Transactions of the American Fisheries Society 128:1151–1162, 1999

Long-Term Trout Production Dynamics in Valley Creek, Minnesota

THOMAS F. WATERS*

Department of Fisheries and Wildlife, University of Minnesota, 1980 Folwell Avenue, St. Paul, Minnesota 55108, USA

Abstract.—Long-term studies in Valley Creek, Minnesota, continued from April 1965 to April 1986. Initially, the brook trout *Salvelinus fontinalis* was the only trout species present, but both rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* later entered the study section. Brook trout declined after severe floods, recovered, declined again after an extreme sedimentation, and continued to decline while brown trout increased. Brook trout biomass, initially at 184 kg/ha, decreased to 4 kg/ha at the end of the period, a reduction of 98%. Rainbow trout entered the study section when floods overflowed private ponds, but their population did not reach high levels. After its entrance, the brown trout increased to predominate the trout fauna with a final biomass of 201 kg/ha. At the end of the study period, brook trout biomass remained at 2% of all trout species, rainbow trout at 5%, and brown trout at 93%. Maximum annual production by brook trout, near the beginning of the 21-year period, was 171 kg/ha. Annual production had declined to only 9 kg/ha (3% of all-trout production) by the end of the study. Rainbow trout annual production remained low at 8 kg/ha (2%) by the end of the study. Annual production by brown trout increased to 322 kg/ha (95%). Density and mean annual biomass varied similarly over the study period. The ratio of annual production to mean annual biomass (P:B) varied with species, reflecting length of life span: 1.4 for brook trout and rainbow trout, and 1.2 for brown trout. Annual P:B ratios varied among age-groups, being highest for younger fish. The importance of long-term studies was emphasized by results of the severe environmental disturbances that ensued during the 21-year period. The selection of any 1- or 2-year period for study would not have produced an accurate representation of the stream's long-term biological status.

Science has recognized the importance of long-term ecological research, but such studies are rare. Reasons for this scarcity no doubt include the lack of a recognized immediate need. Furthermore, the requirement of an effective length of a long-term project may be intimidating. With fish, a number of years equal to a full life cycle is a minimum, but the value of even longer terms is obviously preferable.

Elliott (1990) pointed out several major objectives of long-term research: recording base-line variation, detecting trends, detailing of rare events, and acquiring information upon which hypotheses can be formulated. Most important may be base-line data for comparison with later, unpredictable ecological disturbances. Long-term research has had a relatively short history in fresh waters, with some notable exceptions. An outstanding example is the contribution of the Freshwater Biological Association (Lake Windemere, England), where several fishery programs began in the 1930s and 1940s and are continuing (Elliott 1990).

The seminal contributions by Ricker (1946) and Allen (1949), who provided formulations for calculating production, had major influences on the estimation of annual production by fish. Their methods and the development of highly efficient field sampling by electrofishing now permit production estimation with good precision.

Annual production by fish has been defined as the elaboration of fish tissue, by all year-classes present in the population, on a given area of stream over the year. The most common units are kilograms (wet mass) per hectare per year. The expression ''annual production'' includes all of the tissue synthesized by all fish in the area during all or part of the year. The final estimate integrates many underlying variables influencing productivity. The level of annual production has been described as one of the most significant indicators of population success (Le Cren 1969; Hunt 1974; Benke 1993).

Production dynamics includes many variables such as reproductive success, growth and survival rates, numerical abundance, and biomass. Additionally, some special relationships have attracted special interest—for example, the ratio of annual production to mean annual biomass (P:B) (Hunt 1974; Mortensen 1977; Waters et al. 1990).

Although many production data have been ac-

* E-mail: tomfwaters@uswest.net

Received March 23, 1998; accepted January 14, 1999

cumulated, only a few long-term studies of salmonid production dynamics have been forthcoming. Bergheim and Hesthagen (1990) reported production by Atlantic salmon and brown trout in a Norwegian river over 5 years. Two longer examples are Hunt's (1974), 11 years of annual production estimation for a stream population of brook trout S*alvelinus fontinalis* in Wisconsin, and Elliott's (1993) 25-year study of brown trout S*almo trutta* in England. Hunt's study was primarily a test of effectiveness of instream habitat manipulation; the results included increases in both annual production and angler catch. Elliott's (1993) studies, although limited to juvenile migratory trout, provided information on many production dynamics, especially those relating to the early setting of year-class strength.

In the present study, the population dynamics of three trout species were investigated over many life cycles in Valley Creek, a small Minnesota trout stream. Annual production and the associated variables of biomass, density, and P:B ratios for brook trout, rainbow trout *Oncorhynchus mykiss*, and brown trout (when present) were measured for a 21-year term.

A severe flood occurred in Valley Creek immediately after the first mark–recapture estimate, reworking the streambed and destroying all instream structure. Thus, the time seemed propitious for initiating a long-term study. Estimates were continued from spring 1965 to spring 1986, for 21 continuous years. Several major floods, a severe sedimentation, and an almost complete species replacement occurred during that time.

This study was begun when few production estimates had been published. Consequently, the initial objective was simply to measure the annual production of an apparently stable brook trout population, the only trout species present in Valley Creek at the time. Methods for statistical treatment of production did not exist.

Some early years' estimates on annual production, biomass, and annual P:B ratios for Valley Creek trout have been published previously (Elwood and Waters 1969; Hanson and Waters 1974; Waters 1983), a sum of 15 years. To these, 6 additional years, P:B ratios by age-groups, and standard errors on all estimates are added in the present report.

The main objective was to acquire a long-term base of data that could be used to evaluate the effects of future environmental events.

