Relationship of Salmonine Production to Lake Trophic Status and Temperature

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Data on trout, char, and salmon from lakes in several geographic areas indicate that salmonine production (P, kilograms per hectare per year) increases with total phosphorus concentration (TP, micrograms per litre) as log_{10}P = 0.47 + 0.95 log_{10}TP (r^2 = 0.61). A positive relationship was also found between P and phytoplankton productivity and this relationship suggests that energy transfer efficiencies from phytoplankton to salmonines are reduced in eutrophic lakes. Lake area and mean depth had no significant statistical effect on P but salmonine production was significantly lower in warmer climates. Analysis of these data suggests that projected global increases in air temperatures could lead to about 50% reductions in salmonine production and yield in the north temperate zone.

Evidence is accumulating that nutrients ultimately control the rate of fish production in lakes (Eggers et al. 1978; Mills 1985; McQueen et al. 1986; Mills et al. 1987; Stockner 1987; Downing et al. 1990), especially in lakes with short trophic pathways (Stockner 1987). It has been frequently observed that increases in anthropogenic phosphorus and nitrogen loading to lakes increase their general productivity (see Vollenweider 1974). Fertilizer has been used to maintain high rates of production in aquaculture (Moav et al. 1977; Knud-Hansen et al. 1991). Some have attempted, therefore, to formulate equations to predict fish yield (Hrbáček 1969), fish biomass (Hanson and Leggett 1982), or fish community production (Downing et al. 1990) in lakes using variables related to autotrophic producers, such as total phosphorus concentration or primary production. Models to predict the production of species, or groups of species, unfortunately usually require knowledge of the standing biomass of fish populations (Downing and Plante 1993), data that are costly to obtain.

Because salmonine fisheries are of special economic importance, the prospect of enhancing their production through nutrient addition is appealing. Indeed, the idea that phosphorus is the primary limiting nutrient in lake ecosystems (Wetzel 1983), and the observation that the growth of fish increases with food supply (Brocksen et al. 1970), has prompted some to experiment with phosphorus addition to oligotrophic lakes as a means of enhancing the production of salmon fisheries (LeBrasseur et al. 1978; Hyatt and Stockner 1985; Stockner 1987). The success of these programs (Stockner 1987) suggests that lake fertilization may be a generally applicable method of increasing the quality of recreational and commercial salmonine fisheries. This approach may not be generally applicable, however, considering that several other factors such as recruitment (Colby et al. 1972; Burgner 1987), allochthonous energy inputs (e.g., Hartman and Burgner 1972), and fish community structure (Hatch and Webster 1961; Colby et al. 1972; Hartman and Burgner 1972; O’Connor and Power 1973) are known to limit salmonine populations. Recently, Stockner (1987) has suggested that analysis of a broad range of data on salmonine production measurements might reveal general empirical relationships between trophic status and productivity. The purpose of this study is to test the hypothesis that there is a general positive relationship between lake trophic status and salmon, char, and trout production. In addition, we test the hypothesis that salmonine production is correlated with lake morphometry and climate.

Methods

Data on the annual production of salmonine populations were obtained from the published literature. Estimates of production were usually calculated using the Allen curve and instantaneous growth methods (Downing 1984). Because we sought data...
reflecting equilibrium conditions, we omitted from consideration populations supported by stocking (e.g. Hatch and Webster 1961; Miura et al. 1976), and populations intentionally over-exploited (Langeland 1986). Annual average phosphorus concentration in the water column (TP, µg·L⁻¹), phytoplankton productivity (PP, g C·m⁻²·yr⁻¹), mean depth (Z, m), lake area (A, ha), and annual mean air temperature (T, °C). Fish production values include all ages in Char Lake and Øvre Heimdalsvatn, 0+ to 2+ juvenile salmon in Lake Washington and Dalnee, 1+ trout and older in the Turkey Lakes and Wishart Lake, and ages 0 to 5+ for Loch Leven. Data sources: Efford (1972); Krogius et al. (1972); Morgan (1972); Rigler (1972, 1975, 1978); Wali et al. (1972); Hall and Hyatt (1974); Thorpe (1974); Kloster (1978); Lien (1978, 1981); Tangen and Brettum (1978); Kelso (1985); J.R.M. Kelso (Department of Fisheries and Oceans, Sault Ste. Marie, personal communication); Lam et al. (1986).

