ANALYSE DES MODÈLES DE PRÉDICTION DES POPULATIONS DE SALMONIDÉS EN RIVIÈRE.

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RÉSUMÉ (traduit par les éditeurs)

73 modèles multivariés (empiriques) prédisant les populations de salmonidés à partir de variables biologiques et environnementales ont été analysés.

Parallèlement, les résultats publiés de 15 tests de ces modèles sont brièvement commentés. Les relations entre les sources des différentes variables significatives et la performance des modèles sont discutées à la lumière du développement de HABSCORE, un outil de gestion des pêcheries des salmonidés, basé sur des modèles prédictifs empiriques.

Une évaluation des capacités prédictives des modèles suppose qu'une combinaison de variables (celles qui retracent les traits à large échelle du bassin et celles qui sont reliées aux conditions mêmes du cours d'eau) est plus utile pour prédire les stocks de truite que l'une des sources prise séparément.

Les données de base utilisées dans la formulation de la majorité des modèles détaillés dans la littérature ont souvent une provenance géographique limitée. Par conséquent, de tels modèles n'ont un bon pouvoir prédictif que dans une même région écologique, et sont peu applicables ailleurs.

Pour développer des modèles utilisables comme outils de gestion des pêcheries, il est souhaitable de baser leur développement sur des données issues d'une base géographique étendue.

Bien que certaines définitions spécifiques des différents paramètres diffèrent selon les auteurs, il y a un consensus général sur la nature même de ces paramètres considérés comme utiles ou importants pour le développement de modèles. A partir de définitions rigoureuses de ces paramètres, il devient possible de proposer un système de description de l'habitat qui sera à la fois applicable largement et pourra donner lieu à des résultats reproductifs.

Mots-clés : habitat, HABSCORE, modèle, prédiction, salmonidés.

AN ANALYSIS OF PREDICTIVE MODELS FOR STREAM SALMONID POPULATIONS.

SUMMARY

A total of 73 multivariate (empirical) models predicting salmonid populations from biological and environmental variables were assessed. In conjunction with this, the published results of 15 tests of models are briefly commented on. The relationships between the sources of the significant variables and the performance of the models are discussed in relation to the development of HABSCORE - a management tool for salmonid fisheries which is based on empirical predictive models.

An assessment of the predictive capabilities of the models implied that a combination of variables (those which relate to the large-scale features of the catchment and those which describe the instream conditions) were more useful in predicting trout stocks than either source of variables alone.

Whilst raw data gathered from relatively 'narrow' ecological ranges have been used to formulate the majority of models detailed in the literature, such models often have high predictive power only within the same ecological range, and are consequently restricted in their applicability elsewhere. In order to develop models which can be used as fisheries management tools it is desirable to base the model development on data from a wide geographical base.

Although specific definitions of many parameters may differ between fishery workers, there is general agreement regarding the nature of those parameters perceived to be useful or important for model development. Given the production of a series of rigorous definitions for these parameters it should be possible to propose a system of habitat description that would be both widely applicable and would give rise to reproducible results.

Key-words : habitat, HABSCORE, model, prediction, salmonid.

INTRODUCTION

The evaluation of stream habitats in terms of their suitability for specific fish species is a practice which can be traced back some 30 years (for example MCFADDEN and COOPER, 1962). Although some authors (e.g. BEARD and CARLINE, 1991) have produced evidence to suggest that habitat variables may not be correlated with trout density, a vast array of multivariate models have been produced by fisheries scientists over the last 20 years or so. These models have all been designed to predict standing crops of stream fish (in terms of number or biomass per unit length or area) from measurable characteristics of the stream and catchment environment. Such models cover a variety of warm- and cold-water fisheries and refer to both salmonid and non-salmonid fish species.

A series of multivariate models, relating salmonid population size to habitat features, have been derived using data from over 600 sites throughout England and Wales. These models form the basis of the latest version of HABSCORE, a system which enables predictions of salmonid abundance to be made from information on stream habitat features. An early version of HABSCORE is in operational use in the Welsh Region of the National Rivers Authority (NRA) (MILNER *et al.*, 1985 ; WINSTONE, 1993) where it is proving to be of practical value.

To facilitate the development of the models which underlie HABSCORE, stream habitat evaluation methods documented in the published literature were assessed to provide information on the nature of variables used by workers to predict fish populations ; the subsequent testing of models ; and their predictive power when applied to independent data sets.

It was not intended that this should be an exhaustive review of freshwater fish standing crop prediction models, but rather a selective assessment of those models which predict salmonid standing crop in river and stream systems, and relate to conditions to be found within the UK. A reference list detailing the full set of models that were assessed may be obtained from the first author.

