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Production Dynamics of Smallmouth Bass in a Small Minnesota Stream

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Abstract.—Annual production by smallmouth bass *Micropterus dolomieu* in Bear Creek, Minnesota, was 43.8 and 24.1 kg wet weight per hectare in 1985–1986 and 1987–1988, respectively. Corresponding annual production/biomass ratios were 1.6 and 0.9. Densities and standing stocks changed little between years. Twenty-five additional fish species were present in Bear Creek. Age-0 smallmouth bass (shorter than 11 cm total length) fed most heavily on corixids, whereas older, larger fish fed most heavily on other fishes. Annual production by smallmouth bass was much lower than trout production in similarly fertile streams in southern Minnesota and Wisconsin. This lower production may be attributable to the many more coexisting fishes with which the smallmouth bass must share the food resources of its habitat. More-restrictive creel regulations may be needed for smallmouth bass than for trout, even in streams of similar basic productivity.

The smallmouth bass *Micropterus dolomieu* is noted for its sporting qualities and is held in great esteem by stream anglers (Holschlag 1990). The first professional efforts to understand the biology of the species and improve its management began in the past century (e.g., Henshall 1881; Bower 1897). Outstanding long-term studies include those on Courtois Creek, Missouri, by Funk (1975a, 1975b) and his associates. Other insightful contributions to smallmouth bass biology include those by Surber (1939), Larimore (1961), Reynolds (1965), Paragamian and Coble (1975), Covington et al. (1983), Paragamian (1984a), Lyons et al. (1988), and Forbes (1989). The most definitive review of smallmouth bass biology and management was by Coble (1975).

Smallmouth bass, rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, and brook trout *Salvelinus fontinalis* support the major fisheries in streams and small rivers of the eastern and midwestern United States. Angling interest and management efforts for smallmouth bass are increasing rapidly in midwestern states relative to that for trout. Yet, despite the extensive literature and two major symposia on smallmouth bass (Clepper 1975; Jackson 1991), our knowledge of the species' population dynamics and production ecology lags far behind that for stream trout—for which productivity now can be approximately predicted from stream type and locality (Waters 1992a).

Relatively few data are available on annual production by stream-dwelling smallmouth bass (Vannote and Ball 1972; Funk 1975b; Mahon et al. 1979; Covington et al. 1983; Paragamian 1987; Rabeni 1992; Roell and Orth 1993). Although the literature suggests that annual production of smallmouth bass is much lower than production of trout, even in equally fertile streams, the number and kinds of habitats studied are insufficient to permit generalizations or predictions of smallmouth bass production.

Few accounts of smallmouth bass research in Minnesota have been published, despite the recognition of potentially excellent fisheries there (Buckman 1968; Waters 1977a). Smallmouth bass in Minnesota are best known in the larger rivers such as the St. Croix River, shared with Wisconsin (Simonson and Swenson 1990), and the Mississippi River headwaters above Minneapolis (Swenson et al. 1989). However, many smaller streams in southern Minnesota hold productive smallmouth bass populations. Most of these lie in extreme southeastern Minnesota, in part of the "driftless area," and are tributary to the Mississippi River. In the past, these streams have received little research effort or special management; no production estimates have been made on their smallmouth bass populations. However, recent research and management studies reflect an increasing concern for and attention to this resource (Hayes 1990; Aadland et al. 1991).

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The principal objective of this study was to estimate the annual production of smallmouth bass in a small but fertile southern Minnesota stream. Secondary purposes were to compare smallmouth bass production with published levels of annual production by stream trout in the same region, to relate bottom fauna standing stock to smallmouth bass feeding habits, and to relate smallmouth bass abundance to that of coexisting species. Most of the data in this paper for 1985–1986 were taken from the thesis by Polomis (1988).

Study Site

Bear Creek in southern Minnesota flows eastward for approximately 62 km in Mower and Fillmore counties to its confluence with Deer Creek, forming the Middle Branch of the Root River, which ultimately flows to the Mississippi River. The Bear Creek catchment comprises 213 km^2. The stream's upper reaches flow across flat plains, whereas the lower third lies in a more deeply incised valley characteristic of southeastern Minnesota. Much of the drainage is developed for agriculture.

