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Theory on fish yield versus water quality in lakes

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For many years water quality in lakes has been seen as an important linear predictor of fish yield (kg/ha/yr). However, in Finnish lakes prediction fails. Therefore, we have explored a theoretical basis for such empirical models. With a niche-theory-based model, built on the assumption that each species exhibits a bell-shaped distribution around some optimal water quality value, we are able to show that a linear relationship between water quality and total fish yield is extremely unlikely to result. To illustrate this we shall present data on yield of eight fish species in 148 Finnish lakes. In accordance with the model, the empirical data show roughly bell-shaped yield responses along an environmental gradient for each of the species. This also results in the total yield's peaking at intermediate gradient values, and yield decreasing as we move to either direction from the modal point.

1. Introduction

One of the goals of inland fisheries management is to find methods capable of predicting fish yield (kg/ha/yr) in lakes with known characteristics (Rawson 1951, Ryder 1982). Advances in yield estimation were divided by Deriso (1987) into biological models relating yield (i) to population processes and (ii) to empirical relations between yield and certain characters of the lake ecosystem. Because data for successful application of models of the first type are often tedious to obtain it is obvious that a great number of empirical models have risen, as recently summarised by Leach et al. (1987). These models are founded on production theory (Fig. 1), which states that limnological characters of a lake affect its productivity. Because annually harvested fish yield is part of a lake's production, it is only a short step to infer a link between it and water quality. The prevailing approach is that lake-specific fish yield is a linear function of water quality (Ryder 1965, Ryder et al. 1974, Matuszek 1978, Schlessinger & Oglesby 1977, Kerr & Ryder 1988). Should this hold it would have considerable use both in fisheries management and in assessing effects of long-term environmental changes.

For some years our theme has been to explore the relationship between water quality and total fish yield in Finnish lakes (Lindström & Ranta 1988, Ranta & Lindström 1989, 1990, 1992, Ranta et al. 1992a, b). To stimulate further dis-

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cussion on this topic we will here suggest one possible theoretical relationship between water quality and fish yield in lakes. We will focus on the total fish yield, though recognising the fact that it is composed of yields of individual target species. For this reason our approach closely relates to the niche theory (e.g., Whittaker & Levin 1975, Gauch 1982).

2. The model

2.1. Water quality

We shall explore the theoretical grounds for empirical models predicting fish yield on the basis of water quality. Water quality refers here to routinely analysed chemical and physical characteristics of lake water. No individual parameter is singled out, as many of the variables measured by authorities (Table 1) are strongly intercorrelated. Instead, linear combinations (i.e. *principal components*) of the original variables shall be extracted. Logarithmic transformation of the variables enhances normality by reducing skewness, thus rendering data suitable for parametric statistical calculations. Lake-specific component scores are normally distributed with a zero mean and unit standard deviation (Chatfield & Collins 1980). For an elaborated usage of such an approach, see Ranta & Lindström (1989, 1990).

We assume, in accordance with the niche theory (as pioneered by Hutchinson 1965, Whittaker & Levin 1975), that different species of fish have differing requirements in regard to water quality, with decreasing population sizes distributed around their individual optimum values (Fig. 2). This assumption is supported by data from Finnish lakes (Fig. 3). Under such conditions it is most convenient to describe the

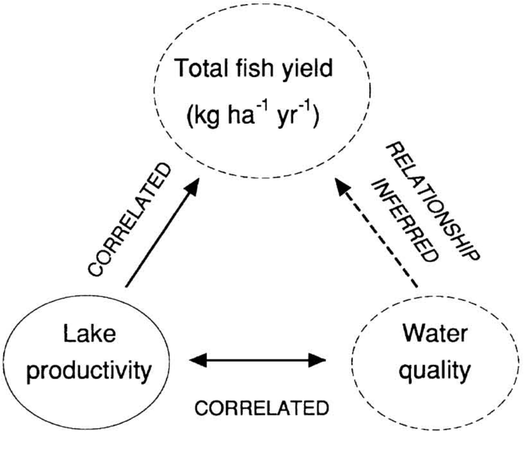

Fig. 1. The productivity concept says that limnological charactersitics of a lake (referred to as water quality) affect productivity of a freshwater ecosystem (the two-headed arrow indicates uncertainty between cause and effect). Harvestable fish yield, in turn, is a function of lake productivity. Therefore, it has repeatedly been assumed that there is a linear link between water quality and annual fish yield. This presumed link (as indicated with broken lines) is the foundation of many empiric models aiming to predict lake-specific yield. For a balanced discussion of such models and their major proponents, see Leach et al. (1987).

