Trout Production Dynamics and Water Quality in Minnesota Streams

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Abstract.—We sampled fish assemblages and quantified production dynamics of brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss* in 13 southeastern Minnesota streams during 1988–1990 to examine the influence of water quality on fish populations in fertile trout streams. Fish assemblages in 15 stream reaches were abundant, but low in diversity; 13 species were collected. Parameter means (ranges) over the reaches were species richness, 4.1 (1–8); density, 29,490 (1,247–110,602) fish/ha; and biomass, 253.5 (49.6–568.6) kg/ha. Means (ranges) for salmonids were annual mean density, 2,279 (343–8,096) fish/ha; annual mean biomass, 162.0 (32.5–355.5) kg/ha; and annual production, 155.6 (36.7–279.6) kg/ha. Salmonid production and mean biomass were greater during the spring–fall interval than during fall–spring; young cohorts (ages 0–1) contributed the greatest proportion to population biomass and production. Salmonid annual production-to-mean-biomass ratio ($P/\bar{B}$) averaged 1.06 (0.64–1.42), and means were significantly different among species (1.03 for brown trout, 1.54 for brook trout, and 1.92 for rainbow trout). A significant linear model was developed that describes $P/\bar{B}$ as an inverse function of population age structure and may be used to improve accuracy in approximations of annual production from mean biomass. Fish density, biomass, or production were not correlated with eight water quality variables describing ionic and nutrient content in these streams, but when data from other United States streams with a wide range in alkalinity were incorporated, salmonid production was strongly, positively correlated with alkalinity. The wide range in fish population and production statistics and their lack of correlation with water quality suggest that no uniform fish carrying capacity exists among these streams and that factors other than water fertility limit fish density, biomass, and productivity at this spatial scale, but the overall maximum production rate in the region may be governed by water quality.

Fish ecologists agree that the dynamic measure of production rate is the best single indicator of a species' ecological success (Le Cren 1969; O'Connor and Power 1976; Mann and Penczak 1986). Production is a synthesis of population biomass, recruitment, growth, and mortality and is especially responsive to the welfare of a population and environmental change (Mann and Penczak 1986). The methods and terminology for estimating fish production have evolved to a generally accepted convention (Waters 1977a; Chapman 1978). Stimulated in part by several landmark publications (Northcote 1969; Waters 1977a; Mann and Penczak 1986), the International Biological Program (IBP), and recent computer software applications (Newman and Martin 1983; Railsback et al. 1989; Kwak 1992), estimates of production are becoming increasingly abundant in the literature.

A considerable body of data is available on an-

nual production of salmonids in small streams (Hunt 1974; Waters 1977a, 1992; Chapman 1978; Mann and Penczak 1986; Elliott 1994). Studies and descriptions of salmonid density and biomass are even more numerous in both recent and historical literature. The abundance of such work is likely due to interest in the sport fisheries these streams support and to the development of efficient electrofishing techniques in these environments.

Spatial and temporal patterns in populations and ecosystems are fundamental themes in ecology, and the influence of observational scale on the description of those patterns is a critical issue in understanding nature (Levin 1992). Appropriately, production dynamics of stream-dwelling salmonids have been studied at a variety of spatial and temporal scales. Many production estimates have been published for a single stream reach during a 1-year period (Waters 1977a; Mann and Penczak 1986), and these data in aggregate can reveal informative biological trends (e.g., Waters 1988, 1992). Of more value in demonstrating ecological patterns, however, are studies that examine production dynamics over an expanded temporal (e.g., Hunt 1974; Waters 1983; Elliott 1993) or spatial

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scale (e.g., Mortensen 1977; Scarnecchia and Bergersen 1987; Newman and Waters 1989).

Comparative data compilations (Waters 1992; Mann and Penczak 1986) and research on a broad spatial scale (Cooper and Scherer 1967; Le Cren 1969; Crisp et al. 1975; Scarnecchia and Bergersen 1987) generally indicate that stream salmonid production rates are influenced by water quality. In such comparisons, measures of water ionic strength (e.g., alkalinity, conductivity, or hardness) are often considered as general indices of fertility, and a positive relationship between water fertility and fish production has been suggested. This relationship is further supported by manipulative stream enrichment experiments (Warren et al. 1964; Mills 1965; Mundie et al. 1983; Deegan and Peterson 1992). However, increasing evidence suggests that many streams do not reach the potential level of salmonid production predicted by their corresponding water fertility, and that the association between water quality and production may exist primarily in streams of infertile waters (Mortensen 1977; Mann and Penczak 1986). In geographic regions with relatively uniform stream water quality—especially those of high ion and nutrient concentrations—other proximate physical factors may limit and account for variation in fish production (e.g., temperature, physical habitat structure, flow regime).

In addition to providing insight into ecological patterns and limiting factors, production dynamics research can contribute quantitative information and relationships useful in the management of stream-dwelling salmonid populations. Because production rate is a superior measure of the status of fish populations, management objectives, decisions, and evaluations could be refined and improved if they were based on production estimates, rather than on static population measures, such as density or biomass. Accordingly, Waters (1992) reviewed the annual production, the ratio of annual production to annual mean biomass ($P/\bar{B}$), and the ecotrophic coefficient (annual harvest/annual production) of salmonid populations in streams and discussed their management implications. Incorporating production dynamics into fishery management may provide a simple but comprehensive quantitative assessment of the effects of varying management practices on the proportion of energy removed from the system by angling relative to that fixed by production.

In this study, we examined the relationships between fish population and production dynamics and stream water quality. Our primary objectives

were to quantitatively describe the variability of population dynamics of all fishes and production dynamics of brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss* in 13 southeastern Minnesota streams and to compare estimates of fish populations and production to corresponding measures of water ionic and nutrient content. We then placed our results in perspective by comparing them with those of other relevant research and expanding the spatial scale of our analyses. We present our findings here and then discuss their ecological and management implications.

Study Area

This study took place in southeastern Minnesota, an area of deeply incised valleys that contain alluvial terraces and a low-relief floor. The valley sides are thickly wooded and include steep, exposed bluffs of limestone and other sedimentary rock leading up to gently rolling, agricultural headwater slopes. The great solubility of the bedrock in the region produces mineralized groundwater and stream waters (Waters 1977b). Elevation in the region varies from 305 m in the lowlands up to a strong plateau of 427 m (Ojakangas and Matsch 1982).

The streams in the area were particularly affected by poor land use in the past (excessive logging, grazing, and cultivation), but since the 1930s, much stewardship and restoration has occurred, and these streams have come to support productive faunal assemblages (Waters 1977b). About 75 identified trout streams in the region total over 450 stream kilometers, and their sport fisheries are intensely pursued and managed. The biomass of salmonids in these streams can exceed 300 kg/ha, and anglers have exerted over 2,000 angler-hours/ha of pressure in a single season on some streams (Thorn 1988, 1990).

