Ann. Zool. Fennici 30:89–100
Helsinki 30 June 1993

ISSN 0003-455X

Review

Water quality and prediction of lake-specific fish yield — a Northern European perspective

Esa Ranta[1] & Kai Lindström

Ranta, E. & Lindström, K., Integrative Ecology Unit, Department of Zoology, Division of Ecology, P.O. Box 17, FIN-00014 University of Helsinki, Finland

Received 21 January 1993, accepted 12 April 1993

We attempted to predict annual fish yield (kg/ha/yr) in four data sets including a total of 390 lakes in Finland, using both water quality variables and variables involving fishing effort. Measures of fishing effort included gear numbers, gear type and number of fishermen. Principal component analysis was used to reduce the number of water quality variables, and to ensure independence of the predictive variables. As a rule, total fish yield could not be predicted reliably on the basis of water quality. At best, water quality explained no more than 15% of the variation in annual fish yield, and this model could successfully be applied to only one sub-area. Fishing effort turned out to be the most useful predictor, with an explanatory power of 50%. In one data set water quality explained more of the variation in fishing effort than in annual yield. Using the catch distribution of individual species in relation to environmental gradients, we constructed a simple theoretical model for yield vs. water quality. The model showed the extreme unlikelihood of finding a linear relationship between water quality and fish yield, because individual species display a bell-shaped distribution around their optimal water quality conditions, and the sum of such distributions likewise is bell-shaped. Finally, we argue that fishing effort should increasingly be taken into account in the development of management tools for inland fisheries.

1. Introduction

Managing fresh water fish resources presupposes knowledge of the kind and quantity of reserves accessible to those exploiting them. Knowledge can be gained by direct and continuous monitoring of the target populations (*high-effort* methods). Alternatively, one can resort to indirect means to assess the quantity and quality of available resources (*low-effort* methods). A list of examples of high-effort methods includes stock/recruit models (Ricker 1954, Beverton & Holt 1957), surplus yield models (Schaefer 1954, Pella & Tomlinson 1969), dynamic pool models (Pitcher & Hart 1982), and time series analysis. Examples of low-effort methods are the Delphi method (Zuboy 1981) and a family of regression

[1] Responsible Editor: Ismo J. Holopainen

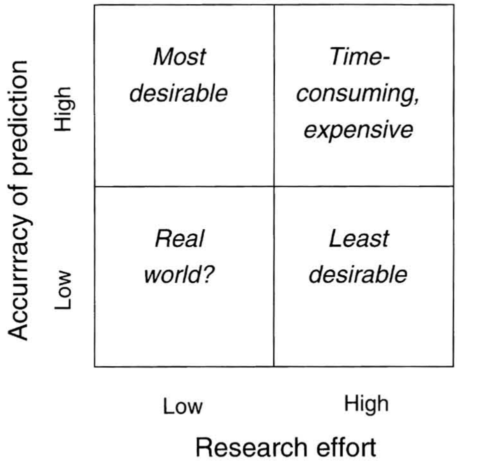

Fig. 1. Prediction of lake-specific fish yield: accuracy graphed against invested research effort. We explore the possibility of producing high-accuracy predictions with low-effort methods.

models in which yield is predicted by characteristics of a lake (Jenkins 1967, Oglesby 1977, Sarvala et al. 1984).

High-effort methods provide data on target populations, and reguire data to be collected for each single population separately. The resultant knowledge can further be used for management programmes tailored on an annual basis at population level. In the high-effort methods with their acquired precision ability to generalise is reduced. Moreover, with these methods precision is gained by spreading the effort over many years. This, however, increases management expenses. The trade-off between the two methods is not necessarily a trade-off between high and low accuracy of yield prediction (Fig. 1).

When monitoring resources are in short supply, an alternative to using high-effort methods is to make the best use of the other methods. Potentially, knowledge gained by means of low-effort methods may be close to that obtainable with high-effort methods (Fig. 1). When erring with low-effort models, not much expense in data collecting is lost. But the error may lead to loss of the target resource. The prevailing paradigm among the low-effort methods is that lake-specific fish yield is a linear function of water quality (Rawson 1952, Ryder 1965, 1982, Ryder et al. 1974, Kerr & Ryder 1988).

As a management tool, a model without feedback loses its foundation entirely. In the high-effort models the feedback is innate, while the low-effort models do not use explicitly any feedback. By use of external variables they just aim at predicting the annual yield as correctly as possible. Such a prediction can serve in traditional management of fish resources. Alternatively, the model expressing the relation between yield and lake water quality can serve as a tool for environmental monitoring.

This paper addresses the performance of low-effort methods in predicting annual fish yield in lakes. We shall limit our discussion to regression models that use water quality as a predictor. In doing this we shall follow the tradition initiated by Rawson (1952) and Northcote & Larkin (1956). Later, several modifications and surrogates of the original plan have been introduced (Ryder 1965, Jenkins 1967, Hrbacek 1969, Melack 1976, Oglesby 1977, McConnel et al. 1977, Matuszek 1978, Schlesinger & Regier 1982; among many others).

We shall first concentrate on establishing possible links — if any exist — between annual fish yield and water quality. In so doing, data on fisheries and water chemistry in Finnish lakes serve as reference material. The performance of empirical models will be tested on different spatial scales. Secondly, we shall outline a theory for fish yield and water quality in lakes. The discussion revolves around total yield viz., pooled annual yield of all species. This article is a review of our recent research (Lindström & Ranta 1988, Ranta & Lindström 1989, 1990, 1992, 1993, Ranta et al. 1992a, b) on the question: *Based on water quality, is it possible to predict lake-specific fish yield?* This review, it is hoped, will activate further discussion on this topic.