Where possible, original papers were reviewed, although FAUSCH *et al.* (1988) provided an excellent overview of much of the work carried out in the United States that is not readily available in the UK. The methods of model assessment which are used in this paper are based on FAUSCH *et al.* (1988).

METHODS

The value of different variable sources

The wide range of variables that can be used to describe stream habitat can be broken down into the local physico-chemical and biological features of a given stream site (i.e. channel morphology/flow conditions and instream habitat) and the larger-scale catchment attributes such as geomorphology, topography, land-use and climate (MILNER *et al.*, 1985).

The origin, or nature, of the independent variables used in empirical models can be used as a means of categorising the broad group of models available for assessment.

All of the independent variables recorded as being significant in the models which were assessed were categorised in relation to their source, allowing the relative importance of variable source to be assessed across the range of model types. For this exercise, the source of variables (as described by MILNER *et al.*, 1985) was subdivided to differentiate between variables pertaining to the following categories :

- drainage basin ;
- channel morphometry and flow ;
- habitat structure and the physical, biological and chemical microhabitat ;
- a combination of several of the above variable types.

The overall model type of any given model was taken as being the source of the majority of its significant variables.

Quality of models

In order to help identify the quality of the models which are documented in the literature, the distribution of models was examined with respect to :

- the r^2 coefficient (the percentage of the variation in the data which is successfully accounted for by the model) ;
- the number of observations involved in the model development ;
- and the number of degrees of freedom (d.f.) for the model.

Tests of models

The testing of a model involves its application to a data set other than the one from which the model was originally developed. Often such a data set is recorded by the authors of the model on a separate reach of the same, or a neighbouring, watercourse and, in addition to testing the applicability of the original model is sometimes used to refine the model further (see, for example, BINNS and EISERMAN, 1979). On other occasions, a published model may be used in an attempt to explain the observed variation in, say, the salmonid biomass of a stream reach, in terms of the habitat or other variables.

The success of tests (or independent application) of predictive models was assessed by looking at the value of the r^2 coefficient resulting from the application of the model to a new data-set (i.e. an assessment of the ability of the model to account for the observed variation in the new data-set). The new data-sets were categorised as being derived from either the same area as the data that were originally used to develop the model being tested, or as coming from a different area. In this way, not only could the success of models be assessed, but also an insight would be gained into the general applicability of the models concerned.

Variable recording

It is not unreasonable to expect that methods employed to record values for any given parameter may differ across a selection of authors. The means by which the common variables used in empirical models are assessed is briefly discussed, although the actual techniques used are not fully reviewed.

DISCUSSION

Sources of significant variables

The distribution of significant variables across the range of models assessed is shown in Table I. The relative importance of the significant variables recorded in the models which were assessed displayed an uneven distribution across the three potential sources which were considered (Table I). The average number of significant variables in a model is around two to three for those models based mainly on variables from one source. However, those models which are based on variables from multiple sources have a higher average number of significant variables (greater than four).

Tableau I : Nombre et nature des différentes variables significatives rencontrées dans différents types de modèles.

Table I : Number and sources of significant variables found in different model types.

	Basis of model type:				
Variable source:	**Drainage basin**	**Channel & flow**	**Habitat**	**Multiple source**	
Drainage basin	27	1	0	11	
Channel/flow	2	36	5	34	
Habitat	0	1	48	58	
Total number of models considered	9	18	23	23	= 73

When the variable sources are examined for the fourth category of models in Table I (i.e. those with significant independent variables from a variety of sources) the importance of drainage basin variables is decreased relative to those pertaining to channel/flow and habitat features. This could be the result of drainage basin characteristics being displaced by other variables which are better able to explain the observed variances in fish populations or, more simply, that they are not considered during the model development phase.

Within the group of nine models which rely primarily on drainage basin variables, r^2 coefficients tend to be on the low side (values ranging from 0.33 to 0.66) although five of the nine are described as being significant at the $P<0.001$ level. This suggests that, when used in the absence of other variable types, drainage basin variables are able to account for at least part of the observed variability of fish stocks.

However, if used in isolation, either channel morphometry/flow variables or habitat variables would be likely to explain more of the variation in instream conditions than drainage basin characteristics. Consequently, it would be expected that models developed using variables from such sources would be able to explain a greater percentage of the observed variation in fish stocks than would models based primarily on drainage basin characteristics.

Model power

The distribution of models within selected r^2 and d.f. categories is given as Table II.