The study site comprised a 278-m reach of Bear Creek approximately midway along the stream's length. Mean width was 12.5 m, surface area was 0.35 hectare, and gradient was 2.3 m/km. Mean low-water discharge during the study periods was 0.23 m^3/s. Stream features included a mixture of riffles and small pools and one large pool. Riffles constituted about 25% of the study site by area. The streambed in the riffle area was primarily cobbles of limestone and other sedimentary rock. Total alkalinity was about 230 mg/L as $CaCO_3$, conductivity was about 390 μS/cm, and pH was 6.8–8.2. Water temperatures ranged from 0°C in winter to normal summer maxima of 21–23°C; in the unusually hot summer of 1985, water temperature reached 27°C.

The stream riparian area was largely in pasture and had virtually no woody vegetation. Aquatic vegetation consisted of the moss *Fontinalis* sp., watercress *Nasturtium officinale,* wild celery *Vallisneria americana,* and several species of pondweed *Potamogeton.* The most common benthic invertebrates were the northern clearwater crayfish *Orconectes propinquus,* mayfly nymphs of several families, caddisfly larvae of several families, several species in the hemipteran family Corixidae, the dipteran families Chironomidae and Tabanidae, and riffle beetles of the family Elmidae. Twenty-six species of fish including smallmouth bass were observed in the study section. No creel census data were available for Bear Creek, and no angling was observed during our field studies.

Methods

Procedures for estimating density, standing stock, and annual production of smallmouth bass were similar to those used in trout production studies (Waters 1983). In 1985–1986, population estimates were made on 26 April, 27 September, and 2 May. In 1987–1988, estimates were made on 22 April, 11 June, 20 August, 13 October, and 19 April. Populations were estimated by a single-census, mark–recapture method (Ricker 1975); fish were captured by electrofishing with a 240-V pulsed direct-current generator mounted in a small boat. On the marking sample date, all smallmouth bass captured were measured to the nearest 1 mm total length and given a partial caudal lobe clip.

Weights and scales for aging were taken from up to two smallmouth bass per 2-mm length-group. During the recapture sample, usually 2 d later, each smallmouth bass was measured and examined for a fin clip, and additional scales and weights were taken if needed to complete length-group records.

Population estimates for smallmouth bass were stratified into 4-cm length-groups, although length-groups represented by low numbers of larger fish were combined for analysis. Population size and its sampling variance were calculated with a modified Petersen estimate (Ricker 1975; Newman and Waters 1989). Population number by size was converted to age-specific estimates with the proportions of fish of given lengths 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 from a Taylor series expansion (Seber 1982; Cone and Krueger 1988).

Standing stock and production were estimated by the age-based instantaneous growth rate method (Ricker 1946; Allen 1949; Waters 1977b), and expressed in kilograms (wet weight) per hectare. All other measures of variance were estimated according to Newman and Martin (1983). Interval production for newly recruited age-0 fish was estimated as standing stock at initial occurrence (Waters 1983).

Estimates of production between sampling dates—that is, for intervals within the production year—were summed to obtain annual production

TABLE 1.—Densities (number/hectare) of smallmouth bass in Bear Creek, Minnesota, by age and date, 1985–1986 and 1987–1988. Ninety-five percent confidence intervals are given in parentheses.

Date	Age (years)							Total
	0	1	2	3	4	5	6	
				1985-1986				
26 Apr 1985	0	41 (12–70)	204 (118–290)	29 (0–61)	0	0	0	274 (178–370)
27 Sep 1985	1,028 (823–1,233)	203 (0–429)	190 (0–383)	15 (0–47)	0	0	0	1,436 (1,073–1,799)
2 May 1986	0	263 (185–341)	41 (0–87)	14 (0–36)	0	0	0	318 (225–411)
Annual mean total								650 (466–834)
				1987-1988				
22 Apr 1987	0	74 (48–100)	663 (492–834)	93 (30–156)	10 (0–24)	10 (0–24)	0	850 (665–1,035)
11 Jun 1987	0	86 (0–177)	190 (126–254)	38 (12–64)	9 (0–21)	9 (0–21)	0	332 (216–448)
20 Aug 1987	34 (0–74)	431 (272–590)	73 (31–115)	72 (27–117)	44 (10–78)	15 (0–35)	7 (0–21)	676 (496–856)
13 Oct 1987	66 (29–103)	490 (319–661)	280 (76–484)	150 (14–286)	83 (0–174)	17 (0–52)	0	1,086 (770–1,402)
1 Apr 1988	0	273 (177–369)	71 (30–112)	24 (6–42)	12 (0–25)	4 (0–12)	0	384 (277–491)
Annual mean total								681 (566–796)

during 1985–1986 and 1987–1988. Density, standing stock, and production per unit area were computed by dividing the estimates for the entire stream reach by its surface area, 0.35 hectare.