Study Area

Valley Creek is a short (6-km), first-order tributary to the St. Croix River in east central Minnesota, a warmwater stream. Valley Creek flows in a deeply incised, limestone–bedrock catchment. Dissolved oxygen was always near atmospheric saturation, midday water temperatures were usually about 15°C in summer and 5°C in winter, and alkalinity (as $CaCO_3$) was constant at 220 mg/L. The study section, located about midway in the course of the stream, was about 0.4 km long with an area of 0.181 ha. In this section, base discharge was about 0.14 m^3/s and mean width was about 4.5 m. Except for minimal angling by some residents, the trout population was unexploited. Waters (1983) gave other details of the stream and study section.

Methods

Field sampling.—Field sampling began in April 1965 and terminated with the estimate of April 1986. Procedures were the same as those reported in previous papers (e.g., Waters 1983). A crew of five persons, we made population estimates either two or three times per year by the Petersen single-census, mark–recapture method (Ricker 1975). Each estimate consisted of a marking sample and a subsequent recapture sample separated by approximately 1 week. We used a direct-current, engine-driven electrofisher, carried in a small boat, to which were attached the electrodes. We attempted to sample all habitats in the stream, applying the degree of effort in accordance with fish abundance. All fish were measured and marked with a small caudal fin clip that was alternated between dorsal and ventral lobes for successive estimates. We collected fish in a continuous upstream direction and returned marked fish near the location of capture. During each estimate, we weighed and scale-sampled 20 fish in each size-group (2.5 cm or 2.0 cm) if available. These fish were also returned immediately to the water.

Estimates were made either twice (April and September, in the 16 years 1965–1971 and 1977–1985) or three times per year (March [occasionally February], July, and November, in the 5 years 1972–1976).

Data analysis.—Analytic procedures were similar to those described by Kwak and Waters (1997). Estimates of production, biomass, and density were computed with procedures described in earlier reports, but current methods for estimating variance and standard error (Newman and Martin

1983) were added and a computer program based upon their procedures was used (Kwak 1992). The adjusted Petersen method (in which 1 was added to all three components of the mark–recapture computation for low numbers; Ricker 1975:78) was included in this computer program. Computer calculations from all data for the 21-year period were made for the present report, including repetition of calculations for the earlier 15 years (Waters 1983). This procedure resulted in small differences from estimates in previous reports but provided consistent methods and variances for the entire set. Units for biomass and production are expressed in wet mass.

Variances were calculated with original data from the study section area (0.181 ha), and area conversions for values and variances were made later to a per-hectare basis. Standard errors were computed from the program of Kwak (1992). However, standard errors for means across years during which environmental disturbances occurred were calculated manually as the standard error of the mean. Although estimates of production, biomass, and density were complete for the entire 21-year period, original field data were not available for the first two years, 1965–1966; consequently, statistical computations were not possible for these first two years.

Results

Overview of Events in Valley Creek: 1965–1986

In early 1965, Valley Creek appeared to have been stable for some time. No floods, droughts, or extreme turbidity had been observed in 1958–1965 during other research. Local residents reported no floods or other disturbance for many more years. Exploratory electrofishing revealed only three fish species, brook trout, slimy sculpin *Cottus cognatus,* and American brook lamprey *Lampetra appendix.* The brook trout was predominant throughout the stream. Rainbow trout and brown trout entered the study area after the present study began, but their age distribution did not stabilize for several years. Reported estimates began for rainbow trout in 1971 and for brown trout in 1973. All analyses continued through the final study year of 1985.

Preliminary electrofishing of brook trout in February 1965 revealed a large population, but almost immediately a series of floods occurred, two in March and one in June 1965 and another in February 1966. The March 1965 floods, occurring when the catchment surfaces were frozen, did not create a sedimentation problem; rather, the floods severely scoured the channel bottom and nearly eliminated the 1965 year-class of brook trout, which would have been in the fry stage at the time. However, the adult population survived almost intact, although temporarily; the April estimate (age 1 and older) did not appear to be affected. The June 1965 flood eroded the land surfaces throughout the catchment and created massive sand deposits in the channel. All cover—pools, riffles, undercut banks, and woody debris—was obliterated. In addition, the February 1966 flood greatly reduced the 1966 year-class. By the spring of 1967, the combined effect of failed reproduction and loss of adult habitat had been to decimate the brook trout population.

During relatively stable conditions for the next few years, the brook trout population recovered. Severe sedimentation occurred in 1970–1971, caused by a housing development in the upper catchment, again reducing the trout population. The sedimentation also depressed invertebrates (Waters 1982). Although brook trout increased in the next few years, an expanding brown trout population gradually replaced the brook trout, and they never again reached initial levels of early 1965.

Rainbow trout appeared in spring 1967 from the previous year's flood and overflow of private ponds in the lower catchment. Some of these fish spawned that same spring; young-of-year rainbow trout appeared in the following fall estimate. Rainbow trout increased in the next few years, reaching a stable population structure in 1973 and a maximum in 1975, but then declined to a population level near that of brook trout by the end of the study period.

Brown trout made their initial appearance in the study section in 1969, apparently having existed in other portions of the stream. They increased through the following years, especially after the sediment loadings of 1970–1971. By the end of the 21-year period, brown trout greatly predominated in the trout population.

Annual Production, Biomass, and Density

Brook trout.—Brook trout fluctuated greatly, especially with the severe environmental disturbances (Tables 1, 2; Figures 1, 2). Although estimates of annual production and mean annual biomass were not available prior to the 1965 floods, the first point estimates of biomass and density for brook trout in April 1965 were 184 kg/ha (Figure 1) and 6,618 fish/ha (Table 2; Figure 2). Because

TABLE 1.—Annual production (P, kg/ha) and mean annual biomass (B, kg/ha) for brook trout in Valley Creek, Minnesota, 1965–1985. Standard errors could not be calculated for 1965 and 1966.

