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Fish yield versus variation in water quality in the lakes of Kuusamo, northern Finland

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Our goal was to ascertain whether fish yield differences (0.2–43 kg ha^{-1} yr^{-1}) among 166 Northern Finnish lakes could be attributed to level and variability of 14 limnological variables. Water quality variables were assessed at shallow and deep water in winter and summer. For most of them, the greatest share of the variation (65%) was due to the season, while that of the water depth averaged 28%. Fish yield tends to increase with increasing levels of oxygen saturation, conductivity, Na and K concentrations. A decreasing fish yield was observed with an increasing chemical oxygen demand of lake water and with increasing N. Intermediate levels of water colour were associated with the highest fish yield. A variable variability accounted for a fair proportion of the total variance in the fish yield together with a variable level only in the chemical oxygen demand of the lake water. For most of the variables examined for variability, no clear covariation with the fish yield could be shown. We selected 25 lakes with the lowest fish yield (mean 0.4 kg), and 25 lakes with the highest yield (20 kg). The 14 variables were compared in the two groups of lakes. We found that the oxygen saturation, conductivity and pH were significantly higher in the high-yield lakes than in the low-yield lakes, whilst Fe levels were much lower in the high-yield lakes. We conclude that water quality affects the lake-specific fish yield. The relationship in Finnish lakes is, however, too weak to enable the usage of water quality as a lake-specific fish yield prediction tool.

1. Introduction

We have investigated whether one can predict a total fish yield (kg ha^{-1} yr^{-1}) knowning water quality in lakes (Lindström & Ranta 1988, Ranta & Lindström 1989, 1990, 1993ab, Ranta *et al*. 1992ab). This is an approach that follows the production theory (e.g., Leach *et al*. 1987) stating that limnological characters of a lake affect its productivity. As annually harvested fish yield is a part of a lake's production it is a short step to infer that there should be a link between it and water quality, as early proposed by Rawson (1952), Northcote and Larkin (1956), and further elaborated by Ryder (1965, 1982). In the hunt of valid yieldprediction models we have used data of about 390 Finnish lakes (Ranta & Lindstrom 1993b) with several water-quality variables (in varying combinations) and data on total fish yield. In some occasions we have been able to use species-specific yields too (Ranta & Lindstrom 1990, Ranta *et al*. 1992ab).

The general answer of our research is that no limnological variable alone, nor in any linear combination with other variables, is powerful enough to serve as a sufficient fish yield predictor. Our conclusion holds unambiguously whatever geographical scale (drainage area, region, country-wide) we have used (Ranta & Lindström 1989, Ranta *et al*. 1992b). We also did not find any predictive relationship between water quality and fish catches in a data set where fishing effort was standardised (Ranta *et al*. 1992a).

In fact, using a simple theoretical model based on the concept of the ecological niche (e.g., MacArthur 1972), we were able to conclude that the linear relationship between water quality and a total yield is an extremely unlikely pattern (Ranta & Lindström 1993a). However, in all phases of our work we stressed that water quality and fish yield are not totally decoupled. Rather, we maintained — and shall continue to do so — that the relationship between yield and lake water characteristics is too weak to be used as a predictive tool in fisheries management.

The scope of the present work is to demonstrate further that total fish yield varies to some extent according to variation in lake water quality. In doing this, we shall acknowledge that the variation can originate from different sources. Besides differences between lakes, our present data incorporate variation caused by season and vertical depth. The fish yield recorded in our data set (166 lakes) ranges from 0.17 to 43.8 kg ha^{-1} yr^{-1}, thus providing ample variation for our purposes. According to the tradition of the field (e.g., Ryder 1965, Jenkins 1967, Oglesby 1977, Matuszek 1978, Schlesinger & Regier 1982, Kerr & Ryder 1988, Schneider & Haedrich 1989), we shall focus on the total fish yield.

2. Material and methods

2.1. General

The analysis is based on data collected by Heinonen and Myllymaa (1974), and Myllymaa and Ylitolonen (1980). Their studies addressed both the water quality variables and the annual fish yield information in 166 lakes in the Kuusamo commune, NE Finland. The scope of their studies was to provide data to help formulate fisheries management plans. We were using a part of their data to address the following question: Is it possible to predict lake-specific fish yield based on water quality? (Ranta & Lindström 1989, 1990, 1993ab). So much of the information about the lakes is given in those papers that only short description suffices here. The lakes are from within about 1 000-km^2 area which comprises three drainage systems (e.g., Ranta & Lindström 1989).

Heinonen and Myllymaa (1974) did not give species-specific fish catches, but they list encountered species. On the other hand, Myllymaa and Ylitolonen (1980) provide data on catches of the most important target species. Both papers give the total annual catch, which is here scaled to kg per hectare. This variable is referred to as the total annual yield (or the yield, kg ha^{-1} yr^{-1}, for simplicity).

To characterise water quality in the study lakes Heinonen and Myllymaa (1974), and Myllymaa and Ylitolonen (1980) took water samples on two occasions, late winter (mostly March) and late summer (mostly August) at two depths, 1 m from the surface and 1 m above the bottom sediment of the deepest part of the lakes. Their data comprises information of 14 limnological variables (Table 1). However, for reasons unknown to us, some variables were not always recorded at the two depths, and all the sampling occasions (Table 1). For this reason Ranta and Lindström (1989) restricted their analysis on the shallow-water summer samples. We have also used the same water quality data in two previous papers (Ranta & Lindström 1989, 1990). Therefore, in the present analysis, the late summer shallow-water sample serves again as a reference. However, as we are presently interested in how much variation in water quality is reflected in variation in fish yield, we shall make full use of all dimensions in the water quality variation (lakes, depth, season). While doing this, the number of lakes included into different calculations may vary due to the missing data (Table 1).