Fish species other than smallmouth bass were sampled separately in the 1985–1986 production year to obtain approximate values of density and standing stock. Population estimates were made by electrofishing to depletion in three successive passes; electrofishing catches on subsequent passes were negligible. Thus, a minimum estimate of standing stock was obtained for each species as the aggregate weight of all sizes from the catch on the first three passes. All fish were returned alive to the stream. Dates of these estimates were 25 July, 21 September, 17 November, and 27 April, and mean annual standing stocks were computed as means weighted by number of days in the time intervals.

Limited collections of benthic invertebrates were made also in the 1985–1986 production year to ascertain potential prey availability to smallmouth bass. Five-minute kick samples of about 1 m^2 of streambed were collected from riffle areas near both ends of the stream reach; a stationary D-net with 253-μm-mesh Nitex mesh was used for this purpose. In addition to the kicking, large stones in the 1-m^2 kick-sample area were hand-scrubbed at the mouth of the D-net. Thirty-two such samples were collected, four from each of two riffles on each of four dates. Invertebrate standing stocks were computed in grams wet weight per square meter. Kick sampling did not adequately sample crayfish. Therefore, an attempt to sample crayfish was made with a 6-m-long, 0.6-cm-mesh seine. Thirty hauls each covering 11.5 m^2 were made with the seine on 8 May 1986.

Food habits of smallmouth bass were determined on 10 July, 23 August, 30 October, and 8 May in the 1985–1986 production year. This sampling was usually done within 48 h of benthic invertebrate sampling. On each date, up to four smallmouth bass were sampled from each of five length-groups: 4.0–10.9 cm, 11.0–14.9 cm, 15.0–18.9 cm, 19.0–24.9 cm, and 25.0 cm and longer. For all fish 11.0 cm and longer, a stomach pump (Seaburg 1957) was used to flush stomach contents from anesthetized individuals. These fish were then fin-clipped and released. Fish 4.0–10.9 cm were killed and preserved whole. Analysis of all stomach contents was by the percent-composition-by-weight method (Bowen 1983). The different prey types were separated and their percentages were estimated visually. The total material was weighed wet after it was blotted, and prey-group percentages were multiplied by total weight to obtain es-

TABLE 2.—Mean density, standing stock, production, and annual production/biomass ($P/\bar{B}$) ratio for smallmouth bass in Bear Creek, Minnesota, 1985–1986 and 1987–1988. Ninety-five percent confidence intervals are given in parentheses.

Interval dates	Mean density (number/hectare)	Mean standing stock (kg/hectare)	Production (kg/hectare)	Annual $P/\bar{B}$
		1985-1986		
26 Apr 1985–27 Sep 1985	340 (183–498)	27.7 (11.6–43.8)	41.6 (23.4–59.8)	
27 Sep 1985–2 May 1986	870 (683–1,056)	28.2 (13.0–43.4)	2.2 (0–6.8)	
Annual	650 (466–834)	28.0 (12.0–44.0)	43.8 (25.0–62.6)	1.6 (0.5–2.7)
		1987-1988		
22 Apr 1987–11 Jun 1987	590 (481–700)	20.8 (16.6–25.0)	5.4 (3.4–7.4)	
11 Jun 1987–20 Aug 1987	483 (378–588)	17.2 (12.9–21.5)	2.1 (0.6–3.6)	
20 Aug 1987–13 Oct 1987	877 (695–1,059)	40.3 (26.5–54.1)	15.0 (8.3–21.7)	
13 Oct 1987–19 Apr 1988	726 (560–892)	30.9 (18.4–43.4)	1.6 (0.5–2.7)	
Annual	681 (566–796)	28.2 (19.1–37.3)	24.1 (16.9–31.3)	0.9 (0.5–1.3)

timated prey weights (Hynes 1950). For analysis, smallmouth bass were separated into two length-groups: 4.0–10.9 cm and 11.0 cm and longer, approximating age-0 and older fish, respectively. Results were expressed as percent by weight for all taxa for comparison with bottom fauna data.

Results

Density and Standing Stock of Smallmouth Bass

Mean annual densities of smallmouth bass for 1985–1986 and 1987–1988 were 650 and 681 fish/hectare, respectively (Table 1). The 1985 year-class was recruited to the sampling program in September 1985 at an estimated density of 1,028 fish/hectare. The density of this year-class decreased in May 1986 to 263 fish/hectare but then increased to 663 fish/hectare in April 1987. Several such instances of apparently increasing density over time of a single year-class occurred during the study. In some samples, densities of older smallmouth bass were higher than those of younger fish, suggesting highly variable year-class strengths. Four age-groups were represented in the samples in 1985 and seven in 1987.