Table 1. Linear correlations between water quality variables in 148 Finnish lakes. Data pooled from Ranta & Lindström (1989) and Ranta et al. (1992b). Logarithmic transformations were used for all variables prior to calculations, except for oxygen % (arc sine square root transformed). Due to inter-correlation of variables, their linear combinations were constructed by applying principal component analysis. The first principal component (eigenvalue 3.12) retains about 45% of total variation in original data. The rightmost column (PC1) gives the loadings of the original variables on the first principal component axis.

Variables	Alkal.	Conduct.	Oxygen	*pH*	Nitrogen	Phosph.	Colour	PC1
Alkalinity	1.000							–0.894
Conductivity	0.608	1.000						–0.864
Oxygen %	–0.351	–0.314	1.000					0.574
pH	0.592	0.287	0.376	1.000				–0.458
Nitrogen	–0.143	0.272	–0.385	–0.442	1.000			–0.165
Phosphorus	–0.112	0.228	–0.375	–0.466	0.734	1.000		–0.151
Colour	–0.212	0.036	–0.417	–0.632	0.610	0.610	1.000	0.048

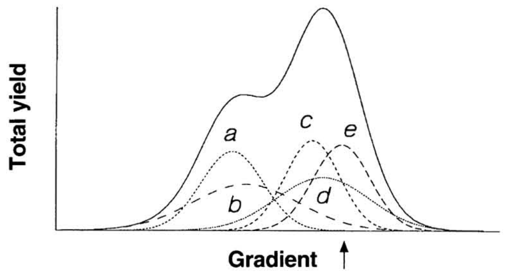

Fig. 2. Frequency distributions of yield of five hypothetical fish species *a* – *e* (broken lines) as a function of an environmental gradient. For each species, modal peak of bell-shaped curve indicates conditions under which highest yield is obtainable. Spread of curve reflects species-specific tolerance. The environmental gradient covers the range of occurrences of the species. For example, a lake, as indicated with an arrow on the gradient axis, has four species. Assume now that each species is trapped in proportion to its occurrence. In our example lake, species *e* dominates the catch followed by *d* and *c* and *b*, while *a* is not found in a lake of this type. The total yield is the pooled sum of the individual species. The theoretical expectation for the total yield is indicated by the solid line.

distributions as bell-shaped using the Gaussian curve (e.g., Gauch 1982). Because the normality of the frequency distributions in Fig. 3 can be questioned, we shall use this curve only to sketch our concept. (Incidentally, we examined the effects of the relaxation of the Gaussian form of the species-specific response function to rectangular or triangular functions; this did not substantially affect our conclusions.)

2.2. Niche theory and fish yield

The Gaussian curve has three parameters: the mode (μ; indicating the position of the curve along the gradient, X), the maximum value (Y_0), and the spread of the curve (σ) in units of standard deviation. Thus, the equation fully describing the yield (Y) of a species along the environmental gradient is

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

We further assume that the modes of species' distributions are located independently along the gradient. Furthermore, some species are restricted to narrower ranges than others (e.g., species *a*, *c* and *e* in Fig. 2) and some species occur more

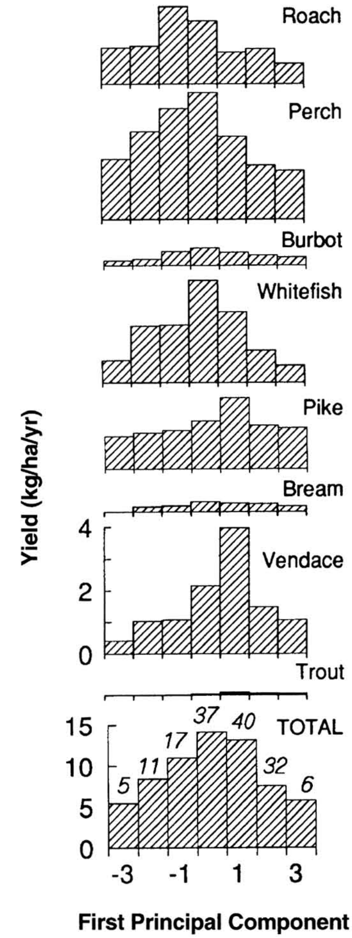

Fig. 3. Yield of eight fish species along an environmental gradient, in terms of linear combinations of the first principal component, based on 148 Finnish lakes (pooled from Ranta & Lindström, 1989; Ranta et al., 1992b). Only species trapped in at least 40 lakes are included. Note that trout (trapped in 44 lakes) has a value of zero for the two lowest classes; the same is true for bream in the lowest class. The length of the bars refers to averages (*y*-axis scale for the species is given with vendace). The lowest panel (with its own scale for the *y*-axis) refers to the total yield. Numbers in italics indicate sample sizes. The interpretation of the environmental gradient is as follows: Negative score values indicate high alkalinity and conductivity, and low oxygen, while positive scores indicate low ionic concentrations and good oxygen conditions (Table 1).

