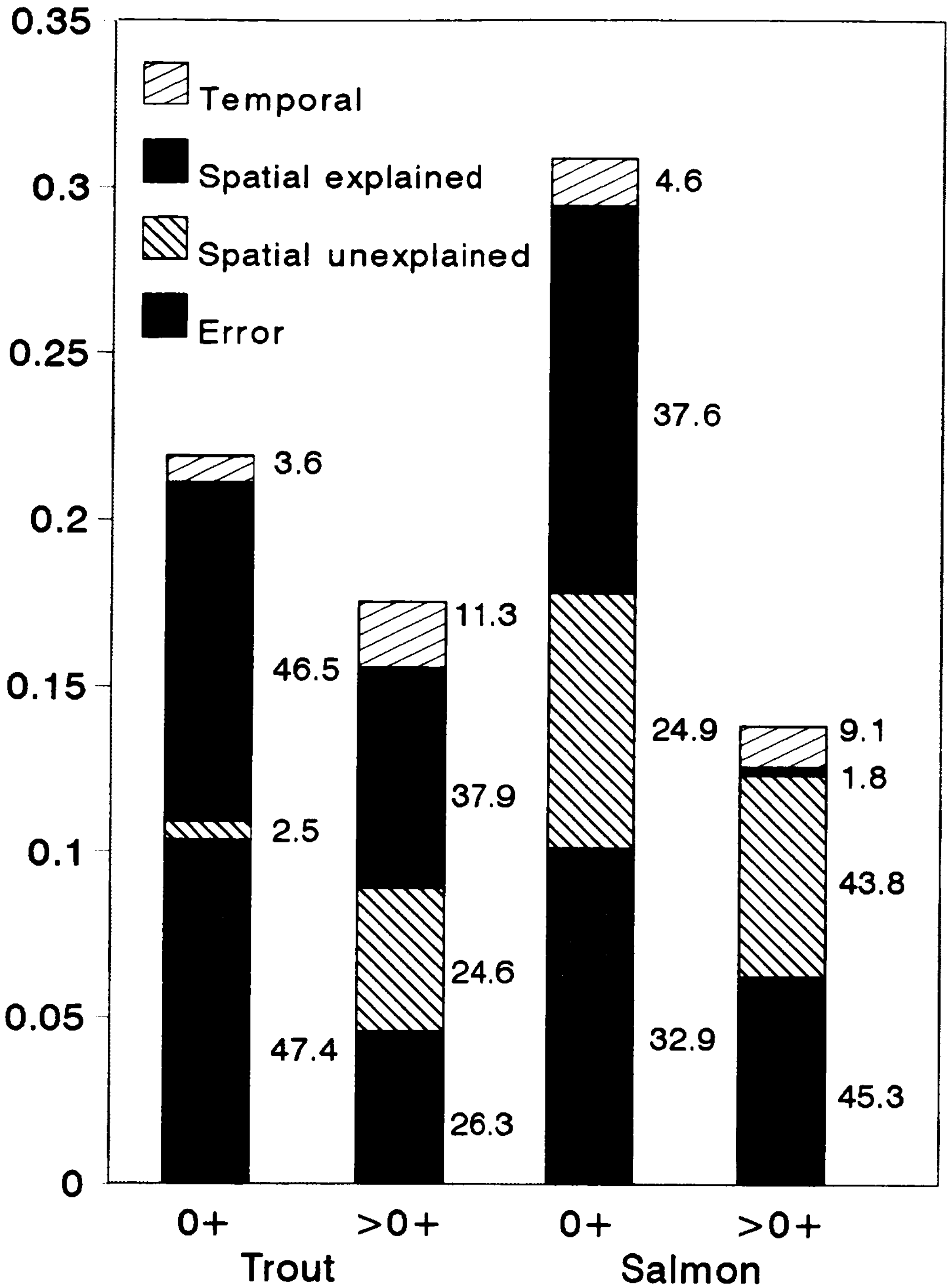


Figure 3 : Partition générale de l'abondance des truites et saumons dans tous les sites de la Conwy.

Figure 3 : Overall abundance partitioning for trout and salmon in all Conwy sites. Percentage contributions shown alongside.