We studied 15 reaches within 13 streams representing all major drainages in the region (Figure 1). Streams were selected to encompass a broad geographic range within the region and to include a wide range of habitats and salmonid biomasses as indicated by unpublished previous surveys conducted by the Minnesota Department of Natural Resources. The sampling sites were in six counties and ranged from 43°52'N to 44°55'N latitude and from 91°30'W to 93°13'W longitude. All streams were first or second order at the sampling reaches. Mean drainage area, gradient, and discharge at base flow varied among sampling reaches (Table 1). Mean length of sampling reaches was 344 m,

FIGURE 1.—Map of trout stream sampling sites in southeastern Minnesota.

TABLE 1.—Descriptive statistics of physical attributes ($N = 15$ reaches) and water quality variables (monitored monthly; $N = 208$ samples) of fish sampling reaches in southeastern Minnesota trout streams.

Variable	Mean	SD	Range
Drainage area (km ²)	44.6	42.9	16.6–167.6
Gradient (m/km)	5.08	1.70	2.85–7.42
Discharge (m ³ /s)	0.16	0.09	0.01–0.34
Length (m)	344	55.7	256–445
Width (m)	5.12	1.54	3.21–9.63
Sampling area (ha)	0.180	0.081	0.090–0.429
Alkalinity (mg/L as CaCO ₃)	235.9	22.0	172–298
Conductivity (μS/cm)	578.8	80.8	425–860
pH	7.90	0.33	7.1–8.7
Turbidity (NTU ^a)	1.92	4.83	0.2–40.0
Nitrate (mg/L as NO ₃ -N)	3.54	1.83	0–14.0
Nitrite (mg/L as NO ₂ -N)	0.015	0.015	0.003–0.100
Ammonia (mg/L as NH ₃ -N)	0.205	0.085	0.01–0.68
Orthophosphate (mg/L as PO ₄)	0.264	1.242	0.01–17.64

^a Nephelometric turbidity unit.

average mean width was 5.12 m, and mean sampling area was 0.180 ha. Detailed and quantitative descriptions of the area, study streams and reaches, and their physical attributes may be found in Kwak (1993).

Methods

Fish sampling.—Field sampling took place over 2 years, from 22 March 1988 to 11 April 1990. Six stream reaches were studied during 1988–1989, eight reaches during 1989–1990, and one reach was studied both years (Figure 1). These sites included two reaches that contained artificial habitat modifications and two corresponding unmodified, reference reaches (see Kwak 1993 for details). Salmonid populations were estimated during the spring (March–April), the following fall (September–October), and the following spring, so that annual population parameters could be estimated. Salmonid sampling was seasonally timed to estimate spring populations before accelerated

summer growth and fall populations before spawning.

Fish were sampled with a variety of electrofishing techniques applicable to small streams. One or two pulsed-DC backpack electrofishers were used in small streams. Larger streams were sampled with a 240-V DC generator that was mounted in a small plastic boat and used with one to three hand-held anodes. Salmonid population sizes were estimated by a single-census mark-recapture method (Ricker 1975). Fish captured on the marking sample date were measured for total length (TL ± 1 mm) and given a temporary, partial caudal fin clip. The recapture sample was conducted approximately 1 week after the marking sample date, when fish were measured and inspected for a fin clip. Fish weights (± 1 g) and scales for aging were collected during both the mark and recapture sampling from up to 10 fish per 1-cm length-group (total from both samples) for each species. Age-0 trout were not collected in spring samples, because they were not sufficiently vulnerable to electrofishing gear.

Nonsalmonid populations in each reach were estimated once during the fall by a three-sample removal method with constant sampling effort (Seber 1982). Because nonsalmonid fishes were present in high densities, they were sampled over only part of each salmonid sampling reach, but each such segment included at least one riffle-pool sequence. Mean length of stream sampled for nonsalmonids (SD; range) was 33.8 m (9.0 m; 28.4–64.0 m); mean sampling area was 159.9 m² (57.0 m²; 90.3–290.9 m²). Large fish were measured (TL ± 1 mm) and weighed (± 1 g) at streamside and released. Small fish were fixed in a 10% formalin solution and later preserved in 70% ethanol. Preserved fish were identified, measured (TL ± 1 mm) and weighed (± 0.01 g) in the laboratory.

Ages of salmonids were estimated by analysis of scale impressions (Smith 1954). Impressions of scales were made on acetate strips with a manual roller press and magnified with a microprojector. Annuli were identified according to criteria specified by Jearld (1983). Fish smaller than 10 cm were assumed to be age 0 if collected in the fall or age 1 if sampled during spring. Aging a subset of these small fish confirmed the validity of that assumption. Length distributions were also used as a comparative tool to support fish age estimates.

Population and production estimates.—Estimates of population size, production, component parameters, and associated variances were computed by microcomputer software developed in as-

sociation with this research (Kwak 1992). Density, biomass, and production were estimated separately for each salmonid species. Population estimates were stratified into 2-cm length-groups to minimize a size bias associated with electrofishing that was observed in most streams. In some instances of low fish numbers, successive length-groups were combined.

Salmonid population size and its sampling variance were calculated for each occasion with a modified Petersen estimate (Ricker 1975). Age-specific population estimates were based on the estimated proportion of fish of a given length for each age (Newman and Martin 1983). Mean weights for size- and age-groups, associated variances, and instantaneous growth rates were estimated according to Newman and Martin (1983). The variance of instantaneous growth was estimated by an approximation of the variance of the natural logarithm of a mean via a Taylor series expansion (the delta method; Seber 1982; Cone and Krueger 1988).

Salmonid biomass and production were estimated by the age-based instantaneous growth method (Ricker 1946; Allen 1949; Waters 1977a). All other component parameters and measures of variance were estimated according to Newman and Martin (1983). The two estimates of interval production between seasonal sampling dates were summed to obtain annual production. The interval production estimate and variance for newly recruited age-0 fish were computed as the biomass estimate and its variance at the initial occurrence of age-0 fish in the catch (Waters 1983). For intervals of negative growth, production and its variance were assumed to be zero (Waters 1977a; Chapman 1978).

Density and biomass were estimated separately for each nonsalmonid fish species. Population estimates for nonsalmonids were initially stratified into 1-cm length-groups; then successive groups around modes were combined. Nonsalmonid population size and its sampling variance were calculated with a maximum-likelihood estimator for the case of three removals (Seber 1982; Bohlin et al. 1989), and mean weight, biomass, and variances were estimated according to Newman and Martin (1983).

All population and production estimates were converted to standard area units (ha) by dividing the estimates for each sampling reach by the surface area of the reach. All reported measures of biomass and production are for wet weight. The

diversity index for fish species in each reach was calculated according to Pielou (1975).