2.2. Numerical analysis

For all statistical treatments involving parametric tests, the original variables were $\log_{10}$ transformed, excepting the percentage of an oxygen saturation. For this variable arcsine square-root transformation was used. The normality of the transformed variables was verified with the rankit test (Sokal & Rohlf 1981). We thus follow the practice adopted early in our research on this topic (Lindström & Ranta 1988). The covariance structure among the limnological variables is different on different sampling occasions. This efficiently prevented us from using principal components to make linear combinations of covarying variables. Therefore, contrary to our previous analyses (Ranta & Lindström 1989, 1990, 1993a, Ranta *et al*. 1992ab), we had to concentrate here on variable level analyses. In doing this, we are fully aware of two statistical pitfalls. Firstly, many of the water quality variables are highly intercorrelated, therefore, they hardly provide independent information. Secondly, multiple testing introduces the Bonferroni inflation to levels of statistical significance (e.g., Bowerman & O'Connel 1990). Due to a great number of tests made, one might end up finding statistically significant values just by chance. To avoid this, significance levels (when used) are corrected for the bias.

The statistical analyses we use are the Pearson correlation, analysis of variance (ANOVA), and Mann-Whitney *U*-test. In the ANOVAs below, the yield is $\log_{10}$ transformed. This allows us to overcome the fact that the lake-specific fish yield is strongly positively skewed. However, to improve readability of our results, when presenting factor profiles for the limnological variables we shall use non-transformed values of the yield.

A limnological variable may affect fish populations in two ways. Firstly, the variable level may be too extreme, and therefore, fish might have difficulties living in the lake. Secondly, high vertical and seasonal variability in the variable level, in turn, may also introduce problems for fish. When attempting to relate the fish yield to the variable level, we adopted the shallow-water summer sample as the base level (Ranta & Lindström 1989). As a measure of variability of each of the limnological variables, the following procedure was used. The values of the three other samples (shallow water in winter, deep water in winter, deep water in summer) had been scaled with this base sample. (Using the other samples as the comparison point does not affect our results). If there was no variation, the measure got a value of 1.0, otherwise it was either smaller or larger. Logarithm (base 10) of the mean of the three figures not only normalised the frequency distribution but also scaled the measure to zero mean (no variation) and, in the present data, to a range from – 1 to 1 (in most cases from – 0.5 to 0.5). However, the missing information caused that the elements Mn, Na, K, Ca and Mg could not be used in these variability calculations.

3. Results

3.1. Water quality

Across the lakes, there is a considerable variation in the limnological variables when measured at the two depths and two sampling occasions (Table 1). The levels of four variables (oxygen saturation percentage, chemical oxygen demand of the water, pH and Na), decreased with depth, while in others they increased (Fig. 1). For most of the variables, the winter-time levels were considerably higher than the corresponding values measured in summer (Fig. 1). To characterise variation at a variable level, we first computed the total sum of squares and then, following Sokal and Rohlf (1981), estimated how large a proportion of it was linked to the seasonal changes and to the differences in water depth. Most of the variation was caused by the seasonal changes, on average

Table 1. Number (*n*) of lakes studied for the different water quality variables together with the coefficient of variation (CV, %) and range of values for the two sampling dates and depths. For units of measurement of each variable see Table 2 (shallow refers to 1 m from water surface, and deep 1 m above bottom at the deepest part of the lake). COD = chemical oxygen demand, mg O_2 l^{-1}.

	Winter						Summer					
	Shallow			Deep			Shallow			Deep		
Variable	*n*	CV, %	(range)	*n*	CV, %	range	*n*	CV, %	range	*n*	CV, %	range
O_2%	163	31	(2–93)	127	68	(1–8 2)	165	5	(69–122)	132	33	(2–102)
Conductivity	166	83	(1.2–100)	128	111	(1.5–380)	164	88	(1.2–105.0)	131	88	(1.3–137.0)
Alkalinity	166	57	(0.02–1.54)	127	58	(0.06–1.71)	165	58	(0.05–1.28)	131	60	(0.03–1.31)
pH	165	4	(5.8–7.4)	128	4	(5.8–7.4)	165	4	(6.2–9.0)	131	5	(6.1–7.6)
Colour	166	95	(25–250)	128	200	(3–1 100)	165	69	(4–104)	127	67	(5–100)
COD	166	45	(1.6–19.9)	128	71	(1.5–43.0)	165	39	(1.6–18.8)	131	31	(1.7–10.9)
N	165	51	(120–974)	126	270	(80–14 000)	160	64	(100–1 790)	127	36	(100–886)
P	166	63	(3–55)	128	486	(3–1 900)	160	61	(4–74)	127	55	(4–54)
Fe	165	203	(10–11 600)	125	242	(27–21 400)	88	88	(11–1 000)	127	116	(10–2 200)
Mn	74	163	(1–701)	51	202	(20–6 700)	88	86	(1–171)	125	320	(4–4 100)
Na	72	73	(0.8–10.5)	46	37	(0.8–3.9)	157	57	(0.5–8.3)	122	56	(0.5–8.5)
K	72	42	(0.4–2.6)	46	41	(0.5–2.8)	157	43	(0.3–2.9)	121	42	(0.3–2.9)
Ca	72	68	(1.5–27)	46	74	(2.1–31.0)	157	64	(0.6–22.5)	121	60	(0.9–15.0)
Mg	72	86	(0.5–10.0)	46	92	(0.6–12.0)	157	63	(0.1–6.3)	121	67	(0.1–6.0)