Examination of Table II suggests that the models which display the greater ability to explain observed variation in field data (i.e. the models with the higher r^2 values) are those which have lower d.f. (degrees of freedom) values. Conversely, those models with higher degrees of freedom tend to have lower coefficients of determination. This is, of course, what would be expected. Given the situation where the total amount of variation in the dependent variable before the fitting of the model and the amount of variation left after the model has been fitted remain constant, an increase in the number of degrees of freedom would result in a concomitant decrease in the r^2 value.

The models which can be viewed as being most 'successful' are those which display both a high value for r^2 and a high value for d.f. (that is a large number of observations relative to the number of independent variables included in the model). Seven models fall into this latter category, those being the models by : RANDOLPH and WHITE, 1984 ; BARBER *et al.*, 1981 ; BINNS and EISERMAN, 1979 ; two models presented by NICKELSON *et al.*, 1979 ; SEKULICH, 1980 ; and one of the models presented by

Tableau II : Nombre de modèles dotés d'un certain taux d'explication en liaison avec le nombre de degrés de liberté.

Table II : Number of models with a certain explanatory power in relation to the number of degrees of freedom.

Degrees of freedom:	Coefficient of determination: r^2=0-0.24	r^2=0.25-0.49	r^2=0.5-0.74	r^2=0.75-1.00
< 20	0	4	10	27
$\geq$ 20	0	14	10	7

N.B. : r^2 value not available for one channel/flow based model with d.f.<20.

JOWETT, 1992. One possible explanation for the relatively small number of models which are to be found in this category may be that a high number of degrees of freedom is only arrived at by using a large number of observations to develop the model. The effort involved in collecting and processing such large amounts of data may, for a variety of reasons, be prohibitive to many workers.

Model power in relation to variable source

Tableau III : Nombre de modèles avec une certaine performance en liaison avec la nature des variables.

Table III : Number of models with a certain performance in relation to the source of variables.

Principal source of variables:	Model performance category: d.f. < 20 r^2 < 0.5	d.f. $\geq$ 20 r^2 < 0.5	d.f. $\geq$ 20 $r^2 \geq$ 0.5	d.f. $\geq$ 20 $r^2 \geq$ 0.75
Drainage basin	3	4	4	1
Channel/flow	14	1	2	1
Habitat	14	1	6	1
Combined	10	8	4	4

N.B. : r^2 value not available for one channel/flow based model with d.f.<20.

Table III classifies the models according to the overall performance of the model (expressed as a combination of d.f and r^2) and the main source of those variables which were significant for the model.

The 16 models which have r^2 values $\geq$0.5 for d.f.$\geq$20 are distributed approximately equally between the classes of principal variable sources. Therefore, for intermediate quality models there is no evidence to suggest that the use of any one particular source of variables in preference to another will result in the production of a better model. However, if the criteria for model performance are raised (e.g. to $r^2 \geq 0.75$ for d.f.$\geq$20, as in the final column of Table III) the seven models in the 'top' category show a clear deviation from this pattern, being based mainly on variables from a variety of sources. The use of variables from a wide range of sources satisfies the requirements which are inherent in the views that site and catchment features should not be considered in isolation from one another in schemes of habitat evaluation, and that the continuum of change of these factors along a given catchment (HUET, 1959) should be recognized.

Tests of models

Tableau IV : Réussite des tests des modèles.

Table IV : Success of model tests.

Test data-set collected from:	Number of tests with: $r^2 < 50\%$	$r^2 \geq 50\%$
'Same' area as original model	2	7
'Different' area as original model	7	0

The results of the assessment of available model tests are given as Table IV. The values presented suggest that, when assessing the relative success of models, the source of the test data (in relation to the source of the data used to formulate a given model) is of crucial importance. Quite obviously, the models tested are far better able to explain the variability in data-sets which have been obtained from the same area (i.e. the same river or catchment) as the data which was used to formulate the original models.

This manifestation of site specificity is most notably demonstated by four reports of the application of Binns and Eisermans' HQI model (BINNS and EISERMANS, 1979). Three of the applications (based on data from different sources to the original data-set) suggested that the model was capable of explaining, at most, only 17 % of the observed variability in the data. However, a fourth application (using data from eight sites on the same streams as were used in the model's development) demonstrated that the model was capable of explaining more than 90 % of the data's variability.

Parameter estimation

Whilst definitions are readily available for the common drainage basin parameters (e.g. BURTON and WESCHE, 1974 ; LANKA *et al.*, 1987) the means of recording the dimensions of the site (i.e. the habitat area which is surveyed, and for which the salmonid population size will be estimated) vary considerably between authors. Consequently, techniques used in one study do not necessarily provide parameter estimates that can be utilised directly in the models developed in another.