Water quality analyses.—Water quality variables were measured monthly during production intervals for each fish sampling site. Alkalinity was determined by titrating a 100-mL water sample with 0.04 N sulfuric acid to an endpoint of pH 4.6, indicated by a methyl orange solution. Conductivity was measured with a Horizon type 1484-10 conductivity meter, pH with an Orion model 399A analog meter, and turbidity with a Hach model 2100A turbidimeter.

Nutrient concentrations were determined by measuring a series of chemical reactions with a Hach DR/2000 direct-reading spectrophotometer (Hach Co. 1992). Nitrate nitrogen was measured with a modification of the cadmium reduction method, in which gentisic acid was substituted for 1-naphthylamine. Nitrite nitrogen was determined by a diazotization method incorporating chromotropic acid as the indicator. Acid-preserved water samples were neutralized before ammonia analysis, which was determined by the Nessler method. Orthophosphate (reactive phosphorus) was determined by an ascorbic acid method that is a form of the molybdenum blue procedure.

We investigated the relationships between fish population and production statistics and water quality variables using canonical correlation analysis (SAS Institute 1989; Manly 1994) and pairwise calculations of the Pearson correlation coefficient (Zar 1984). Two-tailed probabilities and test power for correlation coefficients were computed according to Zar (1984).

Results

Fish Assemblages

Thirteen fish species representing six families were collected from trout streams in southeastern Minnesota (Table 2). Rainbow trout, central stone-roller, and mottled sculpin were each found in only one sampled stream. Brown trout, sampled from 12 streams, was the most ubiquitous species. The number of salmonid species present varied among streams: only brook trout occupied Spring Brook; only brown trout occurred in eight streams; brook trout coexisted with brown trout in three streams; and brook trout, brown trout, and rainbow trout were found in Valley Creek (Table 3), the only stream that contained rainbow trout.

Typical of coldwater streams, species richness of individual fish assemblages was relatively low, averaging only 4.1 species (Table 4). Two stream

TABLE 2.—List of fishes collected in 13 southeastern Minnesota trout streams and the number of streams in which each occurred during 1988–1990.

Family and species	Number of streams
Salmonidae	
Rainbow trout <i>Oncorhynchus mykiss</i>	1
Brown trout <i>Salmo trutta</i>	12
Brook trout <i>Salvelinus fontinalis</i>	5
Cyprinidae	
Central stoneroller <i>Campostoma anomalum</i>	1
Bluntnose minnow <i>Pimephales notatus</i>	2
Blacknose dace <i>Rhinichthys atratulus</i>	6
Longnose dace <i>Rhinichthys cataractae</i>	3
Creek chub <i>Semotilus atromaculatus</i>	5
Catostomidae	
White sucker <i>Catostomus commersoni</i>	7
Gasterosteidae	
Brook stickleback <i>Culaea inconstans</i>	4
Cottidae	
Mottled sculpin <i>Cottus bairdi</i>	1
Slimy sculpin <i>Cottus cognatus</i>	4
Percidae	
Johnny darter <i>Etheostoma nigrum</i>	3

reaches, in Beaver and Trout Run creeks, supported only one fish species—brown trout. Eight species occurred in Money Creek, the greatest number in any stream sampled. The relatively homogeneous nature of the fish fauna was similarly reflected in diversity; mean diversity index was 0.25 and ranged only up to 0.61 (Spring Brook; Table 4).

Although fish diversity in these streams was low, the same may not be said of abundance. Density estimates (including all species) averaged 29,490 fish/ha but ranged widely from 1,247 fish/ha in Cedar Creek to 110,602 fish/ha in the habitat-modified reach of Garvin Brook (Tables 3, 4). Biomass estimates were also widely distributed; mean biomass was 253.5 kg/ha and ranged from 49.6 kg/ha in Pine Creek to 568.6 kg/ha in Garvin Brook (habitat modified reach).

Salmonid Production Dynamics

The site-selection criterion of a wide range of salmonid biomass among streams was clearly met (Tables 3, 4). Mean salmonid biomass among streams was 162.0 kg/ha, but biomass ranged from 32.5 kg/ha in Money Creek and 32.9 kg/ha in Pine Creek to a maximum of 355.5 kg/ha in Beaver Creek. Density of salmonids corresponded with biomass, and estimates ranged from 343 fish/ha in Money Creek to 8,096 fish/ha in Beaver Creek. Mean salmonid density was 2,279 fish/ha.

Annual salmonid production estimates varied less than did mean biomass estimates (Tables 3,

TABLE 3.—Fall densities and biomasses for nonsalmonid fishes and annual mean densities and biomasses, annual production, and ratios of annual production to mean biomass ($P/\bar{B}$) for salmonid fishes in streams of southeastern Minnesota. Values in parentheses are 2 SEs.

Stream	Nonsalmonid fishes			Salmonid fishes				Total	
	Density (number/ha)	Biomass (kg/ha)	Species present ^a	Density (number/ha)	Biomass (kg/ha)	Production (kg/ha)	$P/\bar{B}$	Density (number/ha)	Biomass (kg/ha)
Beaver Creek	0	0	Bn	8,096 (1,073)	355.5 (30.3)	252.2 (33.2)	0.71 (0.11)	8,096 (1,073)	355.5 (30.3)
Big Trout Creek	18,568 (5,480)	17.1 (4.3)	Bn	981 (221)	108.9 (18.6)	107.3 (16.6)	0.98 (0.23)	19,549 (5,484)	126.0 (19.1)
Cedar Creek	679 (94)	36.8 (4.1)	Bn	568 (195)	65.3 (7.9)	66.2 (15.7)	1.01 (0.27)	1,247 (216)	102.1 (8.9)
Cold Spring Brook	26,367 (5,436)	50.5 (9.8)	Bk, Bn	3,965 (636)	245.1 (39.7)	239.3 (36.4)	0.98 (0.22)	30,332 (5,473)	295.6 (40.9)
Garvin Brook (habitat-modified site)	108,840 (24,112)	240.4 (63.4)	Bk, Bn	1,762 (206)	328.2 (30.7)	279.6 (29.3)	0.85 (0.12)	110,602 (24,113)	568.6 (70.5)
Garvin Brook (reference site)	70,925 (20,554)	145.4 (31.1)	Bk, Bn	1,312 (141)	155.0 (12.6)	170.9 (15.6)	1.10 (0.13)	72,237 (20,554)	300.4 (33.6)
Hay Creek	29,158 (2,118)	31.7 (31.7)	Bn	1,783 (124)	257.2 (20.8)	165.5 (16.4)	0.64 (0.08)	30,941 (2,122)	288.9 (37.9)
Middle Fork Whitewater River (habitat-modified site)	17,548 (5,774)	381.1 (44.3)	Bk, Bn	1,833 (193)	171.4 (17.4)	211.1 (22.6)	1.23 (0.18)	19,381 (5,777)	552.5 (47.6)
Middle Fork Whitewater River (reference site)	18,056 (2,746)	71.9 (14.2)	Bk, Bn	872 (109)	61.9 (7.2)	87.8 (10.8)	1.42 (0.24)	18,928 (2,748)	133.8 (15.9)
Money Creek	29,795 (4,578)	115.3 (14.1)	Bn	343 (71)	32.5 (7.9)	36.7 (6.6)	1.13 (0.34)	30,138 (4,579)	147.8 (16.0)
Pine Creek	18,941 (2,380)	16.7 (2.5)	Bn	512 (79)	32.9 (3.6)	46.0 (6.4)	1.40 (0.25)	19,453 (2,381)	49.6 (4.4)
South Fork Whitewater River	18,852 (9,664)	277.9 (67.3)	Bn	1,880 (199)	153.1 (13.9)	179.5 (14.8)	1.17 (0.14)	20,732 (9,666)	431.0 (68.8)
Spring Brook	7,027 (5,194)	3.6 (1.8)	Bk	1,975 (349)	79.2 (9.0)	103.8 (12.1)	1.31 (0.21)	9,002 (5,206)	82.8 (9.2)
Trout Run Creek	0	0	Bn	2,560 (278)	176.1 (15.3)	131.9 (13.2)	0.75 (0.10)	2,560 (278)	176.1 (15.3)
Valley Creek (1988–1989)	49,375 (73,220)	51.1 (51.7)	Bk, Bn, Rb	5,125 (501)	213.0 (14.5)	214.4 (14.0)	1.01 (0.09)	54,500 (73,221)	264.1 (53.7)
Valley Creek (1989–1990)	21,234 (1,761)	25.7 (3.6)	Bk, Bn, Rb	2,899 (221)	155.9 (13.0)	196.6 (15.6)	1.26 (0.15)	24,133 (1,774)	181.6 (13.5)