2. What makes a good prediction model?

2.1. Independency of predictive variables

Before we begin our review in detail, we shall make some comments on the use of regression models as prediction tools. Let us denote by Y_t the annual total fish yield (kg fish ha/yr) in a lake. The entire task of the approach is to find

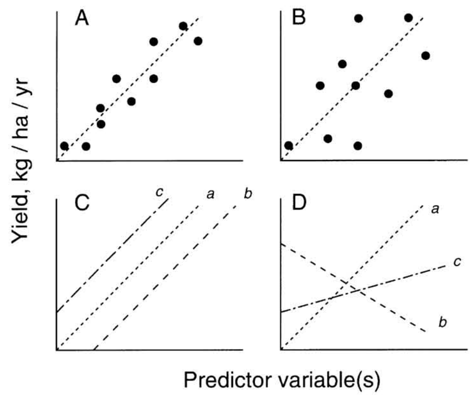

Fig. 2. Performance of empirical regression models ($Y_t = a + b_iX_i$) used to predict fish yield in lakes. Because of smaller residual variance model A is better than model B. When empirical models are derived from data originating from lakes of different drainage areas (a, b, c) the most desirable outcome is a single model (A) for the separate sets of data. The next best result is a family of models differing only in their Y_t intercepts (C). That is, models are adjusted for differences in yield levels among drainage areas. The worst case is depicted in panel D (is this the real world situation?), showing entirely different empirical models needed to characterise relationship between fish yield and predictor variable(s).

out whether such yield can sufficiently be described as a function of one or more characteristics (X_i) of a lake. If so, we shall write

$$Y_t = f(X_i),$$

or in terms of a linear regression model

$$Y_t = a + b_iX_i.$$

Having the data on yield and on predictor variable(s) for a number of lakes one can unambiguously estimate the parameters of the empirical model (Draper & Smith 1966, Edwards 1985). However, there is one point of caution. Water quality (the X_i variables) in Finnish lakes, when described by authorities, is indicated by measuring a number of variables. Many of the variables are strongly intercorrelated and can therefore not be used as such to form independent variables in regression models. Principal component analysis, a multivariate method for overcoming problems of this type, comes in handy to make linear combinations of covarying variables. Lake-specific scores for each principal component are orthogonal and normally distributed. This makes them appropriate as independent variables in further treatments.

Calculating principal components is an objective means to find linear combinations of the original variables. Different affiliations of water chemistry variables may result in differing linear combinations of those variables. In our experience, however, the differences are not that great, because in Finnish lakes the resulting components share elements in common (Table 1).

2.2. Model criteria

An empirical model best suited for management purposes must have high precision and has to be generalisable (Fig. 2). If the residual variation

Table 1. Compilation of the outcome of principal component analyses run for different sets of lakes and water quality variables. Variables labelled with the same character (a, b or c) shared high loadings on the same principal component (column wise). Rows sharing the same characters indicate that the four different data sets (A = Ranta & Lindström 1990, B = Ranta et al. 1992a, D = Ranta et al. 1992b, RL = Ranta & Lindström 1993; as discussed in the text) resulted in closely corresponding principal components. Both the number of principal components extracted and the cumulative variance explained are indicated together with the number of lakes for the four different studies.

	Data set			
Variables	*A*	*B*	*D*	*RL*
pH	a	a	a	a
Alkalinity	a	a	–	a
Ca	a	–	a	–
K	a	–	–	–
Mg	a	–	–	–
Conductivity	c	a	a	a
O_2 saturation	c	b		a
Colour	b	b	b	b
N	b	b	–	b
P	b	b	–	b
Na	b	–	–	–
Chemical O_2 consumption	b	–	–	–
Al	–	–	b	–
Lakes	155	70	80	148
Principal components extracted	3	2	2	2
Cumulative variance explained (%)	70	77	79	75