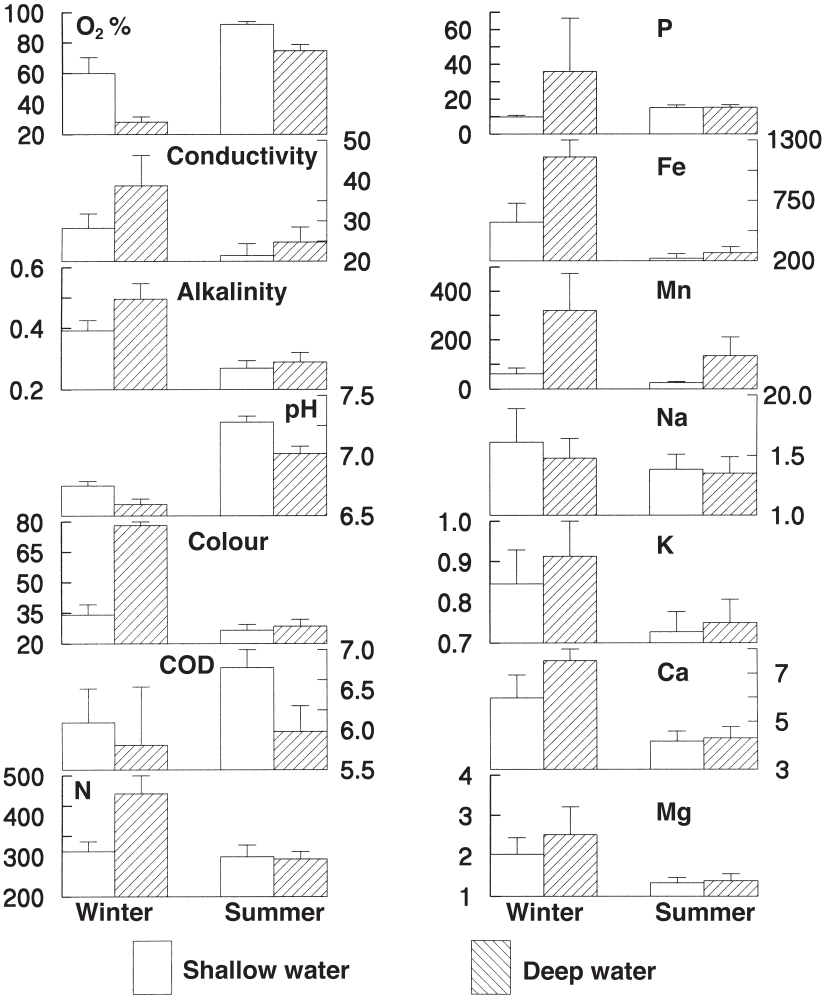

Fig. 1. Mean (+ 95% confidence limit) of the 14 limnological variables characterising water quality in the Kuusamo lakes. The two sampling depths and occasions are treated separately. In calculations transformed values were used but they were returned to linear scale for this presentation. For units of the variable, see Table 2.

65% in over 14 variables, while 28% could be attributed to the water depth differences (Table 2). Only in three variables, chemical oxygen demand, P and Mn concentrations, the variation due to the differences in the water depth overrides the one caused by the changes of the seasons. The smallest variation accountable to the water depth differences was found in the concentrations of potassium, calcium and magnesium.

When the variation was studied at the lake level with the help of correlation analysis, the obvious outcome was that, for most of the variables and comparisons, the correlation coefficients were rather high (Table 2). The most obvious deviation was the oxygen saturation percentage, in which correlations were poor (Table 2). Likewise, the manganese concentration scores low correlations. Pairwise correlations between the 14 water quality variables, calculated for different sampling occasions, revealed high intercorrelations, and temporal and vertical consistency (Table 3). However, this is not always so, sometimes signs of correlation coefficients are reversed indicating substantial changes in their covariation. Such sign reversals mostly occured when correlation matrices for winter and summer were compared (Table 3). In fact, Mantel tests (e.g., Manly 1986), comparison in pairs of the four different correlation matrices, pointed out that covariance structures between the different sampling depths and dates had differed (p at least < 0.01). This means that computing principal components to find linear combinations of covarying variables is effectively hampered.

To analyse the multi-dimensional information in each of the four correlation matrices (Table 3), we performed multi-dimensional scaling analyses. This method is suited to reconstruct variable associations in multi-dimensional co-ordinate systems. When run with the present data no more than two dimensions were needed to encompass at least 90% of the variation between the water-quality variables (Fig. 2). Scatter plots of the results suggest that some variables are always rather closely located in the ordination space (e.g., colour and Fe, alkalinity and K), while some others (e.g., pH, oxygen saturation) seem to move around in the ordination space relative to the other variables, visualising sufficiently the changing covariance structure (Fig. 2).

3.2. Fish yield vs. water quality

In the previous section,we have been able to show that in these lakes there is a considerable variation in limnological variables characterising water quality (see also Ranta & Lindström 1989, 1990). The variation was not only among lakes, also within a single lake considerable changes in water quality were accountable to the water depth and season. The fish yield in these lakes ranged from 0.2 to 43.8 kg ha^{-1} yr^{-1} (Fig. 3) Therefore, it is rather interesting to compare whether there is any link between the yield variation and variation in water quality.