^a Bk = brook trout, Bn = brown trout, and Rb = rainbow trout.

TABLE 4.—Population parameters estimated for nonsalmonid fishes, salmonid fishes, and all fishes in southeastern Minnesota streams ($N = 16$).

Statistic	Mean	SD	Range
Nonsalmonid fishes			
Fall density (number/ha)	27,210	28,395	0–108,840
Fall biomass (kg/ha)	91.6	113.9	0–381.1
Salmonid fishes			
Annual mean density (number/ha)	2,279	2,010	343–8,096
Annual mean biomass (kg/ha)	162.0	98.9	32.5–355.5
Annual production (kg/ha)	155.6	75.3	36.7–279.6
Annual production/mean biomass	1.06	0.24	0.64–1.42
Total			
Density (number/ha)	29,490	28,230	1,247–110,602
Biomass (kg/ha)	253.5	159.7	49.6–568.6
Species richness (number)	4.13	1.86	1–8
Species diversity index	0.25	0.19	0–0.61

4). Mean annual production was 155.6 kg/ha and ranged from 36.7 kg/ha in Money Creek to 279.6 kg/ha in Garvin Brook (habitat-modified reach). The $P/\bar{B}$ ratio computed for each stream reach (salmonid species combined) averaged 1.06 and ranged from 0.64 to 1.42, but $P/\bar{B}$ ratios for individual species at each site were more variable. Salmonid biomass and production estimates were distributed fairly evenly within the range of estimated values; their modes were close to their means (Tables 3, 4). Details of salmonid production rates and associated statistics by stream reach, species, and sampling interval were given by Kwak (1993).

Salmonid production and mean biomass varied by season and were generally greater during the spring–fall interval than during fall–spring (Figure 2). In all but one stream, salmonid production was greater during spring–fall (average, 70% of annual

FIGURE 2.—Seasonal comparisons of salmonid mean biomass and production in southeastern Minnesota streams ($N = 16$). Data are mean ($\pm$ SE) comparisons of interval mean biomass to annual mean biomass and mean ($\pm$ SE) interval production as a proportion of annual production.

P) than during fall-spring. The exception to that trend was Spring Brook, the only stream in which brook trout was the lone salmonid. Salmonid mean biomass also was greater during spring-fall (average, 112% of annual mean biomass), than during fall-spring, but this trend was reversed in four streams.

The relative contribution of annual production and mean biomass of specific age-classes varied among salmonid species (Figure 3). Age-0 rainbow trout contributed the greatest proportion of annual production to the population total of that species (mean, 60%), but the dominant contributing age-class of brown trout (mean, 54%) and brook trout (mean, 59%) was age 1. The age-1 cohort was the greatest overall contributor to mean salmonid biomass. Proportions of production exceeded those of mean biomass for age-0 cohorts in all species, but the trend was reversed in older cohorts (ages 2 and older).

Annual $P/\bar{B}$ ratios varied among the 22 salmonid populations studied (two measures were made of the Valley Creek populations) and were related to species and age structure (Table 5; Figure 4). They averaged 1.26 among all populations and ranged from 0.64 for brown trout in Hay Creek to 2.47 for brook trout in Garvin Brook (reference reach). Mean $P/\bar{B}$ ratios were 1.03 for brown trout, 1.54 for brook trout, and 1.92 for rainbow trout, differing significantly among species ($P < 0.0005$; one-way analysis of variance). Ratios for brook trout and rainbow trout were both significantly different from that for brown trout ($P < 0.005$; Tukey honestly significant difference test), but not from

FIGURE 3.—Mean ($\pm$ SE) relative contributions of specific age-classes to annual mean biomass and production of salmonid populations in southeastern Minnesota streams, according to species ($N = 25$).

TABLE 5.—Mean (SE) numbers of year-classes and ratios of annual production to mean biomass ($P/\bar{B}$) for salmonid populations in southeastern Minnesota streams, according to species.

Species	N	Number of year-classes	Annual $P/\bar{B}$
Rainbow trout	2	3.00 (0)	1.92 (0.12)
Brook trout	8	2.50 (0.27)	1.54 (0.16)
Brown trout	15	5.27 (0.28)	1.03 (0.06)
All species	25	4.20 (0.33)	1.26 (0.09)

FIGURE 4.—Ratios of salmonid annual production to mean biomass ($P/\bar{B}$) related to number of year-classes present in southeastern Minnesota streams.

each other ($P > 0.05$). The inverse relationship between annual $P/\bar{B}$ ratio and number of population year-classes was significant in a linear model incorporating populations of each species ($P < 0.0001$; Figure 4). The mean number of salmonid year-classes did not correspond directly with $P/\bar{B}$ ratio among species owing to variation among populations within species (Table 5).

Nonsalmonid Populations

Nonsalmonid population estimates were more variable than those of salmonids (Tables 3, 4). Density of nonsalmonid fishes averaged 27,210 fish/ha and ranged from 0 in Beaver and Trout Run creeks to 108,840 fish/ha for slimy sculpins in Garvin Brook (habitat-modified reach). Nonsalmonid biomass averaged 91.6 kg/ha and ranged from 0 to 381.1 kg/ha for three species in the Middle Fork Whitewater River (habitat-modified reach).