	Production		Biomass	
Year	P ± 2 SE	% of all trout	B ± 2 SE	% of all trout
1965	61	100	62	100
1966	44	100	33	100
1967	94 ± 9	83	48 ± 4	84
1968	132 ± 11	89	102 ± 11	87
1969	171 ± 11	99	134 ± 7	96
1970	130 ± 18	96	114 ± 9	96
1971	80 ± 11	84	70 ± 4	85
1972	107 ± 12	77	66 ± 6	78
1973	112 ± 11	74	82 ± 5	73
1974	96 ± 9	62	78 ± 6	61
1975	97 ± 13	57	69 ± 7	55
1976	87 ± 11	55	56 ± 5	49
1977	42 ± 5	35	37 ± 5	35
1978	35 ± 6	33	28 ± 4	23
1979	27 ± 5	15	23 ± 3	15
1980	25 ± 3	11	12 ± 2	8
1981	18 ± 3	10	12 ± 1	7
1982	16 ± 2	7	11 ± 1	6
1983	16 ± 2	6	10 ± 2	4
1984	20 ± 3	7	10 ± 1	4
1985	9 ± 2	3	7 ± 1	3

TABLE 2.—Densities (numbers, N, per hectare ± 2 SE) of brook trout, rainbow trout, and brown trout in Valley Creek on spring dates, 1965–1986. Standard errors could not be calculated for 1965 and 1966.

Date	Brook trout (N/ha ± 2 SE)	Rainbow trout (N/ha ± 2 SE)	Brown trout (N/ha ± 2 SE)
Apr 1965	6,618		
Apr 1966	425		
Apr 1967	575 ± 25		
Apr 1968	2,159 ± 208		
Apr 1969	5,416 ± 604		
Apr 1970	6,673 ± 168		
Apr 1971	4,865 ± 470	326 ± 94	
Mar 1972	1,918 ± 254	367 ± 96	
Mar 1973	5,833 ± 843	213 ± 46	61 ± 0
Mar 1974	2,616 ± 411	620 ± 199	134 ± 33
Feb 1975	2,991 ± 693	852 ± 161	420 ± 196
Mar 1976	2,785 ± 355	667 ± 107	607 ± 197
Apr 1977	1,206 ± 179	773 ± 178	533 ± 88
Apr 1978	1,322 ± 193	835 ± 172	1,098 ± 143
Mar 1979	734 ± 129	517 ± 132	1,539 ± 268
Apr 1980	509 ± 101	540 ± 138	2,452 ± 295
Apr 1981	208 ± 33	199 ± 45	1,468 ± 136
Apr 1982	283 ± 59	138 ± 38	2,608 ± 268
Apr 1983	373 ± 59	308 ± 70	4,929 ± 386
Apr 1984	391 ± 76	536 ± 206	5,223 ± 391
Apr 1985	312 ± 64	99 ± 32	5,371 ± 533
Apr 1986	171 ± 88	315 ± 138	7,395 ± 746

these data were obtained prior to the floods, they represent the best estimates of the original population status, although a later peak reached about the same levels.

During the first two years, 1965 and 1966, brook trout annual production was low at 61 and 44 kg/ha (Table 1), and mean annual biomass was also low at 62 and 33 kg/ha (Table 1). These low values appeared to be the result of the floods. Density followed a similar pattern, dropping from its initial high of 6,618 fish/ha in April 1965 to only 425/ha in April 1966 (Table 2; Figure 2). Stable hydrologic conditions prevailed in the subsequent 3 years, and brook trout production, biomass, and spring density all recovered by 1969.

The sedimentation in 1970–1971 dropped the brook trout population again, but after a short period of recovery they reached another peak in 1973 (Tables 1, 2; Figures 1, 2). From 1973 on, however, brook trout gradually decreased as brown trout increased. The study period ended with annual production by brook trout at 9 kg/ha, a drop of 95% from its maximum of 171 kg/ha (Table 1). Mean annual biomass ended at 7 kg/ha, a drop of 95% from its maximum of 134 kg/ha (Table 1). Spring biomass ended the study period at only 4 kg/ha in April 1986, a decrease of 98% from its initial biomass of 184 kg/ha in April 1965 (Figure 1). Density dropped from 6,618 fish/ha in April 1965, to 171/ha in April 1986, a decrease of 97% (Table 2; Figure 2).

Rainbow trout.—The rainbow trout that entered the study section in 1967 were ages 2 and 3. These fish spawned, and their population structure attained a stable condition in 1971, when annual production was 12 kg/ha and mean annual biomass was 9 kg/ha (Table 3). Rainbow trout continued until 1975, when they reached their highest production and biomass (Table 3) and their highest spring density (Table 2; Figure 2). They decreased gradually to finish at 8 kg/ha for both annual production and mean annual biomass (Table 3). Final spring biomass was 11 kg/ha in April 1986 (Figure 1), and final density was 315 fish/ha (Table 2; Figure 2).

Brown trout.—Brown trout first appeared in the study section in 1969 and reached a stable condition in 1973. In that year, both annual production and mean biomass were 11 kg/ha (Table 4), and spring density was 61/ha (Table 2; Figure 2). Brown trout increased from this point, reaching their maximum at the conclusion of the study. Final annual production was 322 kg/ha, and mean annual biomass was 253 kg/ha (Table 4). Spring biomass and density followed similar patterns, reaching maxima of 201 kg/ha (Figure 1) and 7,395 fish/ha (Table 2; Figure 2) in April 1986.