Results and Discussion

Production data were obtained for 10 salmonine populations from nine lakes in diverse geographical areas, representing a wide range of trophic status. Lakes included a range of trophic states from oligotrophic to eutrophic (Wetzel 1983) (Table 1). Salmonine production estimates were obtained for lakes ranging from 47°N to the high Arctic, in North America, Europe, and Asia. Populations were comprised of trout, char, juvenile salmon, and land-locked salmon (Table 1).

Total Phosphorus and Phytoplankton Production

Salmonine production (P) was significantly correlated ($r^2 = 0.61$) with total phosphorus concentration (TP; Fig. 1). This correlation is similar to that found for complete fish community production by Downing et al. (1990). Such a correlation for individual salmonine populations is surprising because correlations between lake trophic status and population production in other taxonomic groups are rarely very strong unless allowance is first made for the biomass of the fish populations under consideration (Downing and Plante 1993). The link between factors influencing primary production and salmonine populations may be stronger than that for other species because food chains tend to be simple in lakes in which salmonines dominate. The fish populations in the lakes examined here consist mainly of planktivores and benthivores. According to Fig. 1, an increase in total phosphorus from 10 to 100 µg·L⁻¹ corresponds to about a 10-fold increase in salmonine production.

**Table 1.** Data on the annual production of trout, char, and salmon populations (P, kg·ha⁻¹·yr⁻¹), total phosphorus concentration in the water column (TP, µg·L⁻¹), phytoplankton productivity (PP, g C·m⁻²·yr⁻¹), mean depth (Z, m), lake area (A, ha), and annual mean air temperature (T, °C). Fish production values include all ages in Char Lake and Øvre Heimdalsvatn, 0+ to 2+ juvenile salmon in Lake Washington and Dalnee, 1+ trout and older in the Turkey Lakes and Wishart Lake, and ages 0 to 5+ for Loch Leven. Data sources: Efford (1972); Krogius et al. (1972); Morgan (1972); Rigler (1972, 1975, 1978); Wali et al. (1972); Hall and Hyatt (1974); Thorpe (1974); Kloster (1978); Lien (1978, 1981); Tangen and Brettum (1978); Kelso (1985); J.R.M. Kelso (Department of Fisheries and Oceans, Sault Ste. Marie, personal communication); Lam et al. (1986).

<table>
<thead>
<tr>
<th>Lake</th>
<th>Population</th>
<th>P</th>
<th>TP</th>
<th>PP</th>
<th>Z</th>
<th>A</th>
<th>T</th>
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<td>31.5</td>
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<tr>
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<td>91.5</td>
<td>487</td>
<td>31.5</td>
<td>136</td>
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<tr>
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<td>5</td>
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**Fig. 1.** Relationship between annual production of salmonine populations and total phosphorus concentrations in lakes. The solid line represents the least squares regression equation and the broken lines represent the 95% confidence intervals of predicted means. The residual mean square of the regression equation is 0.30. Lake names appear near each observation.
Phytoplankton production, closely correlated with total phosphorus concentration (e.g., Brylinsky 1980), is also well correlated with salmonine production ($r^2 = 0.68$; Fig. 2). Such a strong correlation between phytoplankton production and fish production, regardless of fish standing biomass or lake community structure, underscores the suggestion that lake ecosystems can be controlled by primary producers (McQueen et al. 1986). Analysis of the relationship in Fig. 2 (assuming 1 g C = 10 g fresh mass; Oglesby 1977), however, suggests that the conversion efficiency of phytoplankton into salmonine production declines radically from about 1% transfer efficiency in ultraoligotrophic lakes to <0.2% in eutrophic lakes. These results agree with those of Downing et al. (1990) who found that ratios of fish community production to primary production fall as low as 0.002% in hypereutrophic lakes. Such decreases in the transfer of primary production to fish may be due, in part, to the fact that the fraction of phytoplankton biomass that can be ingested by zooplankton declines rapidly above 30 µg TP-L$^{-1}$ (Watson et al. 1992). Our analysis suggests that the transfer of energy from phytoplankton to salmonine production is 10 times more efficient in oligotrophic ecosystems than in eutrophic ones.