The nature of recording techniques may vary from objectivity through to subjectivity according to the nature of the variable being recorded. For example, the adequate description of channel morphology is often dependent on the precise definition of certain critical parameters (e.g. the required frequency of width and depth measurements). In contrast, other parameters (e.g. flow type) may be more usefully defined by robust, descriptive terms.

Other parameters (e.g. substrate composition) can be described by using existing systems (e.g. the Wentworth system the categorisation of particle size-class - CUMMINS, 1962). The key issue regarding substrate particle size-classes relates more to identifying those classes which are important in accounting for observed variations of salmonid standing stocks rather than the standards by which to measure them. It is far more convenient (in terms of on-site parameter estimation) to restrict the number of size-classes to the minimum necessary for the model rather than to record information to a detailed level of resolution. This is often countered, however, by the potential for a habitat survey to be used as a habitat record as well as a means of obtaining information to run a model.

Whilst BINNS and EISERMAN (1979) cite ARNETTE'S (1976) definition of cover as being 'sheltered areas in a stream channel where a trout can rest and hide from predacious enemies' they essentially re-define 'cover' as 'anything that allows trout to avoid the impact of the elements or enemies'. In other instances, stricter definitions have been employed (e.g. WESCHE, 1980 ; KOZEL and HUBERT, 1989).

Many references are available which relate the standing crop of stream fish to alternative independent variables not considered in this broad assessment. Some habitat or environmental variables, although perhaps not determining the standing stock directly, are thought by some authors to be potentially useful predictor variables in that they are responsible for modifying the level of productivity (and hence the perceived standing crop) of stream fisheries. Such variables include stream order, temperature regime and the slope of the river (ZALEWSKI and NAIMAN, 1985) ; water hardness (as a surrogate for catchment geology - MILNER *et al.*, 1985) ; aluminium concentration and pH levels (e.g. WEATHERLEY *et al.*, 1991 ; WEATHERLEY and ORMEROD, 1991) ; thermal input and thermal regimes (HAWKINS *et al.*, 1983 ; BARTON *et al.*, 1985 ; PLATTS and NELSON, 1989).

Finally, it should be noted that habitat requirements may alter with life-stage, size and species (MILNER *et al.*, 1981 ; KENNEDY and STRANGE, 1982 ; MORANTZ *et al.*, 1987). In addition, diurnal (MASON, 1966 ; GIBSON, 1988) or seasonal (HARTMAN, 1963 ; RIMMER *et al.*, 1983) changes in requirements may also be in evidence. Adequate attention should be addressed to such factors and the limitations of the applicability of a model should be clearly stated.

CONCLUSIONS

In conclusion, the analysis of the predictive capabilities of the models assessed implies that a combination of variables (those which relate to the large-scale features of the catchment and those which describe the instream conditions) were more useful in predicting trout stocks than either source of variables alone. In terms of facilitating the development of predictive models (such as HABSCORE), a wide range of habitat variables, encompassing both local (i.e. instream/riparian) and catchment scales, should be considered during model development.

In addition to instream habitat and catchment parameters, several alternative variables are cited by authors as being significant in models developed to explain observed variations in salmonid population densities. However, in comparison to physical measurements of channel morphology and estimates of the abundance of different substrate/flow types, some of the more detailed biological or chemical variables (e.g. benthos biomass) are generally labour intensive and time consuming to record. The relatively small number of models which use such variables, and the fact that there are several high quality models that do not use such variables, suggest that their consideration during model development is not a pre-requisite for the derivation of high quality models.

It would appear that data gathered from relatively 'narrow' ecological ranges have been used to formulate the majority of models detailed in the literature. The published results of model tests or applications serve to warn against the assumption that populations of fish in a given stream can be predicted by using models previously developed on other streams, even if they are in the same local environment. Although models produced from such data often have high predictive power within the ecological range, they are restricted in their applicability elsewhere.

In this sense, it is possible that the nature of the data used for model development may ultimately limit the models' applicability. In order to facilitate the development of empirical models which are better able to explain the variability of fish populations when applied to new data-sets, it is advantageous to have developed such models on data obtained from a wide geographical base. As a consequence of this finding, the development of HABSCORE, from a regional to a national system, was based on a data-set covering as wide a range of river systems as possible.

Whilst precise definitions of many parameters revealed differences of opinion between fishery workers, the same workers generally agree on the nature of those parameters perceived to be useful or important for model development. If a series of closely definitions for these parameters are produced, a system of habitat description can be proposed which can be widely adopted and allow comparisons to be made between sites over wide geographic areas. Accordingly, to facilitate the successful development of HABSCORE as a nationally applicable tool, methods of habitat assessment used to derive the raw data for the development of the models have been formalised and well documented, allowing the techniques to be confidently applied to new sites.

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