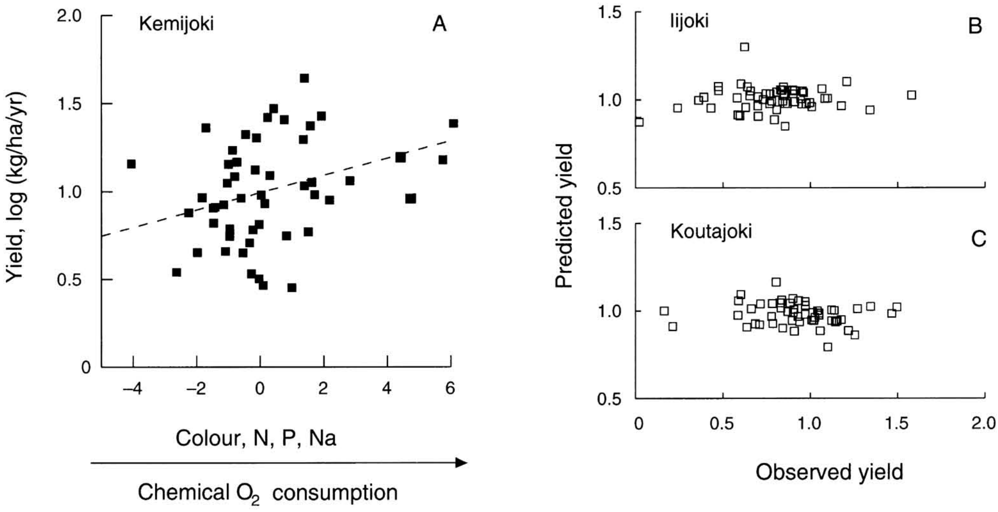

Fig. 3. Three closely located drainage areas (Kemijoki, Iijoki and Koutajoki) in Kuusamo commune used to test whether an empirical regression model derived from Kemijoki data (A) can predict annual fish yield in the two other drainage areas (B, C). Yield in the Kemijoki lakes (n = 49) is regressed against component scores of the second principal component (gradient from oligotrophy to eutrophy, as indicated in panel A). In panels B and C, observed yield is graphed against prediction. It is more than obvious that the Kemijoki lakes model fails entirely to predict correctly annual fish yield in Iijoki and Koutajoki.

between water quality and fish yield is high, or if the parameter values for each specific set of lakes differ greatly the empirical models lose much of their applicability to management problems. Within a limited geographical area there should be no more than one empirical model best characterising the relationship between fish yield and water quality in any one lake (Fig. 2). The residual errors of this model should not exceed the model prediction. At best, the very same model, preferably with no parameter adjustments, should be applicable to lakes in limited biogeographical areas (Fig. 2).

3. Fish yield and water quality in Finnish lakes

Our test materials originate from four different sources (A–D), and we hope that they suffice to underline our major point.

3.1. Data set A, 155 lakes

Ranta & Lindström (1989) examined whether a yield prediction model can be found for lakes from three drainage areas (Iijoki with 54 lakes, Koutajoki and Kemijoki with 52 and 49 lakes, respectively) within an area of about 1000 km^2. Water quality was approximated with principal components based on 12 original variables (Ranta & Lindström 1989, Table 1). For the present purposes it suffices to graph fish yield against lake-specific score values of the second principal component in the Kemijoki drainage area (Fig. 3A). Here we fitted a linear regression model between water quality (PC 2; a gradient from oligotrophy to eutrophy; see Ranta & Lindström 1989 for details) and total yield (log transformed). Though the relationship between the two variables is far from perfect, it still fulfils the statistical goodness-of-fit criteria (Y_t= 0.99±0.04 + 0.049±0.02 × X; $F_{1,47}$ = 4.83, P = 0.033). With these standards, the regression model thus suffices as a management tool. However, using the model as a yield-prediction tool for two nearby drainage areas, Iijoki and Koutajoki, clearly demonstrates that entirely different factors must be responsible for total fish yield in those lakes (Fig. 3B and C). In fact, the covariance between water quality and fish yield in lakes of the three