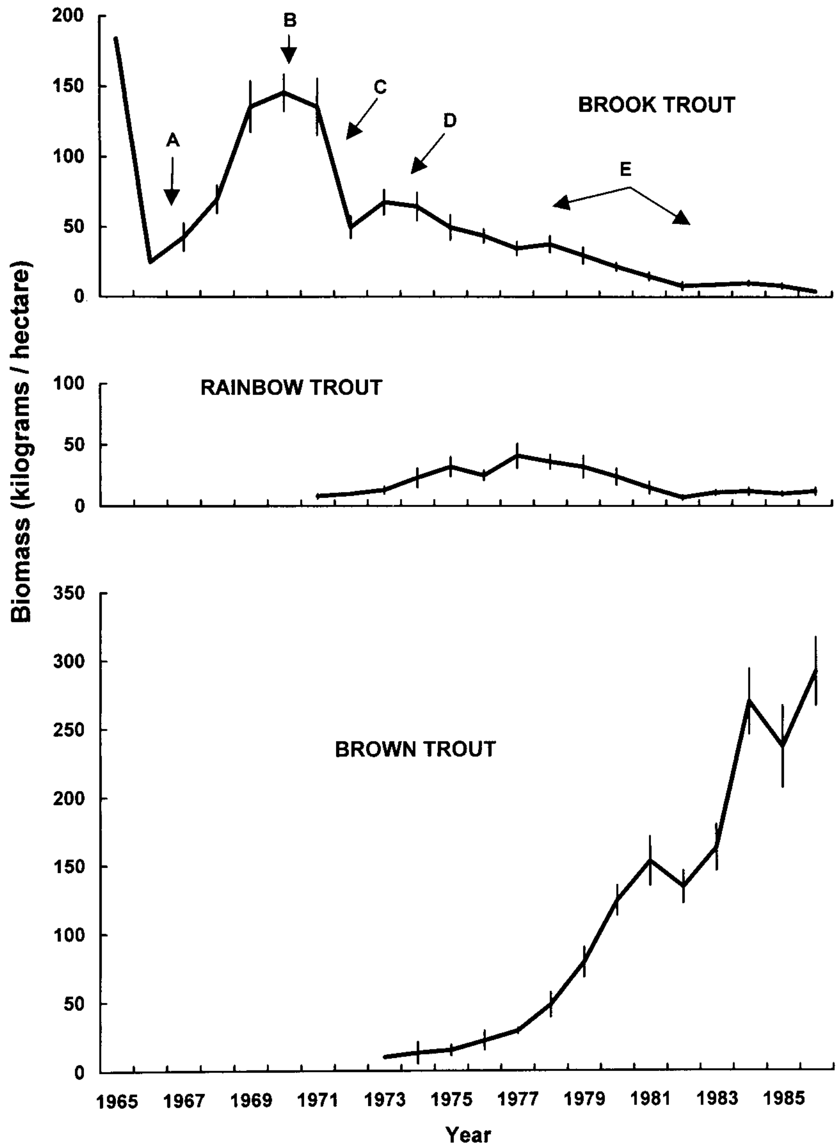

FIGURE 1.—Biomass of brook trout, rainbow trout, and brown trout in Valley Creek, Minnesota, in spring 1965–1986. Top graph shows reduction in brook trout after 1965 and 1966 floods (A), recovery from flood damage (B), reduction due to 1970 sedimentation (C), recovery from sedimentation (D), and gradual decrease in brook trout during brown trout expansion (E). Data are point estimates ± 2 SE.

All trout species.—In the final year, total annual production for all three trout species combined was 339 kg/ha; total mean annual biomass was 268 kg/ha (Figure 3), not much higher than for brown trout alone. For brook trout, the final annual production and mean annual biomass were each 3% of all trout; for rainbow trout, annual production was 2% and mean annual biomass was 3% of all trout. Brown trout final annual production was 95% of all trout, and mean annual biomass was 94% of all trout. In the final point estimate in April 1986, total biomass for all three species combined was 216 kg/ha; total density was 7,881 fish/ha.

Annual P:B Ratios

Annual P:B ratios for brook trout averaged 1.4 over the study period, and the number of age-groups averaged 3.9 (Table 5). For rainbow trout, annual P:B ratios also averaged 1.4, over the 15-year period 1971–1985, and the number of age-