On the average, fish density in these streams was composed mostly of nonsalmonid fishes, but salmonids accounted for a majority of fish biomass (Tables 3, 4). Nonsalmonid fishes were numerically more abundant than salmonids in all streams where both groups occurred. Exceptions to the trend of greater salmonid biomass were found in Money Creek and in all three reaches on the Whitewater River (two Middle Fork sites, one South Fork site).

Water Quality

The streams of this region were fertile, and measures of ionic strength did not vary widely among streams or over time (Table 1). Mean alkalinity was 235.9 mg/L as CaCO_3 , mean conductivity was

578.8 $\mu\text{S}/\text{cm}$, and pH averaged 7.90. Spring Brook had notably higher alkalinity and conductivity than other streams, and Pine Creek's ionic measures were the lowest. Stream water was usually clear; turbidity averaged 1.92 NTU, but ranged widely from 0.2 to 40.0 NTU. Measures of nutrient concentration reflected similarly high fertility (Table 1). Mean nitrate and nitrite concentrations were 3.54 mg/L and 0.02 mg/L, respectively. Ammonia averaged 0.21 mg/L and mean orthophosphate was 0.26 mg/L.

The upper extremes in turbidity, ammonia, and orthophosphate (Table 1) were due to rare occurrences and activities of overwintering waterfowl (mallards *Anas platyrhynchos*) directly upstream of the sampling reach in Trout Run Creek. Turbidity of water from Trout Run Creek sampled during December, January, and February 1989 averaged 33.3 NTU (SD, 9.9 NTU) compared with a mean of 1.29 (0.54) NTU for the remainder of the year. Mean ammonia concentration for the 3-month winter period was 0.52 (0.16) mg/L compared to 0.19 (0.07) mg/L during the remainder of the year, and orthophosphate concentration averaged 6.01 (10.07) mg/L during the winter versus 0.09 (0.02) mg/L during other months. Turbidity was 25.8 times greater during the 3-month winter period compared with the remainder of the year; ammonia was 2.74 times greater; and orthophosphate was 66.8 times greater.

Water Quality–Fish Relationships

Several streams supported exceptionally high fish biomasses, whereas others did not (Table 3), suggesting that a uniform fish carrying capacity

does not exist for these streams. The habitat-modified reach on Garvin Brook ranked highest in salmonid production, second in salmonid biomass, and third in nonsalmonid biomass. Beaver Creek had the greatest salmonid biomass and the second highest salmonid production, but contained no other fish species. Cold Spring Brook ranked third and fourth highest in salmonid production and biomass, respectively. Reaches of the Whitewater River (South Fork and habitat-modified Middle Fork) supported the greatest biomasses of nonsalmonid fishes. Money Creek was lowest in both salmonid biomass and production, but only four other streams had higher nonsalmonid biomasses. Pine Creek was particularly devoid of fish biomass; it ranked next to the lowest in salmonid biomass and production and fourth lowest in nonsalmonid biomass.

Correlation analyses detected no ecological relationship between fish populations and production and water quality in the streams of southeastern Minnesota. Canonical correlation analysis incorporating the variables listed in Table 6 failed to detect a significant relationship between the set of fish population and production statistics and the set of water quality variables (squared canonical correlation = 0.93; $P = 0.51$). No significant pairwise correlation between salmonid density, biomass, or production and eight water quality variables was detected ($P > 0.05$; Table 6), even though test power was sufficient to detect such a relationship if it existed. In all but one of these comparisons, the probability of committing a type II statistical error (β) was below 0.20 (i.e., test power > 0.80 ; Zar 1984).

A marginally significant, positive correlation between nonsalmonid biomass and pH ($P = 0.04$; Table 6) was the only significant water quality-fish relationship detected in our pairwise analyses and is likely a statistical artifact, based on the number of comparisons and the lack of significant correlation with other related measures (e.g., no significant correlation of nonsalmonid biomass with conductivity or alkalinity). Among the 56 pairwise comparisons assigned a 5% significance level (α), 2.8 significant correlations would be expected by chance, and any adjustment in significance level for a Bonferroni inequality (Miller 1981; Milliken and Johnson 1984) would render all pairwise correlations not significant. No significant correlation was detected in comparisons of nonsalmonid density, total fish density, or total fish biomass and water quality variables ($P > 0.05$; Table 6). Test power was sufficiently high to ensure that sample

TABLE 6.—Correlation coefficients (r), their probabilities (P), and the probability of a type II error (β ; power = $1 - \beta$) for comparisons of salmonid (annual means), nonsalmonid, and total fish density (N) and biomass (B) and salmonid production (P) to measures of water quality (annual means) in southeastern Minnesota streams ($N = 16$). Measurement units for water quality variables are given in Table 1.

Fish statistic	Water quality variable	r	P	β
Salmonid N (number/ha)	Alkalinity	0.14	0.61	0.07
	Conductivity	-0.06	0.82	0.04
	pH	-0.07	0.81	0.04
	Turbidity	-0.14	0.61	0.07
	Nitrate	0.05	0.87	0.04
	Nitrite	-0.22	0.41	0.13
	Ammonia	-0.13	0.65	0.07
	Orthophosphate	0.02	0.93	0.03
Salmonid B (kg/ha)	Alkalinity	-0.01	0.97	0.03
	Conductivity	-0.29	0.28	0.19
	pH	0.12	0.67	0.06
	Turbidity	-0.12	0.67	0.06
	Nitrate	-0.15	0.58	0.08
	Nitrite	-0.36	0.18	0.26
	Ammonia	-0.25	0.35	0.15
	Orthophosphate	0.05	0.86	0.04
Salmonid P (kg/ha)	Alkalinity	-0.11	0.68	0.06
	Conductivity	-0.19	0.48	0.10
	pH	0.20	0.46	0.11
	Turbidity	-0.18	0.51	0.10
	Nitrate	0.08	0.77	0.05
	Nitrite	-0.24	0.39	0.14
	Ammonia	-0.28	0.30	0.18
	Orthophosphate	0.01	0.98	0.03
Nonsalmonid N (number/ha)	Alkalinity	-0.44	0.09	0.40
	Conductivity	-0.42	0.11	0.36
	pH	0.45	0.08	0.42
	Turbidity	-0.36	0.18	0.27
	Nitrate	-0.15	0.58	0.08
	Nitrite	-0.16	0.56	0.08
	Ammonia	-0.36	0.18	0.27
	Orthophosphate	-0.28	0.31	0.17
Nonsalmonid B (kg/ha)	Alkalinity	-0.22	0.42	0.13
	Conductivity	0.04	0.89	0.03
	pH	0.51	0.04	0.48
	Turbidity	-0.01	0.99	0.02
	Nitrate	0.18	0.51	0.10
	Nitrite	0.08	0.76	0.05
	Ammonia	-0.14	0.61	0.07
	Orthophosphate	0.07	0.80	0.04
Total fish N (number/ha)	Alkalinity	-0.43	0.09	0.39
	Conductivity	-0.42	0.10	0.37
	pH	0.45	0.08	0.42
	Turbidity	-0.37	0.16	0.28
	Nitrate	-0.15	0.59	0.08
	Nitrite	-0.18	0.51	0.10
	Ammonia	-0.37	0.16	0.28
	Orthophosphate	-0.28	0.31	0.17
Total fish B (kg/ha)	Alkalinity	-0.16	0.55	0.09
	Conductivity	-0.16	0.57	0.08
	pH	0.44	0.09	0.39
	Turbidity	-0.08	0.79	0.04
	Nitrate	0.04	0.90	0.03
	Nitrite	-0.16	0.56	0.08
	Ammonia	-0.26	0.34	0.16
	Orthophosphate	0.08	0.77	0.05