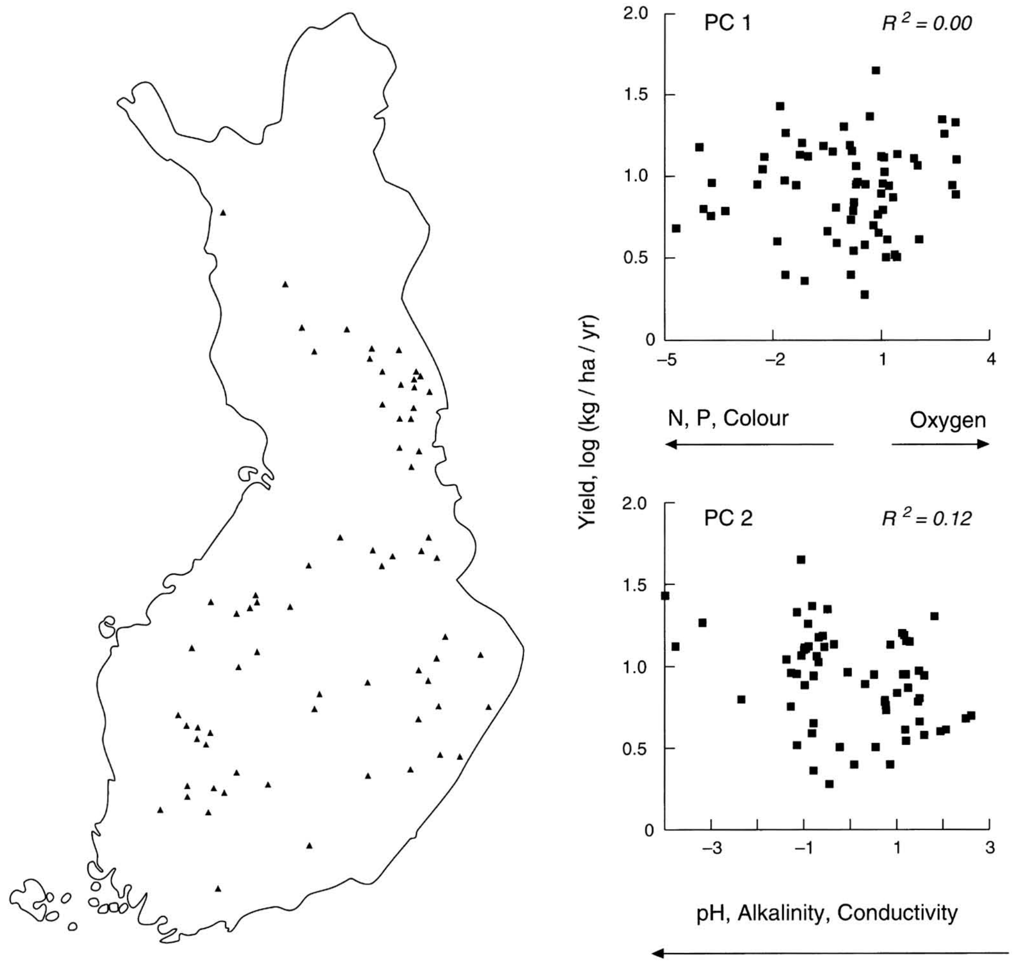

Fig. 4. Ranta et al. (1992a) studied relationship between fish yield and water quality in 70 lakes scattered around Finland. Two principal components extracted from data on 7 water quality variables retained 77% of the variation in the original data (Table 1). Graphing yield against lake-specific component scores indicates that water quality, as measured in terms of lake-specific component scores, does not govern fish yield.

drainage areas is more than confusing. The following tabulation of correlation coefficients should demonstrate the lack of any pattern (Ranta & Lindström 1989):

	Principal components		
	1	2	3
Iijoki	–0.27	0.09	–0.34
Koutajoki	–0.04	–0.14	–0.03
Kemijoki	–0.39	0.31	–0.06.

These observations suggest that it may be impossible to derive a generalisable prediction model (based on water quality variables) for fish yield in lakes of the three drainage areas.

3.2. Data set B, 70 lakes

Ranta et al. (1992b) examined the pattern between fish yield and water quality in 70 lakes scattered all around Finland. They set out to seek a valid empirical relationship, but failed to do so (Fig. 4). It seems that, again, water quality and fish yield have little in common. What they found was that annual fish yield can be predicted *if* fishing effort is known. For example, the coefficient of determination (R^2) between yield and water quality ranged from 0.00 to 0.12 depending on the principal component (Fig. 4; Table 1), while for fishing effort (number of fishermen / ha)

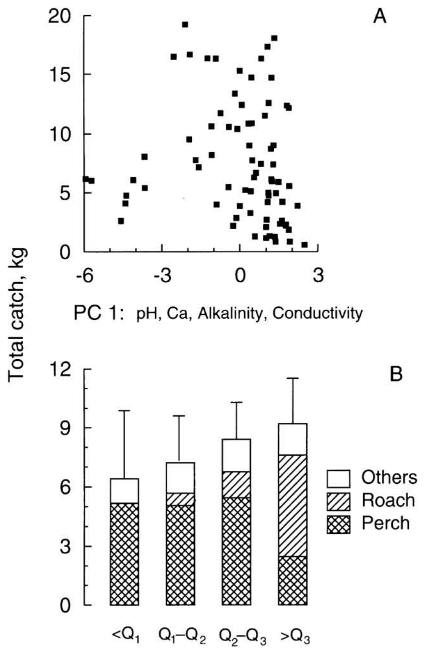

Fig. 5. Fish were trapped with standardised effort from 80 Finnish lakes. Water quality was assessed by determining values of seven water chemistry variables. The relationship between water quality and total catch of fish is non-existent (A; the 1st principal component $R^2 = 0.0$, the 2nd principal component $R^2 = 0.0$). Ranta & Lindström (1990) divided the lakes into four groups according to quartile limits of the 1s' principal component. A trend towards an increasein averaged fish catch (vertical bars indicate 95% confidence limits) is obvious in lakes of the four groups (B). However, the increase from 6.4 kg to 9.2 kg is due to roach (a fish not preferred by fishermen) replacing perch.

the corresponding figure was $R^2 = 0.48$. Partialling out fishing effort improved the relationship between yield and water quality (the first principal component, partial correlation coefficient = 0.26; for the second principal component the corresponding value is 0.34).

With this material it became clear that fishing effort is the best variable governing annual fish yield. This conclusion also holds for individual fish species (Ranta et al. 1992b).

3.3. Data set C, 85 lakes

With the third set of data we reached the same conclusion as with B, viz., fishing effort explains the yield more than does water quality (Ranta & Lindström 1990). This time the data (a subset of A) were accurate enough to allow fishing gear-specific examination. In a forward stepping regression model we attempted to include some of the 16 original water quality variables. The success was poor: for six species not a single variable was powerful enough to enter into the model. With perch (*Perca fluviatilis* L.) the model resulted in to inclusion of water conductivity, but the fit of the model, to say the least, was low ($R^2 = 0.06$). On the other hand, when we began from a full model including the 16 water quality variables plus six variables characterising fishing effort (traps/ha), our success improved. From the total of 22 variables we removed with a stepwise elimination method the variables not needed in the regression model. The results were unambiguous: in no case were water quality variables powerful enough to remain in the model. We found that variables describing fishing effort were the determinants of the species specific yield (Ranta & Lindström 1990).

3.4. Data set D, 80 lakes

Finally, Ranta et al. (1992a) examined fish catch and water quality in yet another set of Finnish lakes. Generally, fishing effort and gear may vary considerably among lakes. Therefore, detection of any relationship between water quality and fish catch may be hampered. To avoid this bias, fish in the study by Ranta et al. (1992a) were trapped with a standardised effort. Thus, instead of fish yield, with these data we are dealing with catch per unit effort, which is a measure of fish biomass.