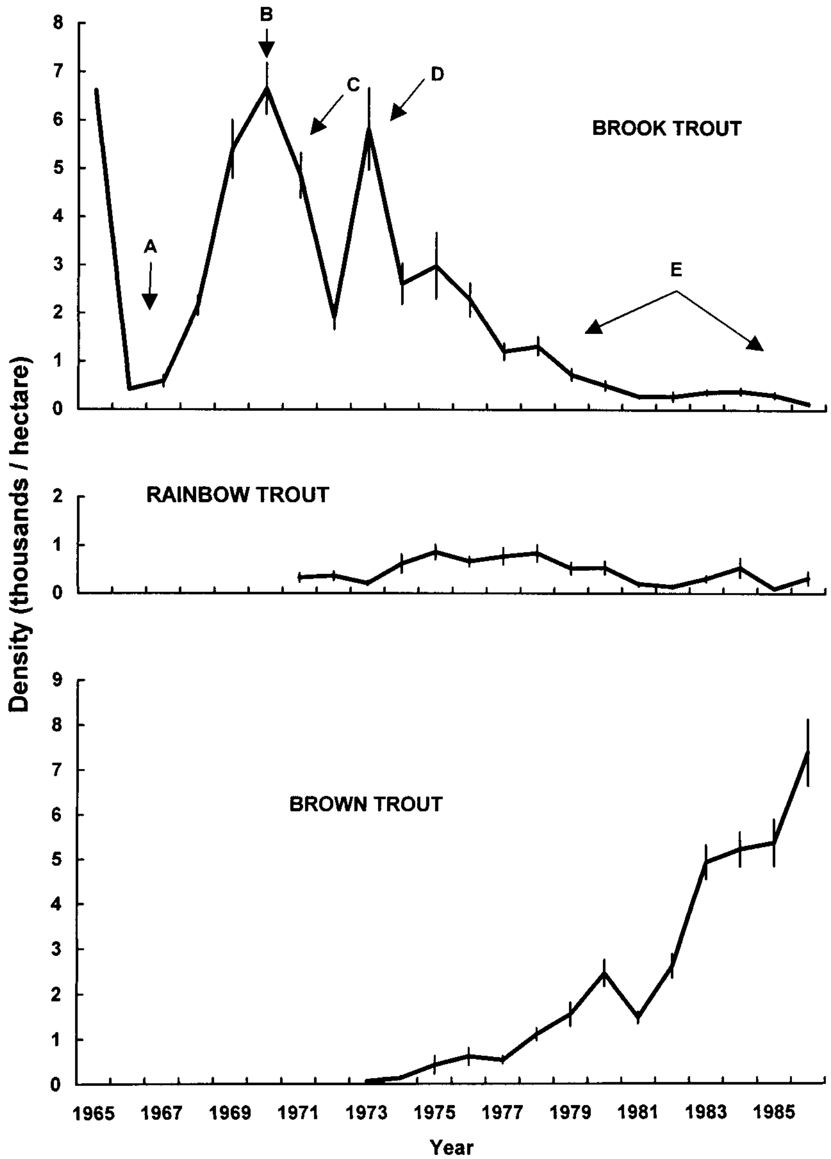

FIGURE 2.—Numerical density of brook trout, rainbow trout, and brown trout in Valley Creek, Minnesota, in spring 1965–1986. Top graph shows reduction in brook trout after 1965 and 1966 floods (A), recovery from flood damage (B), reduction due to 1970 sedimentation (C), recovery from sedimentation (D), and gradual decrease in brook trout during brown trout expansion (E). Data are point estimates ± 2 SE.

groups averaged 3.5 (Table 5). For both brook trout and rainbow trout, the number of age-groups present dropped in later years when both populations were in decline. Annual P:B ratios for brown trout averaged 1.2 over the 13-year period 1973–1985, significantly lower than for the other two species, and the brown trout population included an average 5.3 age-groups (Table 5).

Annual P:B Ratios by Age-Group

Annual P:B ratios were higher for younger age-groups, consistently through all ages. All three species had similar ratios and distributions through the age-groups. Annual P:B was highest (1.9–2.1) for age-group 0 and lowest (0.2 and 0.5) for age-group 4. The number of years in the computations varied (4–17) with age-group and species (Table 6).

TABLE 3.—Annual production (P, kg/ha) and mean annual biomass (B, kg/ha) for rainbow trout in Valley Creek, 1971–1985.

	Production		Biomass	
Year	P ± 2 SE	% of all trout	B ± 2 SE	% of all trout
1971	12 ± 2	13	9 ± 1	11
1972	27 ± 6	19	13 ± 1	15
1973	29 ± 5	19	19 ± 2	17
1974	37 ± 5	24	35 ± 2	27
1975	52 ± 7	31	35 ± 2	28
1976	36 ± 6	23	28 ± 2	24
1977	35 ± 4	29	30 ± 1	29
1978	27 ± 4	25	26 ± 3	22
1979	27 ± 6	14	24 ± 2	16
1980	20 ± 3	9	12 ± 1	8
1981	9 ± 2	5	8 ± 1	5
1982	10 ± 3	4	10 ± 1	5
1983	17 ± 2	6	9 ± 1	4
1984	16 ± 3	6	10 ± 1	4
1985	8 ± 2	2	8 ± 1	3

TABLE 4.—Annual production (P, kg/ha) and mean annual biomass (B, kg/ha) for brown trout in Valley Creek, 1973–1985.

	Production		Biomass	
Year	P ± 2 SE	% of all trout	B ± 2 SE	% of all trout
1973	11 ± 2	7	11 ± 4	10
1974	21 ± 2	14	16 ± 4	12
1975	20 ± 2	12	21 ± 3	17
1976	35 ± 5	22	31 ± 3	27
1977	44 ± 4	36	38 ± 4	36
1978	45 ± 7	42	66 ± 5	55
1979	139 ± 10	71	105 ± 6	68
1980	174 ± 11	80	130 ± 7	84
1981	156 ± 12	85	147 ± 10	88
1982	201 ± 13	89	164 ± 9	89
1983	256 ± 17	88	225 ± 12	92
1984	253 ± 21	87	257 ± 15	92
1985	322 ± 21	95	253 ± 16	94

Discussion

Annual Production, Biomass, Density, and P:B Ratio

Annual production and its associated variables are among the most important of fish population dynamics. Elaboration of trout tissue proceeds mainly during the spring and early summer seasons. However, although minimal production may occur in winter, it is often exceeded by metabolic losses so that fish may lose mass. This loss cannot be considered ''negative production'' (implying a reversal of tissue elaboration), and for calculating production it is usually considered zero, probably producing a slight underestimate in production.

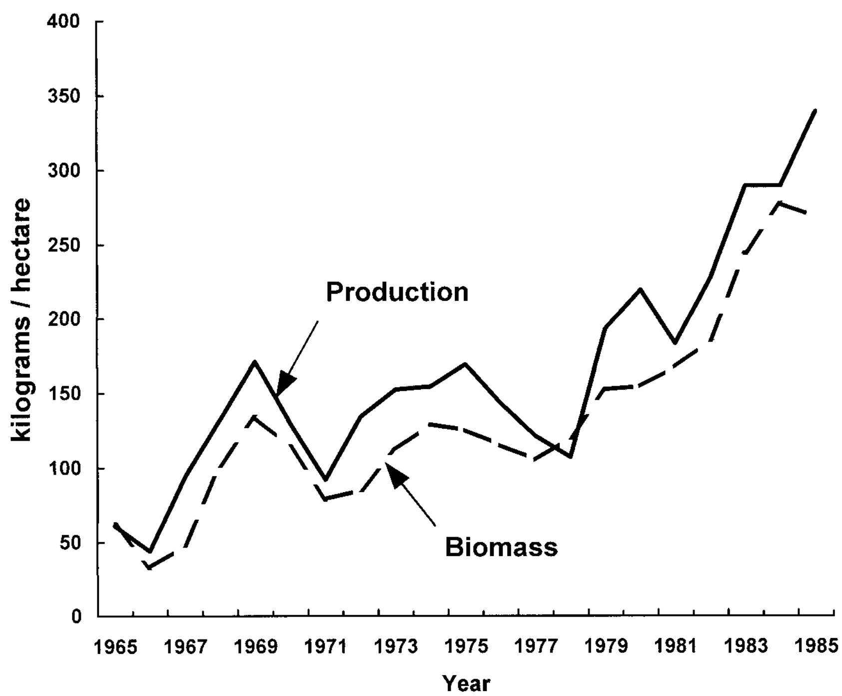

FIGURE 3.—Annual production and annual mean biomass for brook trout, rainbow trout, and brown trout, all species combined, in Valley Creek, Minnesota,1965–1985.

