

Production of Fish Populations in Lakes¹

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Biological production estimates of 100 fish populations from 38 lakes worldwide were gathered from the literature. The relationship between the annual production of fish populations (P , kilograms per hectare per year), annual mean standing biomass (B , kilograms per hectare), and maximum individual body mass (W , grams) was approximately $\log_{10}P = 0.32 + 0.94 \log_{10}B - 0.17 \log_{10}W$ ($R^2 = 0.84$). This relationship is similar to one observed for lotic invertebrate populations and shows that P declines with W . Major axis regression indicated that the $P/B:W$ relationship had an exponent similar to that predicted by allometric theory. The residuals from this multivariate equation suggest that fish production is positively correlated with temperature, lake phosphorus concentration, chlorophyll a concentration, primary production, and with pH. The results suggest a general bottom-up control of lake ecosystem components. The morphoedaphic index is not a good predictor of the production of fish populations. Assuming that sustainable yield is about 10% of production, sustainable yield would be less than 15% of the standing biomass for the majority of fish populations analyzed. Exploited populations were found to be about 70% more productive, on average, than unexploited populations of the same standing biomass and body-mass.

On a relevé, dans les ouvrages publiés, des estimations de la production de 100 populations de poissons vivant dans 38 différents lacs à travers le monde. La relation entre la production annuelle des populations de poissons (P , kilogrammes par hectare par année) la biomasse annuelle moyenne (B , kilogrammes par hectare) et la masse maximale individuelle (W , grammes) est décrite par l'équation suivante : $\log_{10}P = 0,32 + 0,94 \log_{10}B - 0,17 \log_{10}W$ ($R^2 = 0,84$). Cette équation est similaire à celle obtenue pour les populations d'invertébrés lacustres. Elle démontre que P diminue avec W . L'axe majeur entre P/B et W donne un exposant similaire à celui prédit par la théorie allométrique. Les résidus de cette équation suggèrent que la production est positivement corrélée avec la température, la concentration en phosphore total, la concentration en chlorophylle a , la production primaire et avec le pH. Les résultats suggèrent un contrôle des composantes de l'écosystème par la disponibilité en nutriments. L'indice morpho-édaphique n'est pas un bon prédicteur de la production des populations de poissons. En supposant que le rendement de pêche équilibré soit 10 % de la production annuelle d'une population, ce rendement équilibré serait moins que 15 % de la biomasse présente pour la majorité des populations analysées. On trouve que les populations exploitées sont d'environ 70% plus productives que les populations non-exploitées.

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Freshwater fish populations are of major ecological and economic importance. Fish play a major ecological role in structuring the benthic and zooplanktonic invertebrate communities. For example, recent research shows that the presence and relative abundance of fish populations with various trophic characteristics can alter zooplankton size structure and abundance (Benndorf et al. 1984; McQueen et al. 1986), nutrient cycling (Bartell and Kitchell 1978; Mazumder et al. 1988), algal community structure (Mazumder et al. 1988), water clarity (McQueen et al. 1990), and even the heat budgets of lakes (Mazumder et al. 1990). Economically, sport and commercial freshwater fisheries generate about \$2 billion annually in Canada alone (Pearse 1988) and sportfishing's social value lies in its role as a frequently enjoyed recreational experience.

At equilibrium, unexploited fish stocks produce exactly enough biomass to balance natural mortality. One of the principal aims of contemporary fisheries management is to balance the rate of renewal of fish populations as closely as possible

with the sum of natural and fishing mortality (e.g. Schaefer 1968). The renewal of fish biomass is provided by production, which is the "amount of tissue elaborated per unit time per unit area, regardless of its fate" (Clarke 1946). It is thus of interest to fisheries ecologists to know how fish production varies among ecosystems and populations. A first step toward this goal is to determine which characteristics of ecosystems have the greatest impact on this rate of renewal.

Until recently, confusion in this field was fostered by a proliferation of models using differing indices of fish production (reviewed by Downing et al. 1990). Not surprisingly, these models often yielded widely variable, and sometimes contradictory, results, probably in part because models dealt with such disparate measures of fish production as commercial fish yield, sportfishing yield, long- or short-term average catch, net growth increment, fish catch, creel censuses, etc. (Downing et al. 1990). Variables that have been found to be correlated with indices of "fish production" in these studies are lake area, mean depth, alkalinity, total dissolved solids, total nitrogen, total phosphorus, or chlorophyll a concentration of the water column, primary productivity, benthos abundance, air temperature, and fishing effort. In a recent study of fish community

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production in lakes, Downing et al. (1990) followed the suggestion of Oglesby (1977) in establishing fish production models from rigorously defined and repeatable measurements of biological fish production rather than rough indices of catch. They found, in a study of 23 fish communities in 20 lakes covering a wide range of geographical areas and trophic status, that the production of entire fish communities was closely correlated with annual phytoplankton production, mean total phosphorus concentration, and annual average fish standing stock.

Although Downing et al.'s (1990) analysis makes predictions about the rate of energy transfer between trophic levels in lakes of differing trophic status, most ecologists and fisheries managers are more interested in the production of specific populations of central trophic, economic, or recreational importance. Some analyses have been made of the biological production of other aquatic faunae, most notably zooplanktonic and benthic invertebrates in lakes (Plante and Downing 1989) and streams (Morin and Bourassa 1992), but no broad comparative study has been made of the production of fish populations. The most complete analyses of fish population production to date have been those of Banse and Mosher (1980) and Dickie et al. (1987) that relate the production to biomass ratio (P/B) of fish populations to body-mass. Neither of these analyses examines the influence of ecosystem trophic status or health on fish production, and both are based on small data bases, comparing only 11 and 8 populations, respectively.

Many factors have been hypothesized to influence the productivity of aquatic populations (reviewed by Morgan et al. 1980; Downing 1984), but quantitative tests of real relationships between field fish production estimates and population and environmental characteristics are lacking. Ecologists have observed, however, a positive relationship between production and population biomass (e.g. Waters 1977). If this relationship holds for fish populations, then factors affecting fish standing stock should also have an impact on fish production. Rates of growth decrease and longevity increases with body-mass (Peters 1983); therefore, populations of larger fish should be less productive per unit biomass than small ones. The literature contains some empirical support for this expectation, both in fish (Banse and Mosher 1980; Dickie et al. 1987) and in other aquatic populations (Plante and Downing 1989). The positive effect of temperature on fish production can be inferred from its influence on growth rates (e.g. Goldspink 1979; Quiros 1990) and egg production and development time (e.g. Holčík 1970). In addition, factors mediating food availability to fish populations such as lake primary production and trophic status (Mills 1985; Kelso 1988), pH (Rask 1984), alkalinity (Saunders and Power 1970; Kelso 1988), morphometry (Saunders and Power 1970; Kelso 1988), and climate (Efford 1972; Craig 1980; Rask and Arvola 1985) should also influence the productivity of fish populations.