Tableau II : Partition de la variance des populations à différentes échelles géographiques. Variances et valeurs en % sont des valeurs moyennes. Densités en $\log_e$ (n).

Table II : Population variance partitioning at different geographical scales, variances and % values are means for each side, $\log_e$ n (densities).

Sampling scale	Species /age	Spatial variance %	Temporal variance %	Total variance	Range
WITHIN-TRIBUTARIES (CONWY) (n=5)					
	trout fry	21.8	34.7	1.0861	0.6356-1.8635
	trout parr	32.5	33.3	0.9283	0.2399-1.5110
	salmon fry	31.6	38.7	1.3717	0.8396-2.1436
	salmon parr	42.4	23.8	0.9748	0.6037-1.6115
WITHIN-RIVERS (n=9)					
	trout fry	48.2	6.8	1.3611	0.7662-1.8202
	trout parr	42.3	13.0	1.1002	0.2533-3.0243
	salmon fry	27.5	4.2	1.4352	0.6674-2.4640
	salmon parr	21.8	13.9	1.1153	0.4615-1.6760
WITHIN-AREAS (n=3)					
	trout fry	52.7	1.8	1.4905	0.9922-1.8676
	trout parr	58.1	11.1	1.1573	0.9317-1.5532
	salmon fry	53.2	3.4	2.1616	1.7994-2.5370
	salmon parr	40.2	10.8	1.5365	1.0219-2.1100
WITHIN-REGION (n=1)					
	trout fry	64.8	1.0	1.9691	-
	trout parr	60.6	9.0	1.3339	-
	salmon fry	55.8	0.7	2.1224	-
	salmon parr	42.0	7.4	1.3720	-

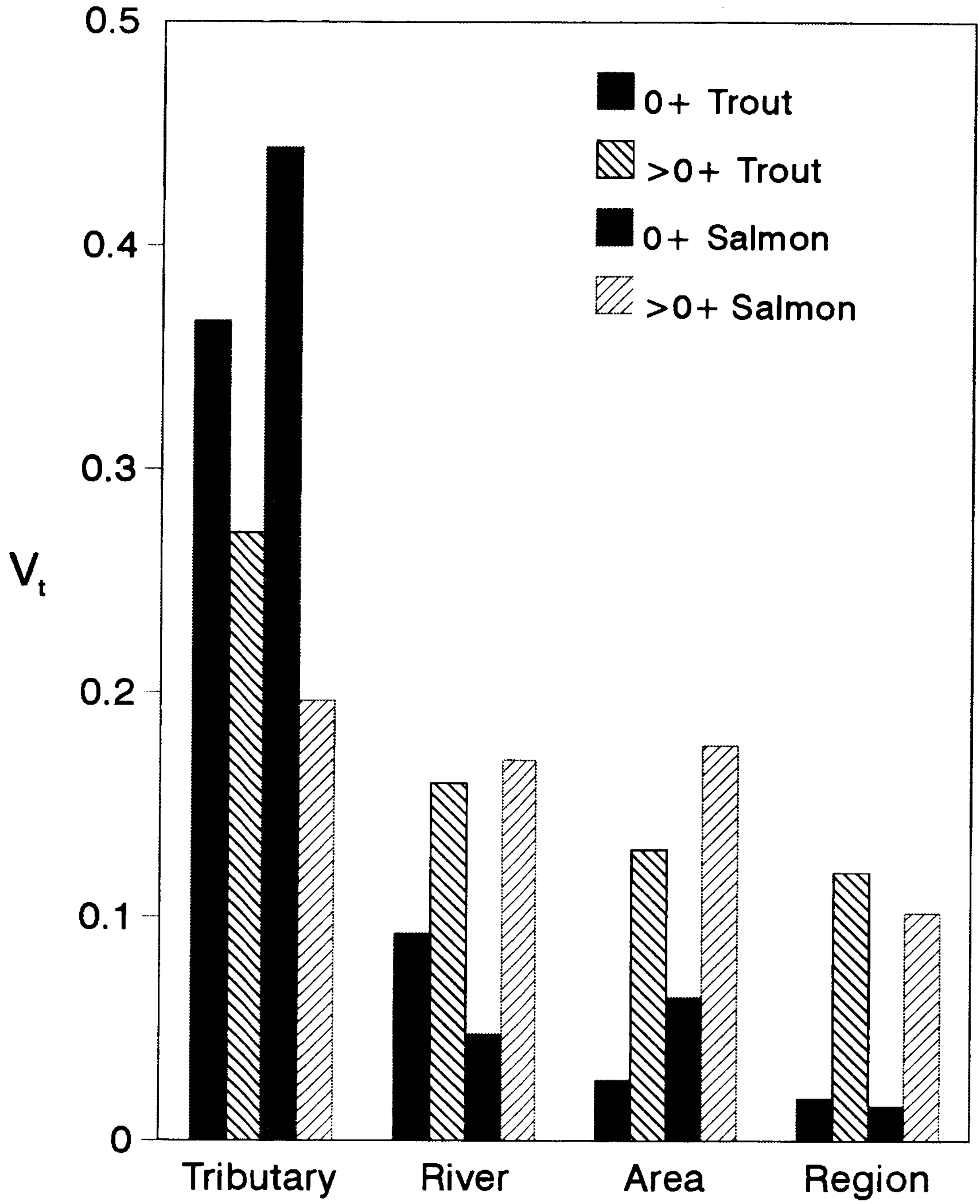
n = numbers of replicates at each scale, eg. 5 tributaries, 3 areas.