TABLE 7.—Summary of selected published annual production estimates (ranges) for stream salmonid populations, presented in order of increasing maxima.

Location	Number streams	Number years	Annual production (kg/ha)	Reference
England	4	5	10–35	Crisp et al. (1975)
Tennessee, USA	1	1	18–48	Whitworth and Strange (1983)
Poland	2	1	3–53	Penczak et al. (1986)
Norway	9	1	1–61	Power (1973)
Quebec, Canada	4	3	14–66	O'Connor and Power (1976)
North Carolina and Tennessee, USA	5	1	1–67	Loar et al. (1985)
England	10	1	2–120	Le Cren (1969)
Idaho, USA	2	1	110–125	Goodnight and Bjornn (1971)
Wisconsin, USA	1	11	106–129	Hunt (1974)
Minnesota, USA	2	1	58–139	Waters et al. (1990)
Poland	1	2	3–160	Zalewski et al. (1986)
Poland	2	1	88–165	Debowski (1991)
Colorado, USA	10	2	15–184	Scarnecchia and Ber- gersen (1987)
Minnesota, USA	1	15	44–190	Waters (1983)
Minnesota, USA	1	3	72–258	Newman and Waters (1989)
Denmark	1	3	169–264	Rasmussen (1986)
Denmark	7	1	47–274	Mortensen (1977)
Minnesota, USA	13	2	37–280	Present study
Pennsylvania, USA	2	1	58–300	Cooper and Scherer (1967)
England	1	24	89–339	Elliott (1993)
Wisconsin, USA	1	6	16–360	Brynildson and Bry- nildson (1984)
Wisconsin, USA	1	3	23–396	Brynildson and Ma- son (1975)
New Zealand	1	1	544	Allen (1951)

size was not a limiting factor in detecting significant water quality–fish relationships in comparisons involving nonsalmonid or total fish biomass (power > 0.80 in 14 of 16 comparisons), but results of density comparisons were less certain due to limited test power (power < 0.80 in 10 of 16 comparisons).

Although no water quality–salmonid relationship was evident for southeastern Minnesota streams, an analysis at a broader U.S. spatial scale including Minnesota streams (Table 7) clearly showed a significant correlation of salmonid production with stream water alkalinity (Figure 5, $P < 0.0001$). Within the broader data set, the lack of correlation for our Minnesota streams is evident.

Discussion

Worldwide Comparisons

Salmonid production estimates from southeastern Minnesota streams in this study varied widely

(Tables 3, 4) but spanned a range well within extremes reported by other investigators worldwide (Table 7). In an early review of fish production in streams, Le Cren (1969) suggested 120 kg/ha as the maximum annual production of natural salmonid populations in small streams. At that time, Allen's (1951) estimate of 544 kg/ha annual production for a brown trout population in a New Zealand stream had been revised to lower estimates of 450 kg/ha (Chapman 1967) and 380 kg/ha (Le Cren 1969), but was still considered an anomalous exception. Contrary to Le Cren's early projection, salmonid annual production estimates in our study ranged up to 280 kg/ha and over one-half of these estimates (10 of 16) exceeded 120 kg/ha (Table 3).

Many other more recent estimates have also considerably exceeded Le Cren's suggested maximum, and it is clear that annual salmonid production rates of 120 kg/ha and higher are common. In a later review, Waters (1977a) cited over 20 instances of annual salmonid production estimates exceeding 100 kg/ha and suggested a higher annual production limit of about 300 kg/ha. Mann and Penczak (1986) noted 37 salmonid annual production estimates in excess of 100 kg/ha and 3 that equaled or exceeded 300 kg/ha. Although an upper limit of salmonid annual production of 300 kg/ha is commonly accepted, no precise ceiling has been defined. None of the salmonid populations that we studied were exceptions to the 300-kg/ha limit. Waters (1992) summarized current thinking when he suggested that a range of 100–300 kg/ha defined highly productive streams ranking in the upper categories of stream trout fisheries.

The upper limit of annual salmonid production that we estimated for southeastern Minnesota streams was generally high compared with those of worldwide populations. Our maximum (280 kg/ha) is higher than those for streams in Norway, Poland, Quebec, Tennessee, North Carolina, Idaho, and Colorado and equivalent to those for Danish and Pennsylvania streams. It was lower than that of one English stream (339 kg/ha, Elliott 1993; but other English values are 35–120 kg/ha) and the Horokiwi Stream of New Zealand.

The range of salmonid production that we estimated (37–280 kg/ha) was similar to that for other midwestern trout streams (Table 7). In Wisconsin, Hunt's (1974) annual production estimates for brook trout in four sections of Lawrence Creek over 11 years ranged from 51 to 258 kg/ha. Annual brown trout production estimates from other Wisconsin streams ranged even higher: 360–396

FIGURE 5.—Salmonid annual production (y) related to total alkalinity (x) for streams in southeastern Minnesota and others throughout the United States. Data for others streams are means (among years or sites) from applicable references cited in Table 7.

kg/ha; the highest estimate, however, was from a stream influenced by organic pollution (Brynildson and Mason 1975).

Previous production estimates from southeastern Minnesota trout streams fell into a range similar to that of our study (Table 7). Newman and Waters (1989) estimated annual brown trout production from eight sections of South Branch Creek over 3 years, which ranged from 72 to 258 kg/ha. Over 15 years of study by Waters (1983), salmonid annual production in Valley Creek ranged from 44 kg/ha in 1966, a year of intense flooding when brook trout was most abundant, to 190 kg/ha in 1979, after brown trout had largely replaced brook trout. In our study on that same stream reach, brown trout remained the most prevalent salmonid from 1988 to 1990, and total salmonid annual production had increased slightly to 214 kg/ha (1988–1989) and 197 kg/ha (1989–1990) (Table 3), compared with the 15-year maximum of 190 kg/ha estimated by Waters (1983).