No broad general synthesis of fish population production rates or analysis of the combined influence of fish population characteristics and environmental conditions on fish population production has yet been published. So far, the multivariate relationship between fish population production and eutrophication, lake morphometry, geography, and climate has not been examined. Such knowledge would be of theoretical importance in identifying the biological and physical characteristics most closely correlated with production, and of practical importance in improving knowledge about factors influencing the rates of renewal of important freshwater fish populations.

This research draws together existing measurements of fish population production to find how the annual production of fish

populations is related to their population biomass and body-mass. We also test several hypotheses regarding the influence of lake trophic status and primary production, physical characteristics of the environment, water chemistry, and lake morphometry on rates of fish population production.

Methods

Data on the annual production and standing biomass of fish populations were gleaned from an exhaustive survey of the primary ecological literature published since 1969. We did not consider data on populations supported by stocking, populations stocked every year, or production rates calculated excluding age classes <3 yr to be sufficiently accurate measurements of natural fish production to be included in the analysis. Production and biomass data are expressed in fresh mass. All estimates were actual measures of biological production (as opposed to catch or yield) and were mostly estimated using cohort, Allen curve, or instantaneous growth methods (Chapman 1971; Rigler and Downing 1984). Conversions from energetic or dry mass units were made using published constants (Cummins and Wuycheck 1971). Body-size estimates of individuals in the populations were collected as the maximum individual body-mass (W , grams fresh mass) and were usually determined as the upper limit of largest length class included in production calculations. For a few populations, W was estimated from data on similar species in other lakes or from Scott and Crossman (1973). Data on biotic and abiotic characteristics of lakes were derived from published works or in some cases were obtained through direct communication with the authors of the production studies. Morphometric characteristics collected were lake area and mean and maximum depth. Lake productivity indicators were phytoplankton productivity, total phosphorus, total nitrogen, and chlorophyll a concentrations in the water column, and conductivity (as a measure of total ion concentration). Chlorophyll, total nitrogen, and total phosphorus concentrations were collected as annual averages. The concentration of total dissolved solids of several lakes were estimated from conductivity measurements (Schlesinger and McCombie 1983) in order to permit the calculation of the morphoedaphic index (Ryder 1965). Annual mean air temperature, which is closely correlated with surface water temperature (Straškraba 1980), was used instead of water temperature (see also Schlesinger and Regier 1982) because of its greater availability in climatic reports (Wernstedt 1972). Exploitation of populations was simply recorded as presence or absence of fishing activity in lakes. The trophic level of fish populations (i.e. planktivore, benthivore) was determined using information presented in data sources wherever possible or from the diet of similar species in other lakes. Latitude and altitude were also noted where available.

Analyses of relationships between fish population production, population biomass, and body-mass were performed using simple and multiple regression (Gujarati 1978; Draper and Smith 1981) after logarithmic transformation, which stabilized the variance, linearized the responses, and normalized the residuals. The validity of each regression analysis reported below was verified by extensive residual analysis (Draper and Smith 1981). Because data on lake characteristics were rarer than data on fish standing stock and body-mass, analyses of the influence of trophic, physical, and chemical characteristics of lakes were performed by analyzing the residuals of multiple regression equations (Downing et al. 1990), following the standard protocol of Draper and Smith (1981). Analysis of var-

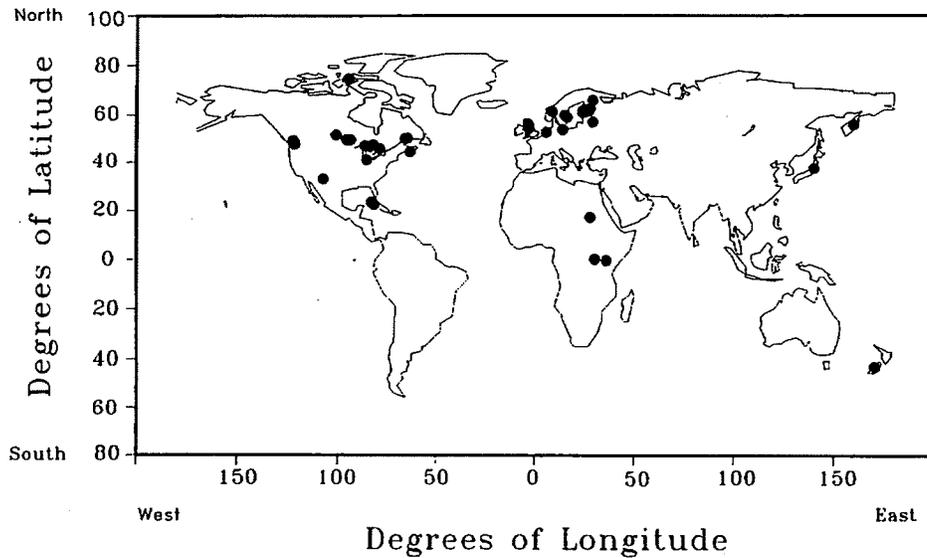


FIG. 1. Location of 38 lakes for which fish population production data were obtained from the published literature. Only 32 different points can be distinguished because many of the Scandinavian lakes are closely spaced.

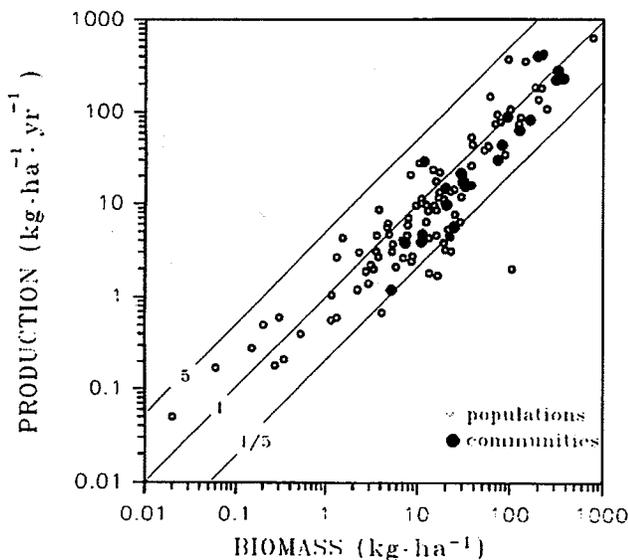


FIG. 2. Relationship between the annual production and annual mean standing biomass of fish populations (data from this study) and communities (data from Downing et al. 1990). The lines represent P/B ratios of 0.2, 1, and 5.