scale. Stream flow has been suggested as the likely dominant factor operating on the Conwy, possibly through effects on local recruitment variation (MILNER *et al.*, 1993). Within rivers, areas and at regional level, synchrony exhibited a progressive reduction with increasing scale, such that <10 % of overall variance at regional level was explained by temporal factors. Such factors may represent climatic variation acting at these scales.

Synchrony was more pronounced in parr than fry (Fig. 4) at river, area and regional levels, possibly indicating a response to common climatic factors influencing survival after the first summer of life. The reversal of this pattern at the within-tributary level in the Conwy may be indicative of tributary-specific factors, e.g. flow, which dominate the control of egg deposition or first year survival but which have less effect on survival or movements of older fish. Change in abundance through density-dependent mortality, probably the most important biological process influencing first year numbers in many sites (e.g. ELLIOTT, 1987), would normally be expressed within the site-year interaction component of total variance.

Figure 4 : Variance temporelle des densités de population de truites et saumons en fonction de la répartition géographique. Les variances moyennes des alevins et des parrs sont indiquées respectivement par des traits pleins et grisés.

Figure 4 : Change in temporal variance in trout and salmon population density with geographical scale. Mean variances for fry and parr are shown by solid and shaded bars respectively.



The spatial component of variance (V_S) for trout decreased progressively from regional to within-tributary levels. This is to be expected as the scope for spatial factors to operate will decrease as sites become more homogeneous, especially when moving to within-tributary level where the fluvial and geomorphological processes governing local habitat are common to most sites.

Spatial factors are those associated with the location of sites and their physiographic and environment features on both local and catchment scales. Such factors represent the independent variables typically used in habitat models (FAUSCH *et al.*, 1988). The potential for explaining or predicting site population size is controlled by the contribution of spatial factors to total population variance. At regional level this ranged from 42 to 65 %, and was only slightly less, at 46 to 62 %, within the Conwy. This represents the maximum that habitat models could ever explain, for these data sets. The HABSCORE models were explaining 60-95 % (except salmon parr) of this spatial variance component (Fig.3), equivalent to 38-46 % of total variance. The failure with salmon parr is unexplained at present and may indicate that their abundance is influenced by some habitat feature poorly measured by the survey methods.

Many habitat models developed on data sets restricted to one year's data are reported to explain >75 % of the variance in fish abundance (FAUSCH *et al.*, 1988), as estimated by R^2 values. Within a stream at any one time, local features are demonstrably important (e.g. LEWIS, 1969 ; GORDON and MACCRIMMON, 1982 ; KENNEDY and STRANGE, 1982), but over time they may explain only small proportions of overall variance, particularly if random factors keep the population below levels where habitat is limiting. Thus, caution should be applied to model performance expressed in this way which disregards the temporal variability, some of which will be synchronous and some of which will be contained as site-year interaction within the error variance. Synchrony is much stronger within tributaries than at whole catchment or regional level. This supports the principle that transportable habitat models should be based on data from a diversity of stream types, preferably over a range of major catchments.

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