Graphing the total catch against the first principal component suggests no relationship whatsoever between these variables, $r = 0.06$ (Fig. 5A; the same is true for the second principal component, $r = 0.04$; Table 1). We do not, however, wish to say that water quality has no effect on fish catch at all. When the score values of the first principal component are split into four groups according to quartile values, a clear pattern emerges (Fig. 5B). The total catch is obviously affected by water quality, but this relationship does not help us very much in predicting lake-specific fish catch. Another complication, in fish resource management terms, is that the increase in the total catch is due to roach (*Rutilus rutilus* L.), a species not valued highly by Finnish fishermen.

In conclusion, after searching for any relationship between fish yield and water quality in 390 Finnish lakes we have repeatedly failed. Therefore we are inclined to say that data on this relationship are difficult to obtain. Against this background we felt rather well motivated to seek theoretical reasons why annual fish yield and water quality are not linearly related, as argued in the *MEI*-models.

4. Theory on fish yield vs. water quality

The idea behind the approach which uses water quality as the predictor of fish yield is straightforward. Because nutrient levels and element balance affect the productivity of any lake ecosystem, the expectation then is that the harvestable proportion of a local fish stock is a function of lake productivity. Therefore, one expects water quality to reflect the level of annual fish yield in lakes.

As shown above, we have had poor success in finding proof for any linear relationship between water quality and fish yield in Finnish lakes (Lindström & Ranta 1988, Ranta & Lindström 1989, 1990, Ranta et al. 1992a, b). This conclusion holds equally as well on a local and a regional scale as it does for total yield and for individual species (Ranta & Lindström 1989, 1990, Ranta et al. 1992b). In our explorations, fishing effort has turned out to be far more relevant in affecting fish yield than is water quality (Ranta & Lindström 1990, Ranta et al. 1992b). Even with a data set in which the fishing effort was initially kept constant we did not succeed (Ranta et al. 1992a).

In what follows we shall explore theoretical grounds for the relationship between fish yield and water quality. Also, we shall concentrate on the likelihood of finding indications of a linear relationship between the two variables. This theme has originally been explored by Ranta & Lindström (1993).

Water quality forms an environmental gradient. Such a gradient could range from oligotrophy

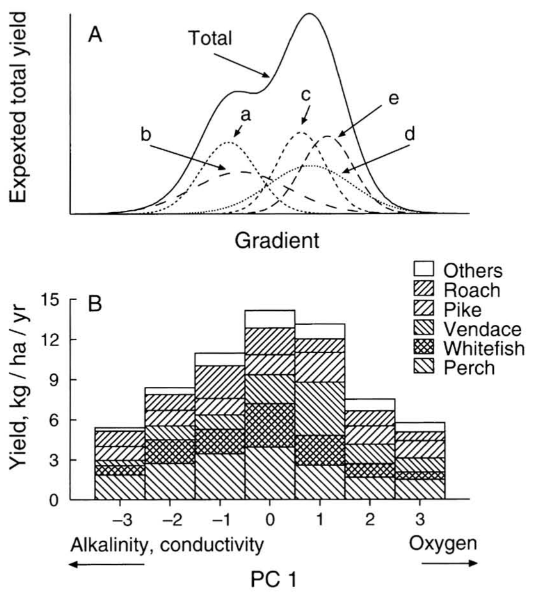

Fig. 6. (A) Frequency distributions of yield of five hypothetical fish species a, b, c, d and *e* (broken lines) as function of an environmental gradient. For each species the modal peak of the bell-shaped curve indicates conditions under which highest yield is obtainable. The spread of the curve reflects species-specific tolerance. The environmental gradient covers the range of occurrences of the species. Assuming that each species is trapped in proportion to its occurrence along the gradient, total yield is the pooled sum of individual species. The theoretical expectation for the total yield is indicated by the solid line. — (B) Expected total yield as function of environmental gradient: The environmental gradient is measured in terms of the second principal component. Negative score values indicate high alkalinity and conductivity, and low oxygen; whereas positive scores indicate low ionic concentrations and good oxygen conditions. The expectation is calculated by using yield data for the eight fish species as indicated by Ranta & Lindström (1993).

to eutrophy, or from acid waters to high-pH lakes, or include a linear combination of several variables. We assume that different fish species have differing requirements regarding water quality. They show decreasing population sizes distributed around their individual optimum values (Fig. 6A). Different species have these optimal conditions for existence in different points along this gradient. Some species are restricted to narrower ranges than others (Ranta & Lindström 1990). We further assume that the optima for different

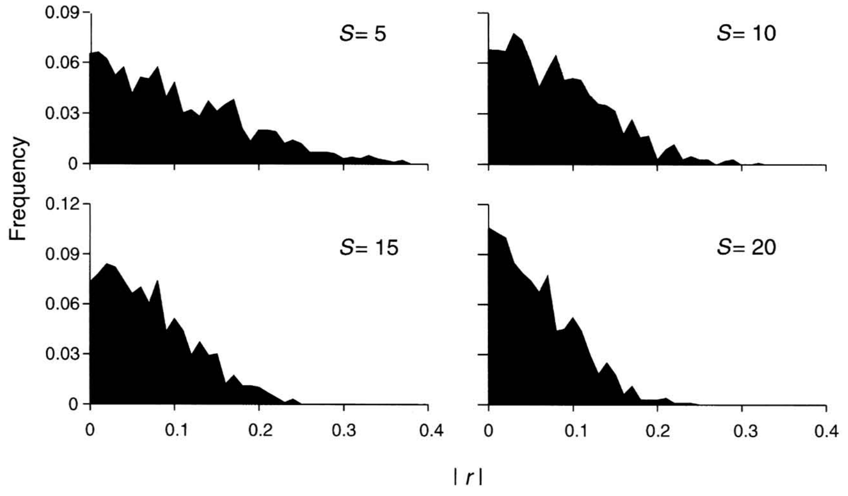

Fig. 7. Frequency distributions of linear correlation coefficients, $|r|$, between total fish yield and the environmental gradient (c.f., Fig. 6A). Graphs are based on 1000 simulations run separately for assemblages of 5, 10, 15 and 20 species. In the simulations species were randomly assigned the following parameter ranges of the Gaussian function: μ [–2 — 2], σ [0.5–2], Y_0 [0.1–4]. More details in text.