Smallmouth bass standing stocks were also consistent; annual means were 28.0 kg/hectare for 1985–1986 and 28.2 kg/hectare for 1987–1988. The total range of standing stocks over the study period was 17.2–40.3 kg/hectare (Table 2).

Production and $P/\bar{B}$ Ratios for Smallmouth Bass

Annual production for smallmouth bass varied substantially—from 43.8 kg/hectare in 1985–1986 to 24.1 kg/hectare in 1987–1988 (Table 2). In 1985–1986, the sampling schedule allowed only two intervals within the production year, essentially summer and winter. The summer interval (April–September) included the greatest production (41.6 kg/hectare), whereas the winter production (September–May) was low (2.2 kg/hectare). In 1987–1988, however, the sampling schedule permitted estimates for four intervals; production was higher in spring and autumn than in midsummer and winter (Table 2).

The different production rates within similar standing stocks yielded $P/\bar{B}$ ratios of 1.6 in 1985–1986 and 0.9 in 1987–1988 (Table 2). The higher production in 1985–1986 probably reflected the higher number of age-0 fish, with higher specific growth rates, that were included in the population.

Densities and Standing Stocks of Other Fishes

Twenty-five species of fish other than smallmouth bass were observed in Bear Creek in 1985–1986, and density and standing stock were estimated for 17 of them (Table 3). Eight other species were observed occasionally but not sampled quantitatively (Table 3). Six families were represented:

TABLE 3.—Mean densities and standing stocks of smallmouth bass and other fishes in Bear Creek, Minnesota, 1985–1986. P = present, not measured.

Family and species	Mean annual density (number/hectare)	Mean annual standing stock (kg/hectare)
Smallmouth bass	650	28.0
Other fish species		
Petromyzontidae		
American brook lamprey *Lampetra appendix*	8	0.1
Cyprinidae		
Central stoneroller *Campostoma anomalum* plus largescale stoneroller *Campostoma oligolepis*	1,849	24.8
Common shiner *Luxilus cornutus*	547	3.3
Longnose dace *Rhinichthys cataractae*	899	3.9
Creek chub *Semotilus atromaculatus*	1,264	4.2
Bluntnose minnow *Pimephales notatus*	420	0.9
Rosyface shiner *Notropis rubellus*	147	0.2
Bigmouth shiner *Notropis dorsalis*	P	P
Sand shiner *Notropis stramineus*	P	P
Spotfin shiner *Cyprinella spiloptera*	P	P
River shiner *Notropis blennius*	P	P
Common carp *Cyprinus carpio*	P	P
Catostomidae		
White sucker *Catostomus commersoni*	1,246	25.8
Northern hog sucker *Hypentelium nigricans*	284	16.5
Golden redhorse *Moxostoma erythrurum*	30	11.0
Quillback *Carpiodes cyprinus*	P	P
Ictaluridae		
Stonecat *Noturus flavus*	98	2.2
Centrarchidae		
Green sunfish *Lepomis cyanellus*	13	0.4
Rock bass *Ambloplites rupestris*	136	2.9
Percidae		
Fantail darter *Etheostoma flabellare*	2,247	2.5
Johnny darter *Etheostoma nigrum*	700	1.2
Banded darter *Etheostoma zonale*	25	0.1
Blackside darter *Percina maculata*	P	P
Mud darter *Etheostoma asprigene*	P	P
Total (other fishes)	9,913	100.0
Total (all fishes)	10,563	128.0

Petromyzontidae (1 species), Cyprinidae (12 species), Catostomidae (4 species), Ictaluridae (1 species), Centrarchidae (2 species other than smallmouth bass), and Percidae (5 species). The Cyprinidae were represented by the most species and the greatest number of individuals, but the Catostomidae was the family with the larger species and the highest standing stock.

The annual mean density of all species other than smallmouth bass was 9,913 fish/hectare (mean of four samples in 1985–1986), and annual mean standing stock was 100.0 kg/hectare (Table 3). Three species exhibited densities of more than 1,000 fish/hectare: creek chub, white sucker, and fantail darter. The central and largescale stonerollers had a combined density of nearly 2,000 fish/hectare.