To analyse the possible relationship between water quality variation and fish yield we proceeded as follows. First, we calculated product moment correlations between the yield and the 14 limnological variables (original variables transformed) at the two sampling occasions, and the two sampling depths. The results were not very encouraging as most of the coefficients were low, or extremely low, to say the least (Table 4).

One could doubt the conclusions drawn from Table 4. For example, correlation coefficients with $|r| > 0.24$ were all significant at $p = 0.05$. To address this, we used the statistical power analysis (Cohen 1988). At $\alpha = 0.05$ we asked, how many lakes one had to have in the sample to be able to recognise, with a known power $(1 - \beta)$, correlation coefficients with a given coefficient of determination. To illustrate our point, let us imagine a situation where one would like to find with 80% $(1 - \beta = 0.8)$ certainty a correlation leading to $r^2 \geq 0.5$. In such a situation, 50% of the variation in the fish yield would be explained by the limnological variable under examination. Power analysis is a handy way to answer such questions. In the present case, only 13 randomly selected lakes would be enough for detecting the 0.707 correlation between the yield and a limnological character (Cohen 1988; see from page 75 onwards). The

Table 2. Proportion of variance observed in the 14 water quality variables as divided between the two sampling occasions (Season: W = winter, S = summer) and water depths (s = shallow, d = deep water). Also, correlation coefficients for the 14 variables are given between the sampling occasions and water depths. Small coefficients are indicated with bold typeface.

	Variance component, %		Correlation coefficients			
Variable	Season	Depth	Ws-Wd	Ss-Sd	Ws-Ss	Wd-Sd
O_2%	61	39	**0.277**	**0.066**	**0.036**	**0.009**
Conductivity, µS	66	31	0.930	0.986	0.952	0.923
Alkalinity, mval l^{-1}	86	12	0.700	0.969	0.864	0.692
pH	84	15	0.740	0.455	0.687	0.322
Colour, mg Pt l^{-1}	54	42	0.522	0.860	0.681	0.470
COD	38	52	0.736	0.930	0.601	0.693
N, µg l^{-1}	46	36	0.679	0.453	**0.268**	0.341
P, µg l^{-1}	14	63	0.435	0.618	0.326	0.346
Fe, µg l^{-1}	71	25	0.495	0.731	0.782	0.705
Mn, µg l^{-1}	42	55	**0.108**	**0.085**	**0.241**	0.423
Na, µg l^{-1}	72	10	0.787	0.970	0.749	0.970
K, µg l^{-1}	87	7	0.725	0.938	0.764	0.673
Ca, µg l^{-1}	93	6	0.895	0.937	0.919	0.782
Mg, µg l^{-1}	93	5	0.916	0.973	0.947	0.915
Mean	65	28	0.639	0.712	0.630	0.590

Table 3. Correlations between water quality characterising variables (log-transformed, except O_2%, which is arcsine square root transformed) at different water depths and sampling occasions. For clarity leading 0's and decimal points are omitted (O_2% = oxygen saturation %, Cond. = conductivity, Alka. = alkalinity.

Winter, shallow water														
(1)	O_2%													
(2)	Cond	–5												
(3)	Alka.	–311	142											
(4)	pH	326	–162	396										
(5)	Colour	–498	–17	188	–416									
(6)	COD	–428	333	–31	–552	670								
(7)	N	–476	–128	194	–244	443	326							
(8)	P	–347	178	95	–234	271	289	421						
(9)	Fe	–511	346	120	–521	572	566	305	384					
(10)	Mn	–581	214	339	–410	645	380	584	543	681				
(11)	Na	–280	187	282	–314	397	217	273	382	488	405			
(12)	K	–196	417	493	139	–52	–127	230	407	154	209	394		
(13)	Ca	–210	502	708	289	11	–110	123	192	100	199	177	755	
(14)	Mg	–121	541	780	324	66	–111	62	–39	172	254	56	349	596
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
Winter, deep water														
(1)	O_2%													
(2)	Cond	–204												
(3)	Alka.	–211	166											
(4)	pH	97	105	720										
(5)	Colour	–508	93	317	–50									
(6)	COD	–106	365	126	–143	721								
(7)	N	–112	0	346	80	579	488							
(8)	P	–252	99	21	–24	426	278	512						
(9)	Fe	–496	159	65	–247	715	546	345	393					
(10)	Mn	–590	31	102	–68	490	247	333	188	500				
(11)	Na	–19	176	44	–71	362	482	221	157	436	198			
(12)	K	–45	597	460	285	77	141	246	42	104	79	381		
(13)	Ca	–24	760	710	528	–117	–167	36	–82	–143	76	20	700	
(14)	Mg	24	778	739	709	–185	–129	–13	–261	–192	–295	93	349	469
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
Summer, shallow water														
(1)	O_2%													
(2)	Cond	–341												
(3)	Alka.	179	328											
(4)	pH	512	62	691										
(5)	Colour	–179	–56	–408	–388									
(6)	COD	–25	–253	–325	–255	807								
(7)	N	337	–375	–134	212	347	506							
(8)	P	56	53	–30	149	396	421	376						
(9)	Fe	–141	–16	–499	–293	861	797	433	436					
(10)	Mn	4	–232	–199	–74	377	402	293	281	407				
(11)	Na	–193	232	223	132	109	41	–20	227	50	53			
(12)	K	95	418	675	584	–255	–297	–123	64	–355	–29	376		
(13)	Ca	156	264	871	647	–322	–254	–137	–11	–442	–42	140	676	
(14)	Mg	162	260	817	528	–157	–105	–54	26	–264	–186	75	475	734
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
Summer, deep water														
(1)	O_2%													
(2)	Cond	–74												
(3)	Alka.	–244	312											
(4)	pH	543	331	451										
(5)	Colour	–262	25	–224	–321									
(6)	COD	259	–122	–240	91	620								
(7)	N	–319	–208	117	–195	281	213							
(8)	P	–146	–57	56	–12	305	240	296						
(9)	Fe	–138	–274	–374	–307	618	529	334	419					
(10)	Mn	–728	–22	255	–409	244	–125	456	160	223				
(11)	Na	–77	155	143	123	249	93	165	300	171	150			
(12)	K	–260	330	747	363	–53	–171	200	128	–157	403	370		
(13)	Ca	–259	250	851	343	–213	–254	56	1	–347	307	53	770	
(14)	Mg	–235	278	886	409	–145	–119	110	–22	–363	185	61	575	680
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)