TABLE 5.—Annual production : biomass (P:B) ratios for brook trout, rainbow trout, and brown trout in Valley Creek, 1965–1985. Standard errors could not be calculated for 1965 and 1966.

Year and mean	Brook trout P:B ± 2 SE	Brook trout Age-groups	Rainbow trout P:B ± 2 SE	Rainbow trout Age-groups	Brown trout P:B ± 2 SE	Brown trout Age-groups
1965	1.0					
1966	1.3					
1967	2.0 ± 0.2	4				
1968	1.3 ± 0.2	4				
1969	1.3 ± 0.1	4				
1970	1.1 ± 0.1	4				
1971	1.1 ± 0.2	4	1.3 ± 0.2	4		
1972	1.6 ± 0.2	4	2.1 ± 0.5	4		
1973	1.4 ± 0.1	5	1.5 ± 0.3	4	1.0 ± 0.3	4
1974	1.2 ± 0.1	4	1.1 ± 0.2	4	1.4 ± 0.5	5
1975	1.4 ± 0.2	4	1.5 ± 0.2	4	1.1 ± 0.3	6
1976	1.6 ± 0.2	5	1.3 ± 0.2	3	1.2 ± 0.2	5
1977	1.1 ± 0.2	5	1.2 ± 0.1	5	1.2 ± 0.2	5
1978	1.2 ± 0.3	4	1.0 ± 0.2	3	0.7 ± 0.1	5
1979	1.2 ± 0.3	5	1.1 ± 0.3	4	1.4 ± 0.1	6
1980	2.1 ± 0.4	3	1.7 ± 0.3	3	1.3 ± 0.1	6
1981	1.5 ± 0.3	3	1.1 ± 0.2	3	1.1 ± 0.1	6
1982	1.5 ± 0.2	3	1.0 ± 0.3	3	1.3 ± 0.1	5
1983	1.6 ± 0.3	3	1.9 ± 0.3	2	1.2 ± 0.1	5
1984	2.0 ± 0.4	3	1.6 ± 0.3	3	1.0 ± 0.1	5
1985	1.3 ± 0.4	3	1.0 ± 0.3	3	1.3 ± 0.1	6
Mean	1.4 ± 0.14	3.9	1.4 ± 0.09	3.5	1.2 ± 0.05	5.3

Production serves as an energy source for the rest of the stream community, and in addition it provides for losses from emigration (volitional or forced by habitat disruption), avian and mammalian predation, and harvest by anglers. If production approximates these losses, biomass remains relatively constant year to year.

Annual production, biomass, and density varied widely over the study period (Tables 1–4; Figures 1–3). The floods and sedimentation affected mainly brook trout, because rainbow trout and brown were not present in early portions of the project. Environmental disturbances—mainly floods and sedimentation—were the main causes of the variation, although some sharp changes occurred without observed disturbance. For example, production and biomass dropped sharply for brook trout in 1977 but not for rainbow trout or brown trout. This decrease in brook trout productivity may have been due to increasing competition from the other two species. In addition, 1981 brought decreases in production and biomass of brook trout and rainbow trout, apparently because of weak 1980 year-classes. Brown trout production also decreased in 1981, but proportionately less. Decreases in brook trout and rainbow trout may have been caused partially by the stress of increasing competition from the brown trout.

Information on hydrologic events was available only in anecdotal form, minimal but still critical. Obviously, quantitative measurement of discharge, water temperature, water chemistry and, especially, sedimentation and suspended sediment would have added greatly to the value of the long-term study. Local annual precipitation data were included in the previous report that covered the first

TABLE 6.—Annual production : biomass (P:B) ratios by age-group for brook trout, rainbow trout, and brown trout in Valley Creek. Years are numbers of data years per age-group.

Age-group	Brook trout Years	Brook trout P:B ± 2 SE	Rainbow trout Years	Rainbow trout P:B ± 2 SE	Brown trout Years	Brown trout P:B ± 2 SE
0	17	2.1 ± 0.18	13	2.0 ± 0.23	9	1.9 ± 0.18
1	17	1.3 ± 0.23	13	1.7 ± 0.19	9	1.4 ± 0.17
2	15	1.0 ± 0.18	12	0.9 ± 0.56	9	0.9 ± 0.26
3	10	0.9 ± 0.24	4	0.6 ± 0.16	9	0.8 ± 0.20
4	6	0.2 ± 0.10			8	0.5 ± 0.19

15 years of this study, but they showed little correlation with events in Valley Creek (Waters 1983). Precipitation was above average in 1965 (the year of the major flood), but even greater precipitation in other years was not correlated with production changes. The catchment of Valley Creek is relatively small, and local storms can have severe effects not mirrored in the broader region.

Several years after the 21-year study, Kwak and Waters (1997), as part of a larger project, found annual production of 214 kg/ha (1988) and 197 kg/ha (1989) for all salmonids in Valley Creek. These estimates were lower than those at the end of the continuous study reported here. Consequently, the annual production values around 250–300 kg/ha for all salmonids (mostly brown trout) in the last 2 years of the 21-year study might have been unusually high and temporary. However, several mean biomass and annual production values above 250 kg/ha were found among 13 streams in southeastern Minnesota (Kwak and Waters 1997) and have been reported commonly in the world literature (Waters 1977; Chapman 1978; Mann and Penczak 1986). The predominance of brown trout continued, and brook trout and rainbow trout still occurred in about the same proportions as in 1986, suggesting a relative stability following the floods and sedimentation of the previous decades.