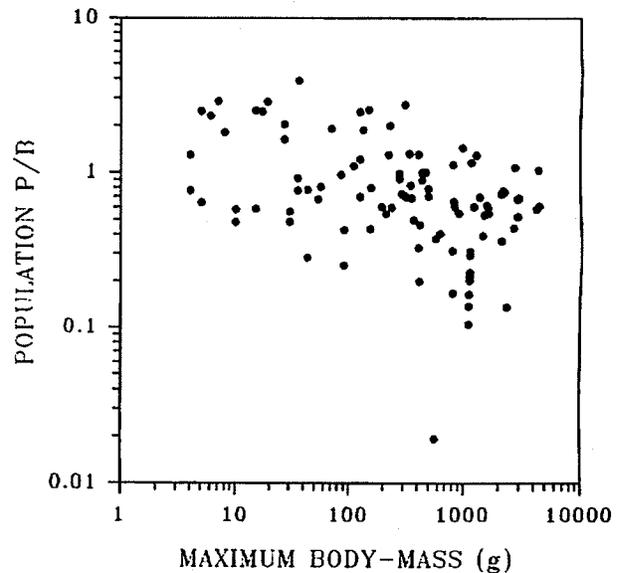


FIG. 3. Relationship between P/B calculated from Table 1 and the body-mass of the largest size class in the populations. The outlying point is the arctic Char Lake.

iance of the residuals of multiple regression analyses was used to test for the effect of trophic level and exploitation.

Results and Discussion

Fish production data were obtained for 100 populations (Table 1) from 38 lakes and reservoirs (Table 2) in a wide range of geographic locations (Fig. 1) representing oligotrophic to hypereutrophic lakes in tropical to temperate climates (Table 2). This is nearly 10 times greater than the number of production estimates used in previous studies of fish population production (cf. Banse and Mosher 1980). Fish species spanned a wide range of sizes and trophic levels (Table 1). Populations varied

in mean annual standing stock from $0.02 \text{ kg}\cdot\text{ha}^{-1}$ for *Micrastes acutidens* in the tropical Lake Kariba (Mahon and Balon 1977) to $771 \text{ kg}\cdot\text{ha}^{-1}$ for *Lepomis macrochirus* in the small, eutrophic, temperate Wyland Lake (Gerking 1962; Mahon 1976).

Biomass and Body-mass

The production of fish populations (P , kilograms per hectare per year) was most strongly correlated with the standing biomass (B , kilograms per hectare) and the body-mass of the largest size class of fish in the population (W , grams):

$$(1) \log_{10}P = 0.32 + 0.94 \log_{10}B - 0.17 \log_{10}W$$

TABLE 1. Production (P , $\text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), biomass (B , $\text{kg}\cdot\text{ha}^{-1}$), and maximum individual mass (W , g) of fish population data drawn from the literature. GR indicates the trophic group (1 = planktivore, 2 = benthivore, 3 = piscivore, 4 = planktivore and benthivore). GR or W values in italics indicate that trophic status or body-mass data were inferred from populations in other lakes. Values of P , B , and W are rounded. Data sources are listed in Table 2.

Lake	Fish species	GR	P	B	W	
226 NE	<i>Coregonus clupeaformis</i> , 1973	1	4.6	15.7	1127	
	<i>Coregonus clupeaformis</i> , 1974	1	6.4	28.3	1127	
	<i>Coregonus clupeaformis</i> , 1975	1	7.7	24.8	1127	
	<i>Coregonus clupeaformis</i> , 1976	1	4.6	21.5	1127	
226 SW	<i>Coregonus clupeaformis</i> , 1973	1	3.8	18.8	1127	
	<i>Coregonus clupeaformis</i> , 1974	1	3.1	22.6	1127	
	<i>Coregonus clupeaformis</i> , 1975	1	3.2	19.5	1127	
	<i>Coregonus clupeaformis</i> , 1976	1	1.7	16.2	1127	
Alinen Mustajärvi	<i>Coregonus muksun</i>	1	11.8	29.1	620	
	<i>Perca fluviatilis</i>	2	15.9	37.0	90	
Big Indian	<i>Esox lucius</i>	3	2.6	6.9	571	
	<i>Salvelinus fontinalis</i>	3	1.9	2.7	320	
Big Turkey	<i>Salvelinus fontinalis</i>	2	0.6	1.1	367	
	<i>Catostomus commersoni</i>	2	0.7	4.1	817	
Bill	<i>Salvelinus fontinalis</i>	3	0.2	0.3	1600	
Botjärn	<i>Perca fluviatilis</i>	3	16.6	29.4	30	
Char	<i>Salvelinus alpinus</i>	1	2.0	104.0	570	
Dalnee	<i>Gasterosteus aculeatus</i>	1	22.0	17.0	4	
	<i>Oncorhynchus nerka</i>	1	350.0	143.0	125	
	<i>Salvelinus malma</i>	3	26.0	37.0	500	
Demenets	<i>Carassius carassius</i>	4	4.6	7.6	841	
	<i>Tinca tinca</i>	2	2.0	3.3	1230	
	<i>Perca fluviatilis</i>	3	78.2	78.0	475	
	<i>Rutilus rutilus</i>	2	107.9	248.0	152	
	<i>Acerina cernua</i>	2	23.5	14.4	27	
	<i>Esox lucius</i>	3	3.7	5.3	1386	
	<i>Scardinius erythrophthalmus</i>	2	8.6	15.7	208	
	<i>Ichtiobus bubalus</i> , 1966	4	38.5	51.1	2252	
Elephant Butte	<i>Carpoides carpio</i> , 1967	—	2.7	3.7	2146	
	<i>Cyprinus carpio</i> , 1968	2	6.1	4.8	1310	
	<i>Tilapia nilotica</i>	1	53.3	37.0	1000	
George	<i>Perca fluviatilis</i>	3	5.9	7.7	35	
Haukilampi	<i>Coregonus pilea</i>	1	10.2	11.2	280	
Horkkajärvi	<i>Perca fluviatilis</i>	4	5.3	21.0	90	
	<i>Perca fluviatilis</i>	2	22.2	28.7	43	
Iso-Mustajärvi	<i>Perca fluviatilis</i>	4	2.4	8.5	43	
Karhujärvi	<i>Schilbe mystus</i>	3	0.2	0.3	53	
Kariba	<i>Hippopotamyrus discorhynchus</i>	—	424.7	227.1	133	
	<i>Heterobranchus longifilis</i>	—	3.1	5.2	4200	
	<i>Haplochromis darlingi</i>	—	8.7	3.8	6	
	<i>Synodontis nebulosus</i>	—	1.1	1.1	35	
	<i>Labeo altivelis</i>	—	4.1	6.8	1630	
	<i>Hydrocynus vittatus</i>	—	20.6	30.2	3000	
	<i>Clarias gariepinus</i>	—	15.7	35.5	2700	
	<i>Tilapia rendalli</i>	1	44.0	38.1	1180	
	<i>Sarotherodon mossambicus</i>	—	178.5	215.7	350	
	<i>Eutropius depressirostris</i>	3	4.7	4.9	85	
	<i>Alestes lateralis</i>	3	366.9	94.8	36	
	<i>Mormyrus longirostris</i>	2	6.4	12.3	2900	
	<i>Sargochromis codringtoni</i>	—	9.6	9.6	440	
	<i>Synodontis zambezensis</i>	—	7.1	7.9	440	
	<i>Micralestes acutidens</i>	2	0.1	0.02	5	
	<i>Mormyrops deliciosus</i>	3	16.3	30.4	1500	
	<i>Malapterurus electricus</i>	—	107.4	99.6	2800	
	<i>Marcusenius macrolepidotus</i>	—	4.6	3.5	222	
	Kiutajärvi	<i>Perca fluviatilis</i>	3	11.2	18.7	235
		<i>Rutilus rutilus</i>	4	4.3	13.1	400
Konnevesi	<i>Phoxinus phoxinus</i>	4	9.6	15.0	5	
	<i>Nemacheilus barbatulus</i>	—	14.3	124.4	15	
Laluisa	<i>Cichlasoma tetracanthus</i>	3	8.4	12.9	830	
	<i>Lepomis macrochirus</i>	1	181.4	184.0	278	
	<i>Micropterus salmoides</i>	3	87.1	128.8	2923	
Little Turkey	<i>Salvelinus fontinalis</i>	3	1.2	2.2	913	
	<i>Catostomus commersoni</i>	2	2.7	8.7	794	
Loch Leven	<i>Salmo trutta</i>	3	17.5	15.6	820	
	<i>Perca fluviatilis</i>	3	27.9	10.2	310	