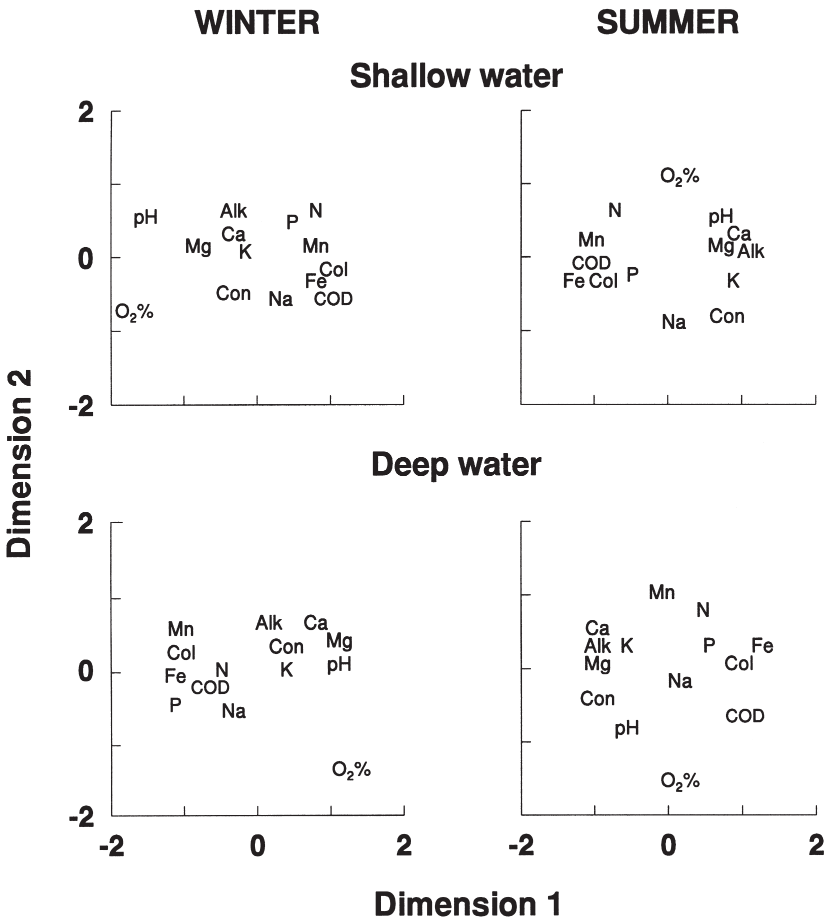

Fig. 2. The relationship between the 14 limnological characters in the two sampling depths and occasions. Strongly associated variables cluster closely in the two-dimensional space. Multidimensional scaling in two dimensions was applied for the correlation data in Table 3. The stress coefficient (S) and proportion of variance explained (R^2) for the four panes are as follows: Winter, shallow water, S = 0.12, R^2 = 0.94; deep water, S = 0.14, R^2 = 0.90; Summer, shallow water, S = 0.07, R^2 = 0.97; deep water, S = 0.11, R^2 = 0.92.

analysis were extended over a suite of $1 - \beta$ values and differing coefficients of determination (Fig. 4). In our calculations for Table 4, there were frequently more than 120 lakes (Table 1). The sample sizes were thus always beyond those needed for detecting reasonable values of r^2 (i.e., those with $r^2 \geq 0.5$; Fig. 4). Consequently, we can conclude that (i) variation in limnological variables, as observed in our lakes, has very little to do with variation in the fish yield, and (ii) had there been such a relationship we certainly would have been able — with this many lakes — to uncover it.

After failing to show strong covariation between the yield and the 14 water quality variables we proceeded as follows. Firstly, for eight limnological variables (Fig. 5) our measure of variability was symmetrically distributed around zero mean; large negative and large positive values indicated high variability. Therefore, we split lakes into two groups: 33% of them around the mean were scored to show low variability, whilst 33% at the low end as well as 33% at the high end were those displaying high variability. Secondly, we further split these groups into lakes with low, medium and high variable level (the class widths were set separately for each variable as 0–33%, 34–66% and 67–100% percentiles). The six groups thus formed encompass the two dimensions of the water quality variation, viz., variable level and variability. For six limnological variables (Fe, Na, Ca, Mn, K, Mg) due to many missing observations (Table 1), we could not score variability, therefore the variable level was classified into three, as above.