Annual P:B ratios have attracted much attention over the past few decades, and many data on stream salmonid production dynamics have accumulated. Reports by Cooper and Scherer (1967), Chapman (1978), and Waters (1983) suggested relatively constant ratios in the range 1.0–1.5. More recently, analyses of annual P:B suggested that ratios differ among species (Waters et al. 1990). Such differences, however, can now be seen as reflections of the number of age-groups present: the more age-groups, the lower the P:B ratio. Elliott (1993, 1994) has been a catalyst for relating P:B ratio to age for trout, brown trout in particular. In most of the 22 year-classes in his long-term study, young, faster-growing age-groups had the highest P:B ratios; the few exceptions could be attributed to the effects of droughts on mortality and growth in some years.

Annual P:B ratio is related to mean growth rate for the entire population. If a population in a given year is heavily weighted by new recruits (i.e., young of year), which have the highest growth rate, the annual P:B ratio will be higher. In contrast, long-lived species comprising several age-groups (such as brown trout among Valley Creek salmonids) have a population structure more heavily weighted by larger fish of lower growth rate, and a lower P:B ratio. Waters et al. (1990) noted that brown trout with five to eight age-groups had an annual P:B of about 1.0, whereas brook trout with four age-groups had an annual P:B of about 1.5 and rainbow trout with two or three age-groups had an annual P:B of about 2.0. Such life-span influences were apparent in the present study: Valley Creek brown trout averaging 5.3 age-groups had a mean annual P:B ratio of 1.2; brook trout and rainbow trout averaging 3.5–3.9 age-groups had mean annual P:B ratios of 1.4. In Valley Creek, the life span of rainbow trout was similar to that of brook trout; in the Waters et al. (1990) study of several Lake Superior tributaries, rainbow trout were migratory with fewer age-groups.

Standard errors for annual P:B ratios in single years were small for Valley Creek trout, reflecting low sampling error on a given estimation date. However, standard errors for mean P:B over the period, reflecting variation across years, were larger. Differences were not statistically significant between species. The larger variation in mean P:B across years appeared to result from fluctuating population structure due to the environmental disturbances. Populations included fewer age-groups in some years of disturbance and relatively strong age-0 groups in years of recovery. The expansion of brown trout probably stressed both brook trout and rainbow trout and affected their population structure; the number of their age-groups dropped substantially in later years, to three each in the final six years of the study.

The timing of the two or three estimates per year suggested that it might be possible to compare Valley Creek production dynamics among seasons. The results suggested high production levels during the spring and early summer. However, the low number of estimates per year precluded significant differences and precise conclusions. When studies would allow more estimates per year (possibly 6), conclusions on seasonal patterns of production might be obtained. Higher production in early seasons has been observed or suggested (Cooper 1953; Hunt 1966; Mortensen 1977; Randall and Paim 1982).

Annual P:B Ratios by Age-Group

New Valley Creek year-classes were recruited into the fall estimate when the fish were at ‘‘fingerling’’ size, considerably larger than the minimum size of free-swimming fry. Consequently, the true minimum size in mass was unavailable. Also

TABLE 7.—Comparison of mean mass by age in fall estimates among brook trout, rainbow trout, and brown trout for years when all three species were present in Valley Creek. Years are numbers of data years per age-group.

	Brook trout		Rainbow trout		Brown trout	
Age	Grams ± 2 SE	Years	Grams ± 2 SE	Years	Grams ± 2 SE	Years
0	6.8 ± 0.8	19	7.3 ± 1.6	15	7.0 ± 1.0	13
1	32.4 ± 4.1	19	54.9 ± 7.5	15	47.2 ± 6.9	13
2	93.2 ± 20.5	19	127.0 ± 18.8	14	124.2 ± 14.8	13
3	147.8 ± 11.2	13	226.9 ± 30.6	8	262.0 ± 34.9	13
4	236.3 ± 100.3	4	310.0 ± 0.0	1	458.9 ± 70.4	11

unknown was the biomass of the fry population, impossible to measure with direct procedures such as electrofishing and mark–recapture methods. The lack of information on minimum size and biomass at an early fry stage is a minor uncertainty in fish production dynamics, although methods to determine values for these would be desirable. Resulting errors produce a fault in most previous literature. Several decades ago, Hunt (1966) faced this problem with two suggested means of calculation. Both were admittedly speculative and produced results differing widely from each other. One method incorporated estimates of fecundity, known survival rate from egg to fry emergence, and the number of the previous year's mature spawners (and thus number of redds). This procedure seems to be compromised by a recent appreciation that later spawners may superimpose their redds on those of previous spawners which ought to severely reduce the survival of eggs produced by early spawners (Sorensen et al. 1995). Such superimposition of redds by other trout had been speculated upon earlier by Greeley (1932). Hunt'second method involved extrapolating back along an exponential curve from numbers estimated in later age-groups, a method that seems to hold greater promise. More than two or three estimates per year would be required for best results.

In the Valley Creek analyses, fall biomass of age-0 fish was taken as equivalent to production during the first season of life, and one-half this value was used as the estimate of mean biomass. Perhaps future imaginative analyses of long-term data can find methods to more accurately fill in this information gap.