TABLE 1. (Concluded)

Lake	Fish species	GR	P	B	W
Marion	<i>Salmo gairdneri</i>	3	9.8	12.3	156
	<i>Oncorhynchus nerka</i>	1	11.6	16.6	125
Matamek	<i>Salvelinus fontinalis</i>	3	2.2	3.1	309
Nakuru	<i>Sarotherodon alcalicum</i>	1	38.6	15.7	17
Øvre Heimdalsvatn	<i>Salmo trutta</i>	4	13.3	16.9	500
	<i>Phoxinus phoxinus</i>	4	1.4	2.9	10
Red Deer	<i>Semotilus atromaculatus</i>	1	0.5	0.2	15
	<i>Pimephalus promelas</i>	4	4.3	1.5	7
	<i>Salvelinus fontinalis</i>	2	0.6	0.3	229
	<i>Notemigonus crysoleucas</i>	1	0.2	0.1	19
	<i>Perca flavescens</i>	2	20.7	8.2	150
	<i>Semotilus margarita</i>	1	2.7	1.3	27
Sabanilla	<i>Lepomis macrochirus</i>	1	135.8	198.3	355
	<i>Cichlasoma tetracanthus</i>	3	41.7	57.2	291
	<i>Micropterus salmoides</i>	3	43.0	56.2	2217
Small Spectacles	<i>Philypnodon breviceps</i>	1	397.8	219.8	8
Tatsu-numa	<i>Moroco steindachneri</i>	4	18.0	31.0	10
Tjeukemeer	<i>Rutilus rutilus</i> , 1967-68	4	94.6	71.9	340
Tjeukemeer	<i>Abramis brama</i> , 1969	4	34.3	86.9	1450
Vitalampa	<i>Perca fluviatilis</i>	1	9.8	20.2	30
Warniak	<i>Esox lucius</i> , 1969	3	13.7	22.4	4425
Washington	<i>Esox lucius</i> , 1970	3	11.3	10.9	4445
	<i>Perca flavescens</i>	3	0.6	1.3	415
	<i>Gasterosteus aculeatus</i>	1	0.4	0.5	4
	<i>Spirinchus staleichthus</i>	1	3.1	3.5	—
	<i>Oncorhynchus nerka</i>	1	5.6	4.6	125
	<i>Cottus asper</i>	3	74.9	67.9	110
	<i>Mylocheilus caurinus</i>	2	3.0	2.3	408
	<i>Ptychocheilus oregonensis</i>	3	1.8	13.2	2385
	<i>Stizostedion vitreum</i>	3	2.1	5.8	2110
	<i>Perca fluviatilis</i>	3	74.6	123.2	192
	West Blue	<i>Salvelinus fontinalis</i>	3	1.2	2.2
Windermere	<i>Catostomus commersoni</i>	2	4.4	22.2	414
Wishart	<i>Lepomis macrochirus</i>	4	625.0	771.4	56

($R^2 = 0.84$, $n = 100$, $RMS = 0.107$, $p < 0.0001$). Analysis of variance of the residuals of this equation showed that there was no significant difference in the production of populations of different trophic levels ($p > 0.05$). The regression coefficients for the effects of biomass and body-mass on production are very similar to those found for aquatic invertebrates (Plante and Downing 1989; 0.79 and -0.16 , respectively). Fish populations tend to increase their production slightly more rapidly with increased biomass than do zooplankton and benthos, but the negative influence of body-mass on mass-specific production is virtually identical. The fact that the slope associated with $\log_{10} B$ is close to 1 in equation 1 suggests that P/B does not vary significantly with B . This is similar to the finding of Downing et al. (1990) for fish communities and is important to note, since several authors have suggested that annual secondary production of populations can be estimated employing an average production to biomass ratio (reviewed by Rigler and Downing 1984). Such a procedure would be invalid if P/B were to vary systematically with B , as is the case for freshwater invertebrates (Plante and Downing 1989). P/B in fish populations generally varied between 5 and 0.2 and was not systematically related to the population biomass (Fig. 2). The fact that the slope associated with $\log_{10} B$ is not significantly different from 1 (Fig. 2) suggests that mass-specific renewal rates are not strongly density dependent in freshwater fish populations and that P/B values should translate well from one population of a given species to another.