For a number of variables. the fish yield tends to increase with the increasing variable level (Figs. 5 and 6). However, the increase was significant in statistical terms for oxygen saturation, conductivity, sodium and potassium. The decreasing fish yield was observed with the increasing

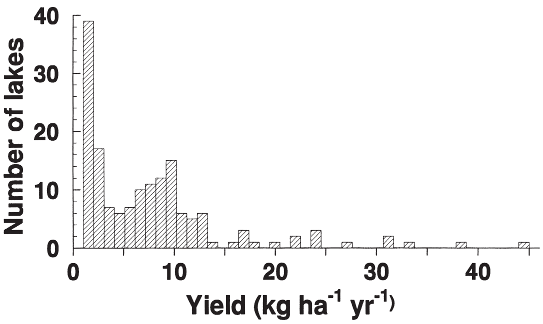

Fig. 3. Frequency distribution of annual fish yield (kg ha^{-1} yr^{-1}) in the 166 lakes studied.

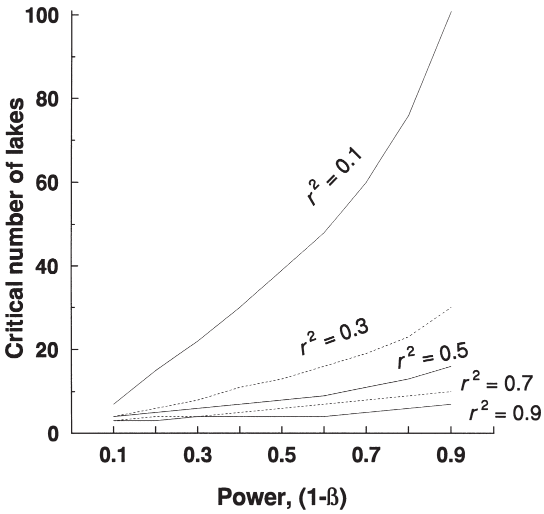

Fig. 4. Sample size curves for different effect sizes (r^2 ranging from 0.1 to 0.9; $\alpha = 0.05$ was applied throughout). Power is defined as $1 - \beta$, where a value of, say, 0.8 would imply that in 80 cases out of 100 one would detect a given coefficient of determination (r^2) with a certain sample size. Here, for example, had there been a limnological variable explaining 90% of variation in the fish yield, one would need, with a power of 0.8, not more than 6 randomly selected lakes to uncover the correlation. Note that with all reasonable values of r^2 the critical sample sizes would be far less than 20 lakes (compare this with the sample sizes, n, as indicated in Table 1).

level of chemical oxygen demand of the lake water and with the increasing nitrogen level (Fig. 5 and 6). It seems that intermediate levels of water colour are those enabling the highest yield (Fig. 5).

Surprisingly, a variable variability did not enter in any case alone as a significant factor in the ANOVA. However, it accounted a fair proportion of the total variance, together with the variable level (but not in the interaction) in a chemical oxygen demand of the lake water (Fig. 5). For most of the limnological variables examined, no clear covariance with the fish yield could be associated (Fig. 5 and 6).

Table 4. Correlation between fish yield (kg ha^{-1} yr^{-1}) and water quality characterising limnological variables in winter and summer samples at shallow and deep water (note that sample sizes vary, see Table 1).

	Winter		Summer	
Variable	Shallow	Deep	Shallow	Deep
O_2%	– 0.035	0.226	– 0.072	– 0.195
Conductivity	0.353	0.313	0.270	0.291
Alkalinity	0.213	0.137	0.275	0.315
pH	0.094	0.342	0.237	0.150
Colour	– 0.089	0.013	– 0.123	0.015
COD	– 0.042	– 0.035	– 0.319	– 0.068
N	– 0.151	– 0.187	– 0.018	– 0.012
P	0.100	– 0.026	– 0.080	0.107
Fe	– 0.031	– 0.198	– 0.071	0.033
Mn	– 0.145	– 0.139	– 0.022	– 0.000
Na	– 0.011	0.049	– 0.142	0.024
K	0.295	0.204	0.244	0.211
Ca	0.175	0.110	0.288	0.359
Mg	0.175	0.164	0.145	0.138