Macroinvertebrate Standing Stocks

Seven orders of aquatic insects were collected in the benthic kick samples. Diptera (mostly Chironomidae) and Trichoptera (Hydropsychidae, Brachycentridae, Helicopsychidae, and Limnephilidae) predominated (Table 4; Figure 1). Ephemeroptera (Baetidae, Siphlonuridae, Heptageniidae, Tricorythidae) was third in total composition by weight, and Coleoptera (Elmidae), Hemiptera Corixidae), and Megaloptera (Sialidae) made up most of the remaining biomass. Plecoptera (Perlodidae) was present but with a very low standing stock. Corixids were visually very abundant, but apparently due to their great mobility or their presence only in nonriffle areas, they were not captured readily in the kick samples. Mean total insect standing stock (wet weight) was 2.06 g/m^2.

In addition to these insect orders, a few miscellaneous taxa were present in low numbers in the samples: oligochaete worms, the amphipod *Hyalella azteca,* water mites, the flatworm *Planaria* sp., and the gastropod *Physa* sp. The northern clearwater crayfish was visually abundant but was not collected in the kick samples, apparently owing to its swimming mobility. Seining in 1985–1986 produced a minimal standing stock estimate of 0.3 g/m^2.

Food Habits of Smallmouth Bass

The taxonomic composition of food items in smallmouth bass stomachs reflected to some extent the invertebrate distribution observed in the bottom samples, but major differences between these two distributions were apparent (Figures 1, 2). Age-0 smallmouth bass (<11 cm long) fed most

TABLE 4.—Standing stocks of benthic insects from riffles of Bear Creek, Minnesota, 1985–1986, by taxon and date. Ninety-five percent confidence intervals are given in parentheses; $N = 8$ samples for each date.

Order	Mean standing stock (g wet weight/m^2)				Annual mean
	7 Jul 1985	20 Aug 1985	20 Oct 1985	10 May 1986	
Ephemeroptera	0.61 (0.33–0.89)	0.10 (0–0.54)	0.16 (0.10–0.22)	0.15 (0–0.30)	0.26 (0.14–0.38)
Plecoptera	0	0.01 (0–0.05)	0.02 (0–0.04)	0.01 (0–0.04)	0.01 (0–0.02)
Trichoptera	0.61 (0.28–0.94)	0.43 (0–1.17)	0.15 (0–0.30)	0.83 (0.25–1.41)	0.50 (0.28–0.72)
Diptera	0.13 (0.03–0.23)	1.57 (0.16–2.98)	1.01 (0.29–1.73)	1.69 (0–4.98)	1.10 (0.31–1.89)
Coleoptera	0.03 (0–0.07)	0.30 (0.12–0.48)	0.14 (0.05–0.23)	0.18 (0–0.45)	0.16 (0.09–0.23)
Hemiptera	0.02 (0–0.05)	0.06 (0–0.19)	0.02 (0–0.05)	0.00	0.02 (0–0.05)
Total	1.40 (0.67–2.13)	2.47 (0.76–4.18)	1.50 (0.62–2.38)	2.86 (0–6.49)	2.06 (1.16–2.96)

frequently on corixids, an invertebrate group present in very low abundance in the bottom samples (Figure 2). Young fish also fed upon chironomid larvae to a moderate extent and on oligochaetes and terrestrial invertebrates to a lesser extent, but fed very little on other benthic invertebrates. Smallmouth bass 11 cm long and longer fed upon a considerably different array of prey (Figure 2). Fish composed the largest single category in their diet, along with moderate quantities of corixids and crayfish and smaller quantities of Ephemeroptera nymphs, oligochaetes, and chironomid larvae. A few of the branchiuran parasite *Argulus* sp. were observed in stomachs of larger smallmouth bass in late summer, when some fish, particularly northern hog suckers, were infested with this parasite. Presumably the smallmouth bass incidentally ingested *Argulus* while feeding on parasitized forage fishes.

Discussion

Smallmouth Bass Production

Annual production by smallmouth bass was relatively high, especially in 1985–1986, when compared with most other estimates in the literature (Table 5). This suggests that Bear Creek, or at least the study reach, was especially productive. The study reach was selected only because it was accessible and included representative habitat types (runs, riffles, pools), and a longer reach might have helped ensure that the results were more representative of the entire stream.