species are independent of each other. Under these conditions the distributions can be conveniently described with bell-shaped Gaussian curves. The reasoning below can easily be generalised to a multi-dimensional space. For clarity of argumentation, however, we shall restrict ourselves to a one-dimensional presentation.

The Gaussian function can conveniently be described by three parameters: the mode (μ; indicating the position of the curve along the gradient, X), the spread of the curve (σ, in units of standard deviation) and the maximum value (Y_0). The parameter Y_0 is a combination of many factors. Fish species differ in terms of population sizes. Some species are target species for fishermen, whereas other species are more a by-catch. Some species are trapped with very effective gear, such as the drag seine. Fishing effort and efficiency therefore are likely to vary among the species. It seems to us that the parameter Y_0 is very hard to break down into components. Presently it suffices to know that it encompasses much of the basic biology of the fish species as well as the behaviour of fishermen attempting to catch the species as efficiently as possible.

By using the Gaussian curve the yield (Y) of a species along the environmental gradient is

$$Y = Y_0 \exp\left(-\frac{(X - \mu)^2}{2\sigma^2}\right).$$

Assume now that species in a target lake contribute to the total yield according to their Gaussian functions. Under these conditions, the expected total yield is the sum of the yields of the individual species along the gradient. Some support for this is found in the data of Ranta & Lindström (1993, Fig. 6B).

Note that the resulting function of the expected total yield is *not* linear. The shape of the total yield graph depends on the spacing and spread of the species-specific responses. With aggregated component curves a multi-modal and often skewed total yield function follows (Fig. 8). Only if the individual species are located randomly along the gradient will the yield function be a unimodal bell-shaped curve.

This approach suggests that linearity between water quality and fish yield is hard to attain. To examine this further we made the following

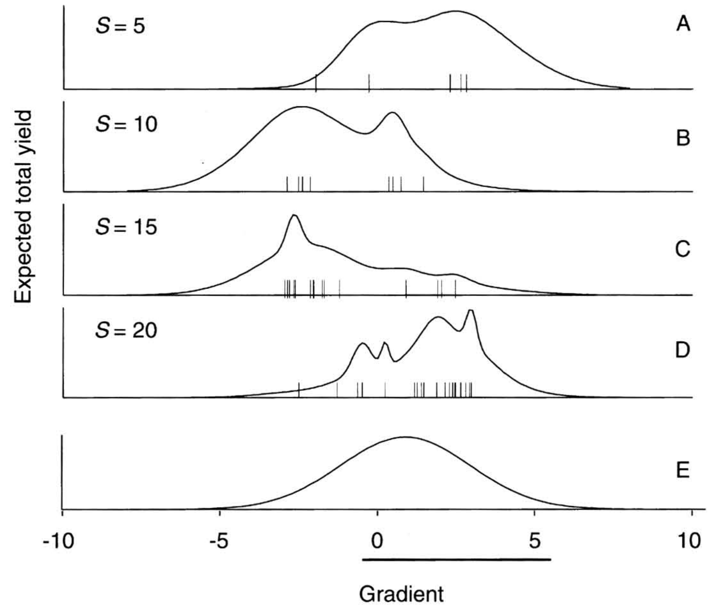

Fig. 8. Examples of species packing in the four assemblages of species (5, 10, 15 and 20 species) giving the highest correlation coefficients between total yield functions and water quality in the simulations for Fig 7. Vertical bars above the x-axis in each panel indicate species-specific modal values (μ) of the Gaussian function. Panel E exemplifies how a truncated gradient (stippled bar below the x-axis) yields to relatively high correlation between

Monte Carlo simulation. Four sets of imaginary species, with 5, 10, 15 and 20 species in them, were chosen. Each species was randomly assigned values of μ (range –2 – 2), σ (0.5–2) and Y_0 (0.1–4). The parameter ranges were selected according to data in Ranta & Lindström (1993). These figures were then used to generate Gaussian curves. The total yield was calculated as a pooled value of the component functions for the whole gradient. A linear correlation coefficient was then computed between the total yield and the gradient. For each of the four sets of species the procedure was repeated a total of 1000 times.

Based on the simulations we conclude that high linear correlation coefficients are rare between total yield and the environmental gradient. Increasing the number of species lowers correlation coefficients between the two variables (Fig. 7). Consequently, the likelihood of finding a linear relationship between fish yield and water quality in lakes is very low.