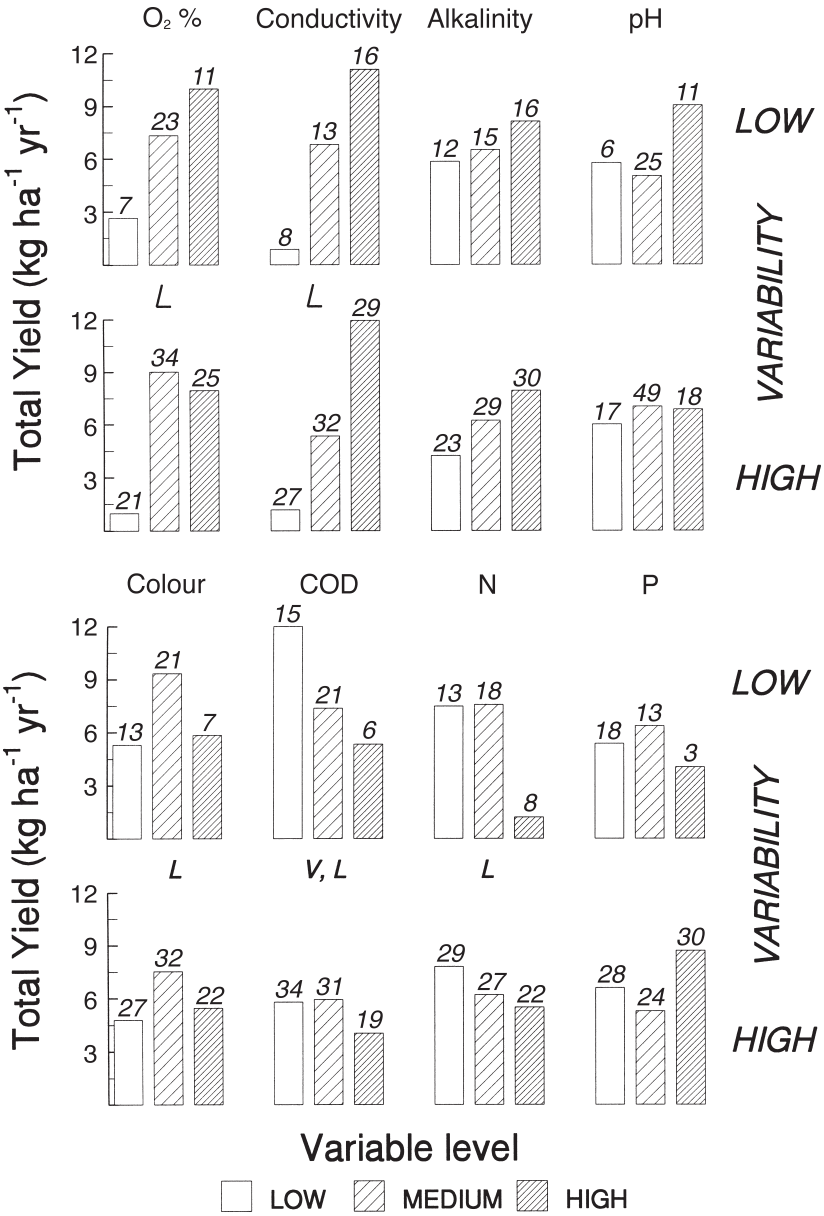

Fig. 5. The fish yield (mean) in the lakes with a different level and variability of eight limnological variables. The variable level is split into three categories and the variability into two categories. The figures above the columns refer to numbers of the lakes in each class. The two italicised letters, *L* (variable level) and *V* (variability of the variable) refer to statistical significances in a two-factorial design. For example, *V, L* with chemical oxygen consumption capacity of the water indicates that both main factors had a significant contribution to variation in fish yield.

3.3. The worst and the best

There was a considerable variation in fish yield in these lakes. A fair number of the lakes give an extremely low yield but there are also lakes with a rather high yield (Fig. 3). Our task here was to characterise the low-end and high-end lakes in terms of water quality variables. For this purpose we selected two groups of lakes, 25 lakes with the lowest yield and 25 lakes with the highest yield. The yield in the two groups averaged 0.40 and 19.65 kg ha^{-1} yr^{-1} (corresponding figures for lake area were 715 and 650 ha, and for the water depth 8 and 11 m). To simplify the presentation of the results, we again selected the shallow-water summer sample as the reference point. Though variable levels in different seasons and from different depths differed (Fig. 1), there was still a relatively strong covariation in their values (Table 2). Furthermore, we also checked the results of this analy-

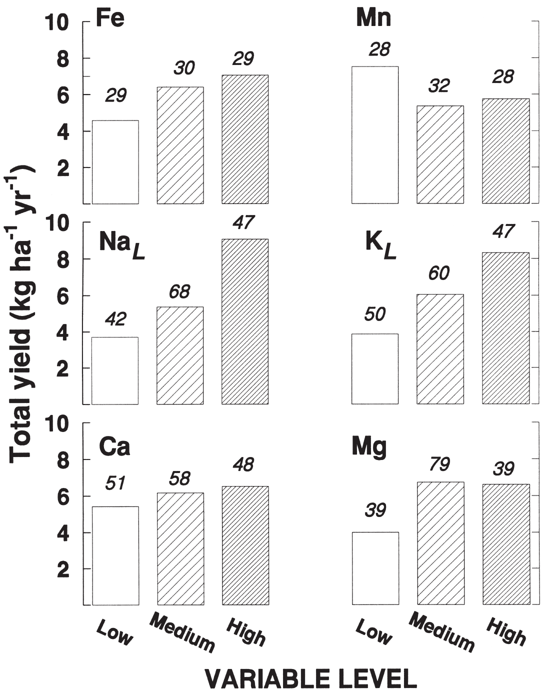

Fig. 6. Total fish yield (mean) in lakes with low, medium and high levels of six elements. Variables are split into the three categories. The figures above the columns refer to numbers of lakes in each class (cf. Table 1). Statistical significances are shown with the italicised *L* for natrium and potassium.

sis with the other samples. We got results generally agreeing with each other. In the comparisons, we used Mann-Whitney *U*-test (for Fe and Mn sample sizes were 18 lakes in both groups).

We found that, in most cases, the water quality variables tended to score somewhat differing levels in the two groups of the lakes (Fig. 7). However, variation was substantial, and therefore there were only a few statistically significant differences between the two groups of lakes. Those were found in oxygen saturation, conductivity and pH, all scoring higher levels in the lakes with a high yield, while iron in the high-yield lakes was much lower than in the low-yield lakes (Fig. 7).