Fish production was strongly correlated with body-mass. Equation 1 shows that P of fish populations declined as $W^{-0.17}$

where B is entered as a covariate. This shows that P/B declined approximately as $W^{-0.17}$ (Fig. 3). Allometric theory, on the other hand, argues that P/B should decline as $W^{-0.25}$ (Humphreys 1981; Lavigne 1982; Peters 1983; Calder 1984). This expectation was upheld for 11 fish populations by Banse and Mosher (1980). The exponent we obtained by least squares regression in equation 1 is significantly different from -0.25 ($p < 0.05$), but major axis regression (Jolliffe 1990) shows a functional relationship between P/B and W with an exponent of -0.22 . The P/B of a population with W of 5 g would be more than three times, on average, that of a population of 5-kg fish with the same standing biomass (equation 1).

Other Factors Correlated with Freshwater Fish Production

The effect of environmental characteristics was evaluated by examining their correlations with the residuals of equation 1 (Table 3). This procedure is equivalent to the next step beyond equation 1 in a stepwise multiple regression analysis with forward selection (Hocking 1976).

Climatic Variation

Because fish are poikilotherms, temperature should influence rates of energy acquisition and growth. Table 3 shows that fish production was significantly correlated with annual mean air temperature ($p < 0.001$) and latitude ($p < 0.001$). Although highly influenced by the very low rates of production seen in arctic Char Lake (Table 1), the influence of air tem-

TABLE 2. Characteristics of the lakes in which fish production data in Table 1 were estimated. NS = number of species, E = population exploited (yes, no), Alt = altitude of the lake (m), \bar{z} = mean depth (m), Area = ha, T = mean annual air temperature ($^{\circ}\text{C}$), Cond. = annual average conductivity ($\mu\text{mho}\cdot\text{cm}^{-1}$), TDS = total dissolved solids ($\text{mg}\cdot\text{L}^{-1}$), TP = annual average total phosphorus ($\mu\text{g}\cdot\text{L}^{-1}$), TN = annual average total nitrogen ($\mu\text{g}\cdot\text{L}^{-1}$), Chlo = annual average chlorophyll a ($\mu\text{g}\cdot\text{L}^{-1}$), PP = primary production ($\text{g}\cdot\text{C}\cdot\text{m}^{-2}$). Values of TDS in italics were estimated from conductivity measurements (Schlesinger and McCombie 1983). Data sources: 1, D. R. Alexander (Department of Fisheries and Oceans, Moncton, N.B., pers. comm.); 2, Alexander and Merrill (1976); 3, Alexander et al. (1986); 4, Arvola (1983); 5, Balon (1972); 6, Balon (1974); 7, Beattie et al. (1972); 8, Chadwick (1976); 9, Ciepiewski (1981); 10, Coche (1974); 11, Craig (1980); 12, Dunn et al. (1969); 13, W. T. Edmondson (Department of Zoology, University of Washington, Seattle, WA, pers. comm.); 14, Edmondson and Lehman (1981); 15, Efford (1972); 16, Eggers et al. (1978); 17, Eloranta and Palomäki (1986); 18, Ganf (1974); 19, Gerking (1962); 20, Gerking (1964); 21, Goldspink (1978); 22, Goldspink (1979); 23, Gulin and Rudenko (1973); 24, Gwahaba (1973); 25, Holčák (1970); 26, IBP data set; 27, Jester (1971); 28, Jester (1972); 29, Jester (1976); 30, Johansson (1983); 31, J. R. M. Kelso (Great Lakes Fisheries Research Branch, Sault Ste. Marie, Ont., pers. comm.); 32, Kelso (1985); 33, Kelso and Ward (1972); 34, Kelso and Ward (1977); 35, Kloster (1978); 36, Krogius et al. (1972); 37, Lam et al. (1986); 38, LeCren (1976); 39, Lien (1978); 40, Lien (1981); 41, E. A. Lind (Department of Zoology, University of Oulu, Oulu, Finland, pers. comm.); 42, Lind et al. (1973); 43, Lind et al. (1974); 44, Mahon (1976); 45, Mahon and Balon (1977); 46, C. A. Mills (Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Man., pers. comm.); 47, Mills (1985); 48, Mills and Eloranta (1985); 49, Miura and Tanaka (1975); 50, Morgan (1972); 51, Mortimer and Worthington (1942); 52, Nakanishi (1975); 53, Nyberg (1979); 54, O'Connor and Power (1973); 55, G. Power (Department of Biology, University of Waterloo, Waterloo, Ont., pers. comm.); 56, Ramberg (1976); 57, M. Rask (Lammi Biological Station, University of Helsinki, Helsinki, Finland, pers. comm.); 58, Rask (1984); 59, Rask and Arvola (1985); 60, Rask et al. (1986); 61, Rigler (1972); 62, Rigler (1975); 63, Rigler (1978); 64, Särrkä (1972); 65, Saunders and Power (1970); 66, Scheffer and Robinson (1939); 67, D. J. Staples (Department of Zoology, University of Canterbury, Canterbury, New Zealand, pers. comm.); 68, Staples (1975a); 69, Staples (1975b); 70, Tangen and Brettum (1978); 71, J. E. Thorpe (Freshwater Fisheries Laboratory, Pitlochry, Scotland, pers. comm.); 72, Thorpe (1974); 73, Tikka and Paasivirta (1979); 74, Vareschi (1982); 75, Vareschi and Jacobs (1984); 76, Vareschi and Jacobs (1985); 77, Wali et al. (1972); 78, Ward and Robinson (1974); 79, Zachweja (1973).