Our findings that young age-classes contribute the most to salmonid biomass and annual production (Figure 3) generally agree with those of other studies. A majority of other studies reporting data analogous to ours for the same three species in North American and European streams (Table 7), found modal biomass and production in the age-1 cohort. Modal biomass or production was common in the age-0 cohort of other studies and was rare in the age-2 cohort. We found no study that re-

ported the occurrence of a biomass or production mode in a salmonid cohort of age 3 or older.

Water Quality–Production Relationship

The high salmonid production rates estimated for streams of southeastern Minnesota in this and other studies contrast sharply with the much lower rates in northern Minnesota streams. Annual salmonid production in two Lake Superior tributaries was only 58 and 139 kg/ha (Waters et al. 1990). The disparate stream productivity among regions in Minnesota has been attributed to variation in water alkalinity caused by differences in geologic history (Krueger and Waters 1983; Waters et al. 1990).

Worldwide summaries of salmonid production estimates in streams suggest that production is correlated with ionic strength or fertility of stream water (Waters 1977a; Chapman 1978; Mann and Penczak 1986; Figure 5), and this has been specifically demonstrated in several field studies (Cooper and Scherer 1967; Mortensen 1977; Scarnecchia and Bergersen 1987). Despite these compelling findings, alkalinity, conductivity, pH, or nutrient concentrations were not correlated with fish population or production measures in our study. This seemingly anomalous finding may be explained by the geographic scale and variation with which we worked. Studies that include streams with wide variation in ionic strength are likely to identify fertility as a limiting factor (Coo-

per and Scherer 1967; Mortensen 1977; Scarnecchia and Bergersen 1987), but others that embrace less variation in ionic strength or that are conducted in areas where fertility is sufficiently high probably will not identify it as a limiting factor (O'Connor and Power 1976; Bowlby and Roff 1986; present study).

The ionic and nutrient content of water is uniformly rather high in streams of southeastern Minnesota and may exceed the range that limits fish populations. Studies that have revealed an alkalinity limitation on salmonid populations included observations from softwater streams and ranged much lower in alkalinity than our study did. For example, Scarnecchia and Bergersen (1987) reported an alkalinity range of 17–120 mg/L in high-elevation streams of Colorado, compared with 172–298 mg/L that we measured in southeastern Minnesota streams. Apparently, factors other than ionic and nutrient concentrations limit salmonid production in southeastern Minnesota streams; such factors may include hydrologic regime, in-stream habitat, landscape features, and biotic processes. Water fertility may, however, influence the overall maximum annual production rate within a region (280 kg/ha for salmonids in southeastern Minnesota).

Management Implications

The management of salmonids and their stream environments has traditionally and currently received much attention (Meehan 1991). Production is clearly the best descriptor of the status of a fish population and thus should be incorporated into management decisions. Many fish managers routinely gather the information necessary to empirically estimate production of salmonids in small streams, and this task may be facilitated by computer software. However, Waters (1992) proposed a simple method for approximating production of a salmonid population as the product of a biomass estimate and a generalized $P/\bar{B}$ ratio for a particular species ($P/\bar{B}$ ratio method). This method would provide more accurate production estimates if the number of age-classes contributing to a biomass estimate were known, compared with a species level $P/\bar{B}$ estimate. Salmonid $P/\bar{B}$ ratios from southeastern Minnesota streams varied widely, but much of that variance was explained by species and population age structure (Table 5; Figure 4). This finding supports the validity of using the $P/\bar{B}$ ratio method to approximate production, and the model describing $P/\bar{B}$ as an inverse linear function of the number of age-classes in a population pro-

vides a useful means of determining an appropriate $P/\bar{B}$ ratio to incorporate into the procedure to improve accuracy. However, direct empirical estimation of production will provide the most accurate estimates, because it may include data from atypical occurrences (e.g., unusually strong or weak year-classes or very slow-growing populations).

Our results on water quality–fish relationships and spatial scale considerations may assist cold-water stream managers in setting realistic management goals. If production is used as an assessment tool to monitor changes in fish populations associated with management strategies and techniques, then a realistic annual production goal can be developed by considering upper limits for a region based on water fertility. For example, it would be unrealistic to expect annual salmonid production in a region containing softwater streams (alkalinity < 50 mg/L) to reach or exceed 100 kg/ha—a rate that would be considered low for a hardwater stream. It is clear that an increasing knowledge of the influence of water quality on fish populations will improve our management and ecological understanding of these systems. We expect that future empirical analyses and simulations will further define the relationship between fish productivity and the lotic environment at varying spatial and temporal scales and thus better identify local limiting factors.