The present model suffices to outline a theoretical foundation showing why the differing sets of lake and fishery data (Ranta & Lindström 1989, 1990, Ranta et al. 1992a, b) failed to disclose linear relationships between fish yield and water quality. However, for present purposes, we were curious to see what type of fish assemblages will produce the highest and produce the lowest correlations between fish yield and water quality (Fig. 7). Examples of species "packings" producing the highest correlations in the previous runs are shown in Fig. 8. From this it is obvious that the highest correlations are achieved in assemblages with aggregated species arrangements along the gradient. Another possibility for truly high correlations is achievable with truncated responses of species to the environmental gradient. In such cases only one slope of the total yield graph (Fig. 8E) is included. However, as correlation between total yield and the environmental gradient are, as a rule, low (Fig. 7) not much value should presently be put on data as graphed in Fig. 8. Low correlations are scored when the total yield graph is a normal bell-shaped function; this follows from evenly or randomly placed μ values along the gradient X.

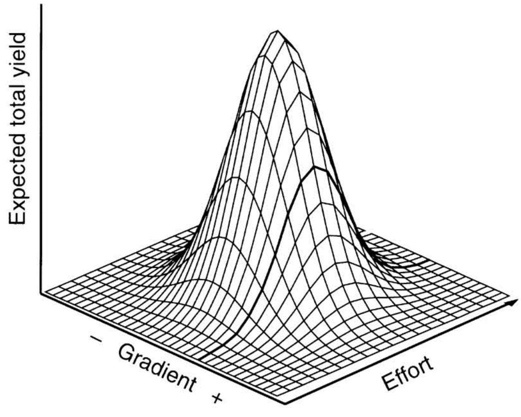

Fig. 9. Effect of fishing effort on expected total yield obtainable along different parts of the environmental gradient. First, total yield is assumed to follow the theoretical model of Ranta & Lindström (1993). Further presume that yield is a non-linear function of effort so that yield first increases with increasing effort but starts to decrease (due to overfishing) after reaching a turning point. Effect of varying effort exemplified by connecting with a line all lakes with a given value on the gradient axis.

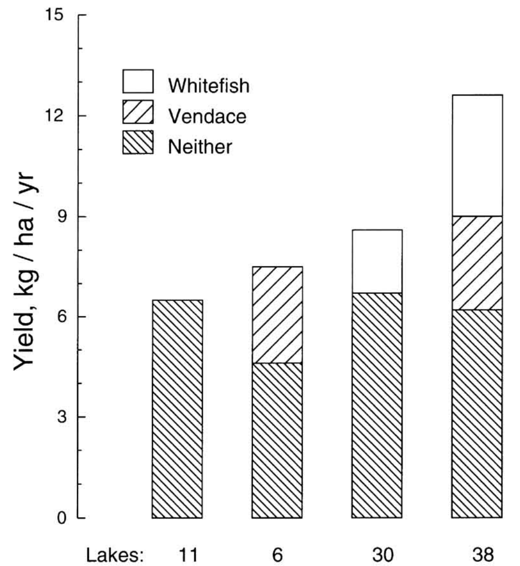

Fig. 10. Total fish yield in lakes with four differing fish assemblages (modified after Ranta & Lindström 1990). Differences in total yield are significant in statistical terms (Kruskal-Wallis, H_3 = 9.63, P= 0.02), but no differences remain if yield of the two species is subtracted (H_3 = 0.58, P= 0.90), which proves the importance of highly valued target species.

5. Whither?

The significance of fishing effort complicates the relation between water quality and total yield. Assume, for the moment that expected total yield follows the model (Ranta & Lindström 1993) as described above. General fishing effort models tell us, however, that increasing effort increases yield. It is also an established (theoretical) fact that those models describe the relation between yield and effort as curvi-linear (e.g., Pitcher & Hart 1982). That is, with increasing effort the yield increases until a turning point is reached, after which increasing effort no longer increases yield. Rather, the yield starts to decrease due to overfishing. Merging the effort function into the yield model results in a revised model, best described in three dimensions (Fig. 9).

Again, as in the previous version, lakes with given environmental characteristics are represented as points along the environmental gradient. Let us now examine the model message for the family of lakes with an identical value on the gradient *X* (Fig. 9). These lakes differ in but one respect: fishing effort varies. Evidently the yield obtained varies considerably, as described by the yield-effort function. Assume that, in the data set to be used for the search for the relation between yield and water quality, fishing effort differs among lakes — even among lakes of similar nature. The exact values of lake-specific efforts are, however, unknown to us. This uncertainty, or lack of knowledge, may considerably increase residual error around the yield vs. gradient model (Fig. 9).

The refinement of the basic model further tells us that even the curvi-linear relationship between total yield and water quality — as suggested by the model — might be hard to verify from data of the type usually available. To sum up our major point: attempting to predict lake-specific total yield based on water quality is a futile task, unless the effort level is known for each lake. For example, in the data analysed by Ranta & Lindström (1989), water quality explains twice the variation in fishing effort (R^2 = 0.20) compared to annual yield (R^2 = 0.08). One must remember that in many cases catch statistics is the raw variable used for measuring a lake's value in fisheries terms. The variation in total yield is mainly explained by fishing effort (e.g., Ranta & Lindström 1989, Ranta et al. 1992b), *the* variable that many of the management decisions will directly affect.

As a management implication of our review we shall suggest that research should be re-directed towards more fruitful issues. Among those, the following is particularly relevant: Long-term experience probably affects the fishing effort that will be put into various lakes in a certain area. This includes the number and type of fishing gear applied. For example, gill nets can be used almost anywhere in any lake, whereas use of a drag seine is much more restricted. The operation of a drag seine requires considerable manpower, while a gill net can be easily handled by one person. The use of various fishing gear is therefore likely to reflect not only the fish assemblage but also fishing tradition and the lakes themselves. All of these, along with the prevailing market situation, contribute to the yield obtained(Fig. 10). Therefore, their relevance beyond fisheries statistics should be acknowledged while developing tools for predicting fish yield in lakes.