Lake	NS	E	Alt	\bar{z}	Area	T	pH	Cond	TDS	TP	TN	Chlo	PP	Data source(s)
226 NE 1973	5	No	414	6	8	2	6.5	21	13	5	270	11	54	46, 47
226 NE 1974	5	No	414	6	8	2	6.4	23	15	5	391	19	74	46, 47
226 NE 1975	5	No	414	6	8	2	6.4	24	16	6	470	16	56	46, 47
226 NE 1976	5	No	414	6	8	2	6.5	26	17	6	510	10	76	46, 47
226 SW 1973	5	No	414	6	8	2	6.6	20	13	4	241	5	44	46, 47
226 SW 1974	5	No	414	6	8	2	6.5	23	15	4	352	3	32	46, 47
226 SW 1975	5	No	414	6	8	2	6.5	24	16	4	429	8	32	46, 47
226 SW 1976	5	No	414	6	8	2	6.6	27	17	3	469	6	28	46, 47
Alinen Mustajärvi	3	—	—	3	1	3	5.8	24	16	39	1545	10	7	4, 59
Big Indian	5	No	—	3	106	6	5.5	42	27	—	—	—	—	1, 2, 3
Big Turkey	2	—	372	12	52	5	—	41	27	4	—	—	2	31, 32, 37
Bill	5	—	96	—	154	1	5.8	23	15	—	—	—	—	54
Botjäm	2	—	280	3	10	5	5.6	25	16	14	400	—	3	30, 53, 56
Char	1	—	30	10	53	-9	—	196	128	4	—	—	4	61, 62, 63
Dalnee	3	—	—	32	136	2	—	—	—	92	—	—	487	36
Demenets	7	—	—	3	7	5	—	—	—	—	—	—	—	23
Elephant Butte	26	No	1646	6	8100	16	8.3	700	303	800	—	—	—	27, 28, 29
George	32	Yes	914	3	27000	22	9.0	220	264	—	2600	100	367	6, 10, 12, 18, 24
Haukilampi	3	—	—	—	2	3	6.8	43	28	23	580	—	—	73
Horkkajärvi	2	—	—	7	1	3	5.7	43	28	115	973	10	6	4, 59
Iso-Mustajärvi	3	—	—	—	3	3	6.9	62	41	20	290	—	—	73
Karhujärvi	1	—	158	5	1	3	4.4	43	—	148	582	26	16	57, 58, 60
Kariba	28	Yes	485	29	5364	25	8.0	73	58	—	—	—	—	5, 6, 10
Kiutajärvi	5	Yes	225	15	45	0	7.1	51	43	9	350	1	—	41, 42, 43
Konnevesi	2	Yes	95	10	18800	3	7.5	44	29	6	420	2	13	17, 48, 64
Laluisa	7	—	—	1	1	25	—	—	—	—	—	—	—	25
Little Turkey	2	—	375	6	19	5	—	39	25	6	—	—	1	31, 32, 37
Loch Leven	7	Yes	107	4	1330	9	8.3	—	—	95	8250	100	354	38, 50, 71, 72
Marion	2	No	300	2	13	9	—	18	12	246	—	—	8	15, 77
Matamek	4	No	122	—	1620	1	5.9	14	9	—	—	—	—	55, 65
Nakuru	1	Yes	1759	2	4400	18	10.5	18167	11862	9850	17000	1160	881	74, 75, 76
Øvre Heimdalsvatn	2	—	1090	5	78	2	6.9	15	10	15	20	—	12	35, 39, 40, 70
Red Deer	6	—	400	4	6	4	6.9	35	23	—	—	—	—	8
Sabanilla	7	Yes	—	1	3	25	—	—	—	—	—	—	—	25
Small Spectacles	3	Yes	610	3	1	9	8.6	119	78	140	—	—	—	67, 68, 69
Tatsu-numa	2	Yes	790	4	1	12	6.2	—	—	10	400	0.4	8	51, 49, 52
Tjeukemeer 1967-68	7	Yes	-1	2	2130	10	8.0	—	—	263	1700	30	300	7, 21, 22
Tjeukemeer 1969	7	Yes	-1	2	2130	10	8.0	—	—	263	1700	30	300	7, 21, 22
Vitalampa	1	No	280	3	3	5	5.7	18	12	17	425	—	5	30, 53, 56
Warniak 1969	>1	Yes	—	2	38	7	7.8	275	180	—	—	—	130	9, 26, 79
Warniak 1970	>1	Yes	—	2	38	7	8.0	226	148	—	—	—	—	9, 26, 79
Washington	7	Yes	4	33	8760	11	7.7	81	53	35	273	15	157	13, 14, 16, 66
West Blue	5	No	670	11	160	2	8.3	160	104	—	—	0.3	38	33, 34, 78
Windermere	>1	Yes	39	22	1482	10	—	—	—	—	—	—	—	11, 38, 51
Wishart	2	—	388	2	19	5	—	33	22	5	—	—	0.7	31, 32, 37
Wyland	5	No	—	—	3	10	8.5	—	—	—	—	—	—	19, 20, 44