4. Discussion

The view that water quality affects fish production reflects the underlying hypothesis that fish populations are constrained by some external features of their habitat, i.e., density independent factors. For such a view, water quality variation presents a special kind of a problem. A lake which at some point in time is very favourable for population growth may at some other time be almost unsuitable. It is probably with this in mind that Ryder (1965, 1982) included the requirement of many years catch statistics in the use of the MEI-index. However, there is no reason to assume that two lakes with the same mean water quality values, but one with double the variation of the other, should have the same fish production. A water quality variation is featured by two major factors: the level around which the variation occurs and the magnitude of the variation. Both factors will affect the extreme conditions under which fish populations will have to survive. In the present data set, the most variation in water quality within a lake was accounted for the season. This variation is problematic for the fisheries manager as different sampling occasions will produce greatly varying results.

That variation in water quality affects an annual yield in northern Finnish lakes is obvious. However, it strikes us — as it has always striken (Ranta & Lindström 1989, 1990, 1993ab, Ranta *et al*. 1992ab) — that, despite the great variation in limnological variables among the lakes, this variation is very weakly manifested in the variation in a fish yield. Only after grouping together lakes with close variable levels, we were able to demonstrate that a fish yield and water quality had been coupled together. Especially, variables such as an oxygen concentration, conductivity, water colour, nitrogen and sodium concentrations seem to covary to some extent with a fish yield. Also, when the extremes of the fish yield variation were examined, viz., the low-yield and high-yield lakes, we were able to demonstrate differences in water quality between lakes of the two types. Thus, there are no doubts that the total fish yield (kg ha^{-1} yr^{-1}), pooled over all species, is linked to a lake water quality.

An interesting feature of the variables that covary with the fish yield is that they also covary with each other in a consistent way. That is, the correlation coefficients for these variables tend to be fairly high and what perhaps is more important, they correlate in the same direction for different water depths and seasons (*see* Table 3).

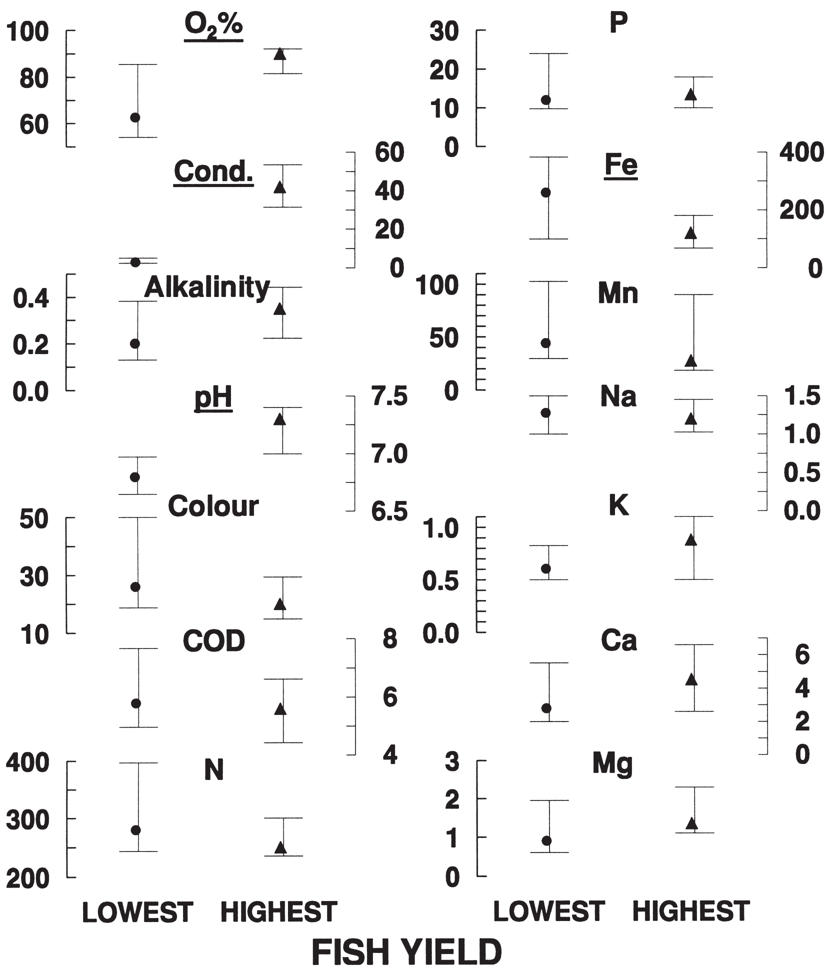

Fig. 7. The level (median with lower and upper quartile) of the 14 water quality variables in 25 lakes with the lowest yield and in 25 lakes with the highest yield. The data refer to shallow-water summer samples. Underlined variable names indicate statistically significant differences between the two lake types.

Conductivity, which is the best correlate of the fish yield, also showed a strong correlation with itself for the different samples. Fish populations certainly cannot track very short term changes in environmental factors but probably reflect a compromise of long-term conditions, and therefore, it is unlikely that variables that show large variations should be very good correlates of the fish production. This may, however, not apply to species which migrate between waterbodies. An environmental variable that is a good fisheries management tool should therefore be fairly constant within a lake and not vary for example between seasons or water depths. Alternatives would be to search for the critical "water quality bottlenecks" that constrain fish populations.

The results of the above analyses are, however, not very encouraging. Especially, if one seeks a predictive tool which could be used to assess fish yields in lakes relying on their water quality. This is a task that has turned out to be almost impossible with data on Finnish lakes (Lindström & Ranta 1988, Ranta & Lindström 1989, Ranta *et al.* 1992ab).

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