Acknowledgements. Our project "*Is it possible to predict lake-specific fish yield based on water quality?*" was funded by the Kone Foundation. This paper is based on a talk given at the World Fisheries Congress, Athens 1992. Without our collaboration with Kalervo Salojärvi and Martti Rask much of what was said in the present MS would have remained untold; we thank them both and Jari Kouki for many discussions on our project. Kauri Mikkola, Jouko Sarvala and an anonymous referee critically commented on the MS. We also acknowledge the persisting critical attitude by Richard Ryder towards our research.

References

Beverton, R. J. H. & Holt, S. J. 1957: On the dynamics of exploited fish populations. — Fish. Invest. London, Ser. II, 19:1–533.

Draper, N. & Smith, H. 1966: Applied regression analysis. — Wiley. New York.

Edwards, A. L. 1985: Multiple regression and the analysis of variance and covariance. Second ed. — Freeman. New York.

Hrbacek, J. 1969: Relationship between some environmental parameters and the fish yield as a basis for a predictive model. — Verh. Int. Ver. Limnol. 17:1069–1081.

Jenkins, R. M. 1967: The influence of some environmental factors on standing crop harvest of fishes in the U.S. reservoirs: 298–321. — In: Proceedings of the Reservoir Fishery Resources Symposium. American Fisheries Society, Bethesida, MD, U.S.A.

Kerr, S. R. & Ryder, R. A. 1988: The applicability of fish yield indices in freshwater and marine ecosystems. — Limnol. Oceanogr. 33:973–981.

Lindström, K. & Ranta, E. 1988: Is the relationship between the morphoedaphic index and fish yield in Finnish lakes an artefact? — Aqua Fennica 18:205–209.

Matuszek, J. E. 1978: Empirical predictions of fish yields of large North American lakes. — Trans. Amer. Fish. Soc. 107:385–394.

McConnel, W. J., Lewis, S. & Olson, J. E. 1977: Gross photosynthesis as an estimator of potential fish production. — Trans. Amer. Fish. Soc. 106:417–423.

Melack, J. M. 1976: Primary productivity and fish yields in tropical lakes. — Trans. Amer. Fish. Soc. 105:575–580.

Northcote, T. G. & Larkin, P. A. 1956: Indices of productivity in British Columbia lakes. — J. Fish. Res. Board Canada 13:515–540.

Oglesby, R. T. 1977: Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. — J. Fish. Res. Board Canada 34:2271–2279.

Pella, J. J. & Tomlinson, P. K. 1969: A generalised stock production model. — Bull. Inter-Amer. Tropic. Tuna Comis. 13:421–496.

Pitcher, T. J. & Hart, P. J. B. 1982: Fisheries ecology. — Croom Helm, London.

Ranta, E. & Lindström, K. 1989: Prediction of lake-specific fish yield. — Fish. Res. 8:113–128.

— 1990: Water quality versus other determinants of species-specific yield of fish in Northern Finnish lakes. — Fish. Res. 8:367–379.

— 1992: Predicting fish yield in Finnish lakes (in Finnish with English abstract). — Suomen Kalatalous 60:159–174.

— 1993: Theory on fish yield versus water quality in lakes. — Ann. Zool. Fennici 30:71–75.

Ranta, E., Lindström, K. & Rask, M. 1992a: Fish catch and water quality in small lakes. — Fish. Res. 13:1–7.

Ranta, E., Lindström, K. & Salojärvi, K. 1992b: Water quality, fishing effort and fish yield in lakes. — Fish. Res. 15:105–119.

Rawson, D. S. 1952: Mean depth and the fish production of lakes. — Ecology 33:513–521.

Ricker, W. E. 1954: Stock and recruitment. — J. Fish. Res. Board Canada 11:559–623.

Ryder, R. A. 1965: A method for estimating the potential fish production of north-temperate lakes. — Trans. Amer. Fish. Soc. 94:214–218.

— 1982: The morphoedaphic index – use, abuse, and fundamental concepts. — Trans. Amer. Fish. Soc. 111:154–164.

Ryder, R. A., Kerk, S. R., Loftus, K. H. & Regier, H. A. 1974: The morphoedaphic index, a fish yield estimator – review and evaluation. — J. Fish. Res. Board Canada 31:663–688.

Sarvala, J., Aulio, K., Mölsä, H., Rajasilta, M., Salo, J. & Vuorinen, I. 1984: Factors behind the exceptionally high fish yield in the lake Pyhäjärvi, south-western Finland – hypotheses on the biological regulation of fish production. — Aqua Fennica 14:49–57.

Schaffer, W. M. 1954: Some aspects of the dynamics of populations important to the management of commercial marine fisheries. — Bull. Inter-Amer. Tropic. Tuna Comiss. 1:27–56.

Schlesinger, D. A. & Regier, H. A. 1982: Climatic and morphoedaphic indices of fish yields from natural lakes. — Trans. Amer. Fish. Soc. 111:141–150.

Zuboy, J. R. 1981: A new tool for fishery managers: the Delphi technique. — N. Amer. J. Fish. Manag. 1:55–59.