broadly (species *b* and *d*). That is, individual species display differing tolerances. They also have optimal conditions for existence and exploitation in different parts along the gradient (Fig. 2). Our argument below can be generalised to a multidimensional gradient space. However, to keep things simple it suffices to present the concept in a single dimension.

2.3. Total yield vs. water quality

The environmental gradient should represent (in terms of a statistical sampling frame; Stuart 1984) the range of occurrences of the fish species. Further, any lake can be located as a point on the environmental gradient. Assume now that the species in such a target lake are trapped in the proportion as indicated by the species-specific Gaussian functions (Fig. 2). For example, in the Finnish data on 148 lakes (Table 1, Fig. 3) yields of roach and perch are greater in lakes with high alkalinity and conductivity, while the highest yields of vendace and trout come from lakes with high oxygen and low ionic concentrations (Fig. 3). Under these conditions, the expected total yield is the sum of the yields of the individual species along the gradient (Fig. 2).

An important fact to observe is that the resulting function of the expected total yield is definitely not linear. The shape of the graph depends on the spacing and spread of the component curves. If the individual species are located randomly (or evenly) along the gradient, the yield function will be a unimodal bell-shaped curve (Fig. 3, lowest panel), whereas, if the component curves are clustered, a multi-modal total yield function easily follows (Fig. 2).

The parameter Y_0, the maximum of the Gaussian curve, is, in the present model, a combination of many factors. Firstly, fish species differ in terms of biomass production. For example, the trout, a specialised piscivore, seldom reaches high population densities per unit area (Fig. 3). Secondly, some species, such as vendace and whitefish, are special target species for fishermen, whereas other species come more as bycatch. Thirdly, some species (especially pelagic plankton feeders) are trapped with very effective gear, such as the drag seine. Fishing effort and efficiency therefore are likely to vary among the species. Presently the parameter Y_0 is very hard to break down into components.

3. Discussion

Recently we have repeatedly failed to find evidence of any linear relationship between water quality and fish yield in Finnish lakes. (Linearity here refers to linear statistical models, such as regression models and parametric correlation, as in Bowerman & O'Connell 1990, in which linearity may also be achieved by variable transformations.) Our finding holds as well for the local (Ranta & Lindström 1989) and for the regional scale (Ranta et al. 1992b), as for the total yield and for individual species (Ranta & Lindström 1990, Ranta et al. 1992a,b). Even when we tried to apply the Ryderian *MEI* model (Ryder 1965), we failed (fig. 2 in Ranta & Lindström 1992; see also Lindström & Ranta 1988). Other criticism of the fish-yield versus water-quality approach is provided by Youngs & Heimbuch (1982), Lindström & Ranta (1988), Walters & Collie (1988), Schneider & Haedrich (1989), Downing et al. (1990).

In our research fishing effort has turned out to be far more relevant in affecting fish yield than has water quality (Ranta & Lindström 1990, Ranta et al. 1992b). Even with a data set in which the fishing effort was initially kept constant we were unable to predict fish yield (Ranta et al. 1992a). Unfortunately, fishing effort is a variable usually known only after the annual fishing has taken place. A predictive model built entirely on fishing effort has a low — if not nonexistant — value as an inland fisheries management tool. Furthermore, variation in fishing effort among lakes may greatly hamper location of the pattern as graphed in Fig. 2. Therefore, we think that large sets of data (preferably with known fishing effort) are a necessity when studying the empirical relationship between total yield and water quality.

We feel that the present model demonstrates theoretical reasons why we, with independent sets of lake and fishery data (155 lakes, Ranta & Lindström 1989, 1990; 80 lakes, Ranta et al. 1992a; 70 lakes, Ranta et al. 1992b), have failed to locate any linear predictive relationship between fish yield and water quality. Also, it suggests to us that the factors capable of predicting fish yield in lakes still deserve attention.

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