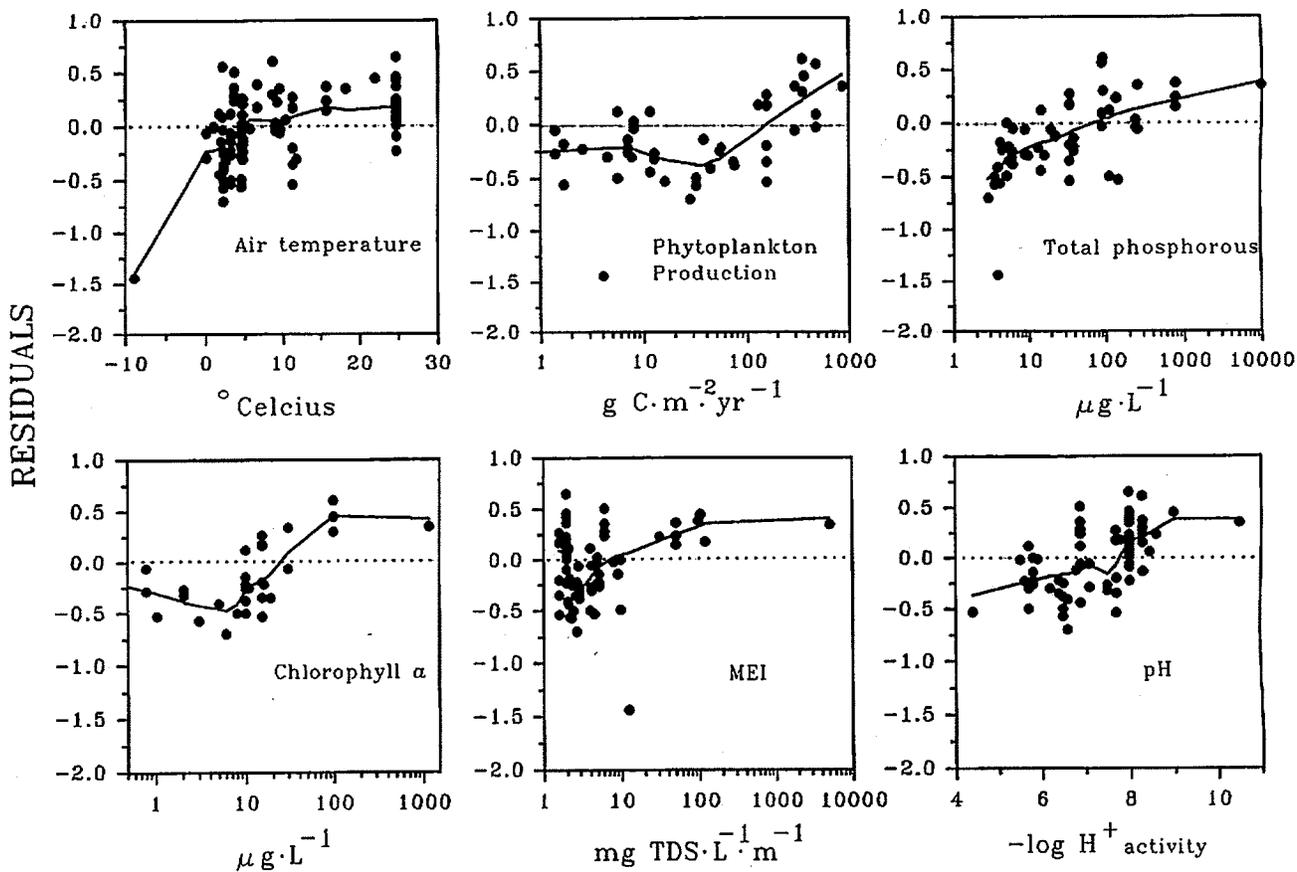


FIG. 4. Relationships of the residuals from equation 1 in \log_{10} form to various characteristics of the study lakes (Table 2). Lines are trends calculated using locally weighted robust sequential smoothing (Cleveland 1979). The outlier in the first three and the fifth panels is the arctic Char Lake.

perature (T , degrees Celsius) on fish production (Fig. 4) can be summarized by the multiple regression equation

(2) $\log_{10}P = 0.20 + 0.93 \log_{10}B - 0.19 \log_{10}W + 0.02T$ ($R^2 = 0.88$, $n = 100$, $RMS = 0.084$, $p = 0.0001$). Analysis of this equation suggests that the ratio of fish production to biomass varies from about 0.9 in temperate oligotrophic Lake 226, on average, to over 2.3 in tropical Lake George for a population of the same body-mass ($W = 5$ g) and biomass ($B = 100 \text{ kg} \cdot \text{ha}^{-1}$). For example, P/B for *Salvelinus alpinus* found in Char Lake ($T = -9$) was only 0.02 (Table 1). Figure 4 suggests that, on average, populations found where the average annual air temperature is 20°C have production rates three times those found in similar populations at 0°C .

Lake Trophic Status and Productivity

The ultimate limit to the rate of production of a population of fish must be set by the primary productivity of the ecosystem in which it lives. Downing et al. (1990) found that the productivity of entire fish communities was well correlated with both algal production and the total phosphorus concentration of the water column, an indicator of lake trophic status. Correlation analyses of the residuals of equation 1 show that fish population production is significantly ($p < 0.001$) correlated with total phosphorus concentration, chlorophyll a concentration, and algal primary productivity. Figure 4 suggests that, if these correlations reflect underlying trophic mechanisms, a change in

total phosphorus concentration from 10 to $100 \mu\text{g} \cdot \text{L}^{-1}$ should be correlated with a threefold increase in P/B of fish populations. Including total phosphorus concentration (TP, micrograms per litre) in a multiple regression analysis with population biomass and body-mass yields

(3) $\log_{10}P = -0.25 + 0.90 \log_{10}B - 0.15 \log_{10}W + 0.29 \log_{10}TP$

($R^2 = 0.81$, $RMS = 0.083$, $n = 52$, $p < 0.0001$). Lakes with low phytoplankton biomass and production also have lower rates of mass-specific fish production than lakes with phytoplankton biomass $>20 \mu\text{g} \cdot \text{L}^{-1}$ and phytoplankton production $>200 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Fig. 4). Other factors related to lake trophic status, such as total nitrogen concentration and total dissolved solids, were also significantly correlated with fish productivity (Table 3). The morphoedaphic index (Fig. 4), a staple predictor of fishing yields from exploited fisheries (Ryder 1982; Leach et al. 1987), was not significantly ($p > 0.05$) correlated with fish production when biomass and body-mass effects were considered (Table 3). The analysis of fish production presented here upholds Downing et al.'s (1990) contention that fish production is more closely correlated with primary production, phosphorus concentration, and fish standing stock than with the morphoedaphic index.

Recent research has attempted to determine the relative importance of producers and consumers in the control of the structure of communities. The positive relationship between fish

TABLE 3. Correlations between residuals from equation 1 (observed minus predicted P) and lake characteristics. Units are in Table 2. p is the probability level associated with the hypothesis that the lake characteristics and the residuals are uncorrelated. Logarithm transformations were performed where necessary to linearize responses and normalize the residuals. Values of p marked with an asterisk are significant at $p \leq 0.05$ after sequential Bonferroni correction for multiple comparisons (Rice 1989).

Lake characteristic	Pearson coefficient	Number of populations	Number of lakes	p
Total phosphorus (log)	0.62	52	26	<0.001*
Primary production	0.58	47	23	<0.001*
Chlorophyll (log)	0.56	32	14	<0.001*
pH	0.56	74	28	<0.001*
Primary production (log)	0.49	47	23	<0.001*
Species richness (log)	0.49	97	35	<0.001*
Air temperature	0.47	100	38	<0.001*
Latitude	-0.45	100	38	<0.001*
Total dissolved solids (log)	0.36	77	29	0.002*
Total nitrogen (log)	0.46	37	18	0.004*
Conductivity (log)	0.33	77	29	0.004
Lake area (log)	0.27	99	37	0.008
Altitude	0.25	73	27	0.03
Morphoedaphic index (log)	0.21	72	28	0.07
Mean depth (log)	0.00	94	23	0.99

population production and phosphorus concentration suggests a "bottom-up" control of these ecosystems, that is, that each trophic level is limited by the subordinate level. This agrees with McQueen et al.'s (1986) model which predicts that the maximum potential biomass of each trophic level in freshwater pelagic ecosystems is controlled by nutrient availability. This has also been hypothesized for terrestrial ecosystems (see White 1978).