Statistics

The addition of statistical treatment was a valuable supplement to this study, not possible in previous reports. Variances were obtained for all variables from the computer output (Kwak 1992), based on the methods of Newman and Martin (1983). Standard errors were calculated from these variances. These standard errors were particularly low, reflecting the high capture efficiency of electrofishing and the large number of fish sampled for age and mean mass determinations. Standard errors were similar for all three species, indicating similar susceptibility to the electrofishing and population estimation procedures among the three species (Tables 1–4). However, mean P:B ratios were calculated over periods of years, during which sharp environmental and species changes occurred, and standard errors (based on variance over years, i.e., standard error of the mean) were correspondingly larger (Tables 5, 6).

Replacement Causes

Possible reasons for the virtual replacement of brook trout by brown trout in Valley Creek were discussed by Waters (1983) based on 15 years of data. At the end of the 21-year period, however, brown trout annual production and biomass were higher than the initial maximum for brook trout (Tables 1, 4). The main reason for this ''exceedence'' of previous norms may be the larger mean sizes reached by brown trout (Table 7). Brown trout live longer and therefore occur in older age-groups (Table 5) and thus larger sizes than brook trout and rainbow trout. Larger size was suggested by Waters (1983) as one of the reasons for this species' replacement of others, perhaps because adult brown trout can dominate spawning grounds. A recent observation of behavior in sympatric populations in Valley Creek suggested that brown trout, by spawning slightly later than brook trout, superimpose their redds on brook trout redds. Thus, the disruption of brook trout redds may severely reduce that species' reproductive potential.

Brown trout, at a larger mean size, may also compete more favorably for better foraging territories and invertebrate foods, as suggested by their faster growth and mean size (Table 7). Fausch and White (1981) observed that individual brown trout tended to crowd out brook trout from resting sites, supporting the preeminence of brown trout density in setting carrying capacity. The data on production and biomass for all species combined (Figure 3) suggests a higher carrying capacity also for mixed species than for one species alone.

Conclusion

Almost any selection of one or two years for study within this 21-year project would have failed to characterize the production dynamics of this stream. The fisheries and stream ecological literature is replete with accounts of disturbances caused by floods, droughts, and sedimentation, not to mention human-caused disturbances. Given the impossibility of forecasting these catastrophic events, the task of selecting and carrying out a long-term study would seem daunting. Yet, modern methods of fish sampling and data analysis make such analysis much more feasible.

Many reasons for the lack of long-term research may be listed: staff turnover, research grants for short-term projects, lack of continuity in administrative missions, shifting priorities within funding agencies, emphasis on graduate student thesis research, and many others. In this context, the National (U.S.) Science Foundation's Long-Term Ecological Research Program, with 20 sites established or planned (Elliott 1990), offers a major advance in long-term research initiatives. Either within this long-term program or without, the inclusion of long-term, ongoing studies of stream fish production dynamics would be extremely beneficial to fishery science and management.

Acknowledgments

Hundreds of undergraduates and graduate students, colleagues, and interested volunteers participated in the field work of electrofishing and associated data collection, for which I am most grateful. I thank Raymond M. Newman for much assistance in statistical treatment and data handling and for critical reading of an early draft that resulted in important revisions. Donald W. Chapman reviewed a draft manuscript and provided many constructive suggestions. Daniel F. Waters produced the computer-generated figures. I am particularly thankful for the enthusiastic cooperation from all the riparian property owners along Valley Creek who generously allowed our access at all times. This is paper 974410004 of the Scientific Journal Series of the Minnesota Agricultural Experiment Station, and it reports research conducted under project 72.

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.

Benke, A. C. 1993. Concepts and patterns of invertebrate production in running waters. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 25:15–38.

Bergheim, A., and T. Hesthagen. 1990. Production of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., within different sections of a small enriched Norwegian river. Journal of Fish Biology 36:545–562.

Chapman, D. W. 1978. Production in fish populations. Pages 5–25 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Wiley, New York.

Cooper, E. L. 1953. Growth of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in the Pigeon River, Otsego County, Michigan. Papers of the Michigan Academy of Science, Arts, and Letters 38:151–165.

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.

Elliott, J. M. 1990. The need for long-term investigations in ecology and the contribution of the Freshwater Biological Association. Freshwater Biology 23:1–5.

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, New York.

Elwood, J. W., and T. F. Waters. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. Transactions of the American Fisheries Society 98:253–262.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

Greeley, J. R. 1932. The spawning habits of brook, brown, and rainbow trout and the problem of egg predators. Transactions of the American Fisheries Society 62:239–248.

Hanson, D. L., and T. F. Waters. 1974. Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. Transactions of the American Fisheries Society 103:431–439.

Hunt, R. L. 1966. Production and angler harvest of wild brook trout in Lawrence Creek, Wisconsin. Wisconsin Conservation Department, Technical Bulletin 35.

Hunt, R. L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wisconsin Department of Natural Resources Technical Bulletin 82.

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., and T. F. Waters. 1997. Trout production dynamics and water quality in Minnesota streams. Transactions of the American Fisheries Society 126: 35–48.

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.

Mann, R. H. K., and T. Penczak. 1986. Fish production in rivers: a review. Polskie Archiwum Hydrobiologii 33:233–247.

Mortensen, E . 1977. Fish production in small Danish streams. Folia Limnologica Scandinavica 17:21–26.

Newman, R. M., and F. B. Martin. 1983. Estimation of fish production rates and associated variances. Canadian Journal of Fisheries and Aquatic Sciences 40:1729–1736.

Randall, R. G., and U. Paim. 1982. Growth, biomass, and production of juvenile Atlantic salmon (*Salmo salar* L.) in two Miramichi River, New Brunswick, tributary streams. Canadian Journal of Zoology 60: 1647–1659.

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.

Sorensen, P. W., J. R. Cardwell, T. Essington, and D. E. Weigel. 1995. Reproductive interactions between sympatric brook and brown trout in a small Minnesota stream. Canadian Journal of Fisheries and Aquatic Sciences 52:1958–1965.

Waters, T. F. 1982. Annual production by a stream brook charr population and by its principal invertebrate food. Environmental Biology of Fishes 7:165–170.

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., 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.