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References

- Allen, K. R. 1949. Some aspects of the production and cropping of fresh waters. *Transactions of the Royal Society of New Zealand* 77(5):222-228.
- Allen, K. R. 1951. The Horokiwi Stream. New Zealand Marine Department Fishery Bulletin 10.
- Bohlin, T., S. Hamrin, T. G. Heggberget, G. Rasmussen, and S. J. Saltveit. 1989. Electrofishing—theory and practice with special emphasis on salmonids. *Hydrobiologia* 173:9-43.
- Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. *Transactions of the American Fisheries Society* 115: 503-514.
- Brynildson, O. M., and C. L. Brynildson. 1984. Impacts of a floodwater-retarding structure on year class strength and production by wild brown trout in a Wisconsin coulee stream. Wisconsin Department of Natural Resources Technical Bulletin 146.
- Brynildson, O. M., and J. W. Mason. 1975. Influence of organic pollution on the density and production of trout in a Wisconsin stream. Wisconsin Department of Natural Resources Technical Bulletin 81.
- Chapman, D. W. 1967. Production in fish populations. Pages 3-29 in S. D. Gerking, editor. *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford, UK.
- Chapman, D. W. 1978. Production in fish populations. Pages 5-25 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Blackwell Scientific Publications, Oxford, UK.
- Cone, R. S., and C. C. Krueger. 1988. Comparison of survival, emigration, habitat use, marking mortality, and growth between two strains of brook trout in Adirondack ponds. *North American Journal of Fisheries Management* 8:497-504.
- Cooper, E. L., and R. C. Scherer. 1967. Annual production of brook trout (*Salvelinus fontinalis*) in fertile and infertile streams of Pennsylvania. *Proceedings of the Pennsylvania Academy of Science* 41: 65-70.
- Crisp, D. T., R. H. K. Mann, and J. C. McCormack. 1975. The populations of fish in the River Tees system on the Moor House National Nature Reserve, Westmorland. *Journal of Fish Biology* 7:573-593.
- Debowski, P. 1991. Production of brown trout (*Salmo trutta* m. *fario* L.) in two tributaries of the Pasleka River. *Polskie Archiwum Hydrobiologii* 38:283-294.
- Deegan, L. A., and B. J. Peterson. 1992. Whole-river fertilization stimulates fish production in an Arctic tundra river. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1890-1901.
- Elliott, J. M. 1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. *Canadian Special Publication of Fisheries and Aquatic Sciences* 118:109-122.
- Elliott, J. M. 1994. *Quantitative ecology and the brown trout*. Oxford University Press, Oxford, UK.
- Goodnight, W. H., and T. C. Bjornn. 1971. Fish production in two Idaho streams. *Transactions of the American Fisheries Society* 100:769-780.
- Hach Co. 1992. *Hach water analysis handbook*, 2nd edition. Hach Co., Loveland, Colorado.
- Hunt, R. L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wisconsin Department of Natural Resources Technical Bulletin 82.
- Jearld, A., Jr. 1983. Age determination. Pages 301-324 in L. A. Nielsen, and D. L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Krueger, C. C., and T. F. Waters. 1983. Annual production of macroinvertebrates in three streams of different water quality. *Ecology* 64:840-850.
- Kwak, T. J. 1992. Modular microcomputer software to estimate fish population parameters, production rates and associated variance. *Ecology of Freshwater Fish* 1:73-75.
- Kwak, T. J. 1993. Influence of physical and biotic factors on trout production dynamics in southeastern Minnesota streams. Doctoral dissertation. University of Minnesota, St. Paul.
- Le Cren, E. D. 1969. Estimates of fish populations and production in small streams in England. Pages 269-280 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Loar, J. M., and ten coauthors. 1985. Application of habitat evaluation models in southern Appalachian trout streams. Oak Ridge National Laboratory, Environmental Sciences Division Publication 2383, Oak Ridge, Tennessee.
- Manly, B. F. J. 1994. *Multivariate statistical methods: a primer*, 2nd edition. Chapman and Hall, New York.
- Mann, R. H. K., and T. Penczak. 1986. Fish production in rivers: a review. *Polskie Archiwum Hydrobiologii* 33:233-247.
- Meehan, W. R., editor. 1991. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Miller, R. G., Jr. 1981. *Simultaneous statistical inference*, 2nd edition. Springer-Verlag, New York.
- Milliken, G. A., and D. E. Johnson. 1984. *Analysis of messy data, volume 1: designed experiments*. Lifetime Learning Publications, Belmont, California.
- Mills, D. H. 1965. Studies of the survival of salmon fry and their application. Report of the Challenger Society 3, (part 17):33-34.
- Mortensen, E. 1977. Fish production in small Danish streams. *Folia Limnologica Scandinavica* 17:21-26.
- Mundie, J. H., S. M. McKinnell, and R. E. Traber. 1983. Responses of stream zoobenthos to enrichment of gravel substrates with cereal grain and soybean. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1702-1712.
- Newman, R. M., and F. B. Martin. 1983. Estimation of fish production rates and associated variances. Ca-

- nadian Journal of Fisheries and Aquatic Sciences 40:1729-1736.
- Newman, R. M., and T. F. Waters. 1989. Differences in brown trout (*Salmo trutta*) production among contiguous sections of an entire stream. Canadian Journal of Fisheries and Aquatic Sciences 46:203-213.
- Northcote, T. G., editor. 1969. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- O'Connor, J. F., and G. Power. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. Journal of the Fisheries Research Board of Canada 33:6-18.
- Ojakangas, R. W., and C. L. Matsch. 1982. Minnesota's geology. University of Minnesota Press, Minneapolis.
- Penczak, T., J. Lobon-Cervia, K. O'Hara, and H. Jakubowski. 1986. Production and food consumption by fish populations in the Pilawa and Dobrzyca rivers, north Poland. Polskie Archiwum Hydrobiologii 33:345-372.
- Pielou, E. C. 1975. Ecological diversity. Wiley, New York.
- Power, G. 1973. Estimates of age, growth, standing crop and production of salmonids in some north Norwegian rivers and streams. Institute of Freshwater Research Drottningholm Report 53:78-111.
- Railsback, S. F., B. D. Holcomb, and M. G. Ryon. 1989. A computer program for estimating fish population sizes and annual production rates. Oak Ridge National Laboratory, Environmental Sciences Division Publication 3245, Oak Ridge, Tennessee.
- Rasmussen, G. 1986. The population dynamics of brown trout (*Salmo trutta* L.) in relation to year-class size. Polskie Archiwum Hydrobiologii 33:489-508.
- Ricker, W. E. 1946. Production and utilization of fish populations. Ecological Monographs 16:373-391.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.
- SAS Institute. 1989. SAS/STAT user's guide, version 6, 4th edition, volume 1. SAS Institute, Cary, North Carolina.
- Scarnecchia, D. L., and E. P. Bergersen. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. North American Journal of Fisheries Management 7:315-330.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edition. Charles Griffin, London.
- Smith, S. H. 1954. Method of producing plastic impressions of fish scales without using heat. Progressive Fish-Culturist 16:75-78.
- Thorn, W. C. 1988. Evaluation of habitat improvement for brown trout in agriculturally damaged streams of southeastern Minnesota. Minnesota Department of Natural Resources, Section of Fisheries, Investigational Report 394.
- Thorn, W. C. 1990. Evaluation of special regulations for trout in southeast Minnesota streams. Minnesota Department of Natural Resources, Section of Fisheries, Investigational Report 401.
- Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. Journal of Wildlife Management 28:617-660.
- Waters, T. F. 1977a. Secondary production in inland waters. Advances in Ecological Research 10:91-164.
- Waters, T. F. 1977b. The streams and rivers of Minnesota. University of Minnesota Press, Minneapolis.
- Waters, T. F. 1983. Replacement of brook trout by brown trout over 15 years in a Minnesota stream: production and abundance. Transactions of the American Fisheries Society 112:137-146.
- Waters, T. F. 1988. Fish production-benthos production relationships in trout streams. Polskie Archiwum Hydrobiologii 35:545-561.
- Waters, T. F. 1992. Annual production, production/biomass ratio, and the ecotrophic coefficient for management of trout in streams. North American Journal of Fisheries Management 12:34-39.
- Waters, T. F., M. T. Doherty, and C. C. Krueger. 1990. Annual production and production : biomass ratios for three species of stream trout in Lake Superior tributaries. Transactions of the American Fisheries Society 119:470-474.
- Whitworth, W. E., and R. J. Strange. 1983. Growth and production of sympatric brook and rainbow trout in an Appalachian stream. Transactions of the American Fisheries Society 112:469-475.
- Zalewski, M., P. Frankiewicz, and B. Brewinska-Zaras. 1986. The production of brown trout (*Salmo trutta* L.) introduced to the streams of various orders in an upland watershed. Polskie Archiwum Hydrobiologii 33:411-422.
- Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.

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