Lake Acidification

Several authors have now discussed the negative impact of lake acidification on fish growth and productivity (e.g. Beamish et al. 1975; Haines 1981; Rask 1984; Schindler et al. 1985; Ingersoll et al. 1990). Whole-lake experiments (Schindler et al. 1985) have shown that fish production falls dramatically with decreases in pH and fish species are nearly completely eliminated in lakes that fall to pH 4 (Haines 1981; Rahel and Magnuson 1983). Analysis of the residuals of equation 1 extend general, worldwide support to the results of manipulations and individual case studies because mass-specific fish production rates rise by nearly an order of magnitude between acid (pH = 4) and alkaline (pH = 9) lakes (Fig. 4). This result agrees with Brylinsky's (1980) work on pH and phytoplankton production and upholds the negative effect of low pH on benthic invertebrate biomass suggested by the work of Roff and Kwiatkowski (1977) and the negative effect of low pH on invertebrate production seen by Plante and Downing (1989). Low production rates of fish populations in acidic lakes may be the result of low food production. For example, Mills et al. (1987) found that certain species of fish in acidified lakes appeared to starve to death even though the pH was within physiologically tolerable limits.

Species Richness

The species richness of fish communities surveyed ranged from 1 to 32. We found that fish populations in lakes with greater numbers of fish species had higher rates of production than lakes with more depauperate faunas (Table 3). This result probably arises from the tendency for eutrophic lakes to have greater species richness as well as greater mass-specific production rates than oligotrophic lakes (Table 2). Comparison of

Downing et al.'s (1990) data on fish community production with our population production data (Table 1) suggests that fish community production is marginally lower (ANCOVA, $p = 0.06$) than fish population production for a given biomass (Fig. 2). Intraspecific competition may therefore lower the rate of production of a given biomass of fish if this fish biomass is partitioned into many species.

Renewal and Exploitation of Fish Populations

An unexploited fish population has a rate of production that, when taken over the long term, balances rates of natural mortality. If this were not the case, then fish populations would either increase toward infinite biomass or fall to extinction. The idea behind scientific fisheries management is that we attempt to replace a portion of the natural mortality with fishing mortality and we hope that removal will be concentrated on the least productive part of the population leading to increased production in the residual population. Fishing yield can therefore never be maintained at a level higher than the production of the population without leading to a decline in the biomass of the exploited populations. Even exploitation near the production rate may lead to recruitment failure. The rate of production examined here therefore sets the extreme upper limit of the rate at which fish populations can be exploited. The real upper limit is closer to the difference between fish production and the irreducible rate of natural mortality found in the population exploited at the maximum sustainable level, as long as adequate recruitment can be maintained.

Simultaneous measures of fish production and sustainable yield are very rare. Downing et al. (1990) found that primary production was a good predictor of fish community production and compared measured production levels with sustained fishing yields found in other lakes of known primary productivity (Oglesby 1977). Although their analyses of this small data base are speculative, they suggest that about 10% of the community fish production can be fished on a sustainable basis although data from extremely large lakes and tropical pisciculture ponds suggest that rates of irreducible natural mortality are proportionately greater in oligotrophic lakes than in eutrophic ones. Downing et al.'s (1990) analysis showed that biological fish production and rates of sustainable yield are strongly corre-

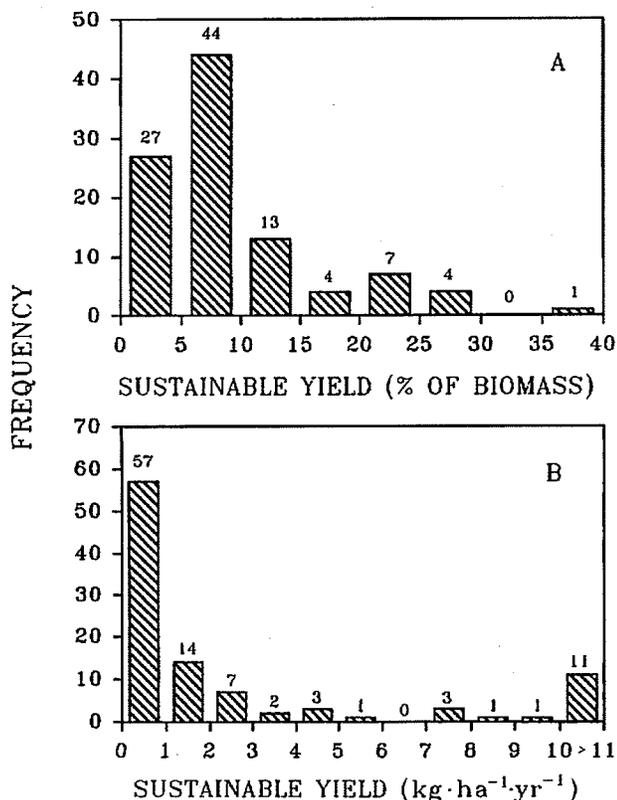


FIG. 5. Frequency histograms of annual sustainable yield (A) as a fraction of biomass, assuming that 10% of the fish production can be removed on a sustainable basis, and (B) in $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, assuming that 10% of the fish production can be harvested on a sustainable basis.

lated; therefore, factors influencing rates of fish population production should also influence sustainable yields.

Assuming that sustainable yields are about 10% of biological production, our data (Table 1) suggest that only a small fraction of the standing fish biomass can be removed on a sustainable basis. Although such calculated sustainable yields go as high as 50% of standing biomass in populations of small, tropical fish, larger fish under arctic conditions (e.g. *Salvelinus alpinus* in Char Lake) can apparently yield as little as 0.2% of standing biomass on an annual basis (Fig. 5). More than one quarter of the fish production data we collected indicated sustainable yields of <5% of biomass, while >85% were <15% (Fig. 5). The data suggest that sustainable yields can be as little as $0.01 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ or as great as $62 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ but the majority of sustainable fish populations yields in lakes are $<1 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, while more than 80% are $<4 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Our calculations are highly speculative due to the lack of data on maximum sustainable fish yield concurrent with production measurements. Equations 1, 2, and 3 and Table 3 show, however, that sustainable fish yields should be lower for larger fish species, at high latitudes, or under acid conditions, and fish yields should be higher at high temperatures or under more eutrophic conditions.

Exploited populations appear to have higher rates of production than unexploited populations of the same biomass and body-size. ANOVA of the residuals of equation 1 shows that the mean residual (in \log_{10} form) of fish populations in unexploited lakes was -0.124 , while the mean residual in exploited lakes was 0.118 ($p = 0.03$). This average difference of 0.24

unit suggests that production rates in exploited lakes are about 70% higher (i.e. $10^{0.24} = 1.74$) than fish population production in unexploited lakes. This is a conservative analysis, since rates of exploitation were not measured but only entered as presence or absence of exploitation, but it agrees well with the general belief that exploited populations are composed of younger, faster growing fish.

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