Our results should not be interpreted to suggest that there can be unlimited increases in salmonine production under eutrophic conditions. Several studies of the effect of eutrophication on salmonid populations were made during the 1970’s (see Colby et al. 1972). These studies suggest that at the onset of eutrophication, salmonid growth generally increases, but the progressive alteration of the spawning areas and competition with other species better adapted to mesotrophic lakes tend to decrease the abundance of salmonid populations over the long term. Equations relating salmonine production and phosphorus or phytoplankton production (e.g., Fig. 1 and 2) probably indicate the potential production of salmonine populations in a lake of a given trophic status. Whether or not this production could be achieved by a salmonine population over long periods depends on other factors influencing the populations. If nutrient addition is to be used as a salmonine production enhancement or management tool, Fig. 1 and 2 represent the potential salmonine production but may not always predict long-term changes in salmonine population production following eutrophication.

Other Factors Related to Salmonine Production

Although it has been suggested that shallow lakes generally support more productive fisheries (e.g., Matuszek 1978; Schlesinger and Regier 1982) and that indices of fish productivity increase or decrease with lake size (e.g., Hayes and Anthony 1964), we found no such correlations for salmonine populations. Correlation analyses of the residuals from Fig. 1 and 2 show that neither lake area nor mean depth was significantly correlated ($p > 0.05$) with salmonine production after accounting for the effects of total phosphorus ($p = 0.21, 0.81$) or phytoplankton production ($p = 0.13, 0.54$). Within the range of lakes studied here, lake depth and area seem to have little influence on salmonine production. Latitudes of lakes in our study range only from 47 to 74°N and, within this range, even shallow lakes like Wishart or Marion probably have temperatures low enough to support healthy salmonine populations. At lower latitudes where surface waters would be warmer (Straškraba 1980), however, lake morphometry may be an important factor mediating salmonine production.

Trout, salmon, and char are all known to be coldwater species (Scott and Crossman 1973); thus, salmonine production should be expected to decline with increased water temperature. Air temperature is probably closely correlated with water temperature in these lakes except in the extremely cold Char Lake where air temperature would grossly underestimate the
annual mean temperature experienced by the fish. If Char Lake is excluded from the data set, there is a negative correlation ($p = 0.03$) between the residuals of Fig. 1 and annual mean air temperature (Fig. 3). A multiple regression of $P$ as a function of TP and $T$ yields the equation \[
\log_{10} P = 0.20 + 1.11 \log_{10} TP - 1.43 \log_{10} T
\] which has an improved $r^2$ (from 0.61 to 0.83) and a greatly reduced residual mean squared error (from 0.30 to 0.16) over the comparable statistics calculated in Fig. 1. This analysis indicates that salmonine production is much reduced in warmer regions. This result implies that global warming would decrease salmonine production. In temperate and cold-temperate countries where salmonine populations are currently found, the two-fold increase in carbon dioxide predicted by 2050 (Nuttle and Linton 1992) is expected to result in an increase in the annual mean temperature of 4–8°C (Washington and Parkinson 1986; Mitchell et al. 1990). Such differences in climate are associated with reductions in salmonine production and yields of around 50% following the trend in Fig. 3. This prediction is particularly grave for northern regions that rely heavily upon salmonines for recreational and economic gains.

Acknowledgements

This research was supported by an operating grant to J.A. Downing from the Natural Sciences and Engineering Research Council of Canada (NSERC), a team grant from the Ministry of Education of the Province of Quebec, an NSERC scholarship to Mario Henri who performed some of the initial search for data, a CAFIR grant from the Université de Montréal, and the support of OMC Canada. We would like to especially thank J.R.M. Kelso who generously supplied us with unpublished data.

References