The disparity in smallmouth bass annual production between 1985–1986 and 1987–1988, 43.8 versus 24.1 kg/hectare, probably reflected the large number of age-0 fish in 1985 and their virtual absence in 1987. Other streams in the region have also shown highly variable year-class strengths in smallmouth bass populations (Cleary 1956; Forbes 1989; Mason et al. 1991). Fish of a younger cohort have higher specific growth rates than fish in older cohorts, and therefore have higher production/biomass ($P/\bar{B}$) ratios. Thus, for the same standing stocks, a population with the larger proportion of young fish will exhibit the higher production rate and $P/\bar{B}$ ratio (Waters et al. 1990). In the present study, the smallmouth bass populations composed of four age-groups in 1985–1986 had a higher $P/\bar{B}$ ratio (1.6) than the population with seven age-groups in 1987–1988 (0.9). High $P/\bar{B}$ ratios have been commonly observed in production studies of anadromous salmonid populations composed mainly of young fish (Hopkins 1971; Elliott 1984) and in populations with fewer age-groups, which tend to have more young fish (Waters et al. 1990).

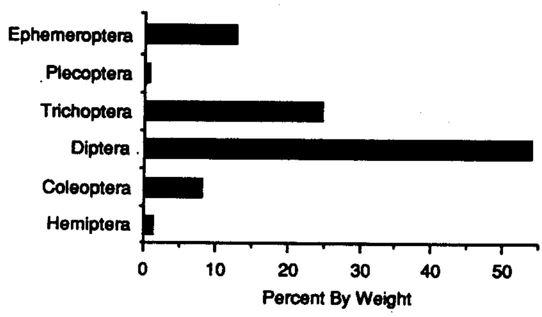

FIGURE 1.—Taxonomic composition (mean percent wet weight by taxon) of benthic insects from riffles in Bear Creek, Minnesota. Means represent four sampling dates and eight samples per date in 1985–1986.

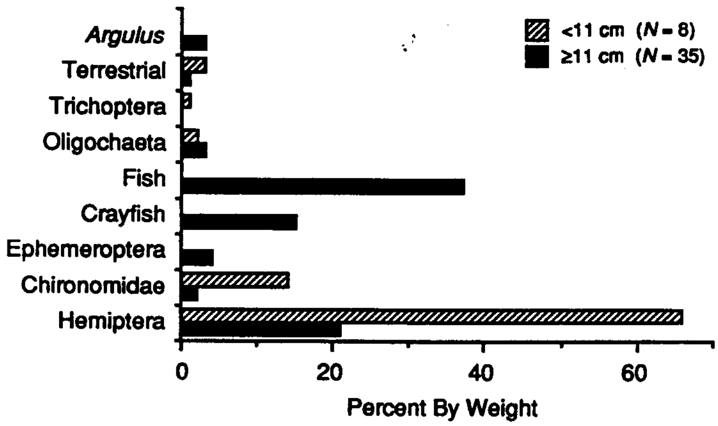

FIGURE 2.—Stomach contents (mean percent wet weight by prey taxon) from 43 smallmouth bass in Bear Creek, Minnesota, by size-group of predator. Means represent four sampling periods in 1985–1986.

Although smallmouth bass densities varied greatly between 1985–1986 and 1987–1988, annual mean standing stocks for smallmouth bass remained similar, suggesting that the carrying capacity (in biomass terms) remained fairly constant. Similar results were observed in trout production studies over 15 years in a Minnesota stream (Waters 1983): trout densities changed greatly due to stream perturbations and varying year-class strengths, but annual mean standing stock and annual production always returned to about the same maximum levels. Long-term studies on smallmouth bass production dynamics should be equally illuminating, especially if both spatial and temporal scales are expanded over those in the present study.

TABLE 5.—Summary of literature values of smallmouth bass annual production.

Source	Stream	Annual production (kg wet weight/ hectare)
Vannote and Ball (1972)	Red Cedar River, Michigan	13.6
Funk (1975b)	Courtois Creek, Missouri	11.5–25.1 (11 years)
Mahon et al. (1979)	Speed River, Ontario	0.17, 0.31
Covington et al. (1983)	Jacks Fork River and Current River, Missouri	2.4–15.9 (4 sites)
Paragamian (1987)	Maquoketa River, Iowa	6.4–15.0 (5 years)
Rabeni (1992)	Jacks Fork River, Missouri	13.1[a]
Roell and Orth (1993)	New River, Virginia	32.1
Present study	Bear Creek, Minnnesota	43.8, 24.1 (2 years)

[a] Converted from dry weight (1 g dry = 5 g wet).

Benthic Invertebrates and Smallmouth Bass Food Habits

The relatively low macroinvertebrate standing stocks recorded in the present study (mean, 20.0 kg/hectare) fell far short of those required to support the recorded smallmouth bass production (mean, 34.0 kg/hectare). This discrepancy is known as the Allen Paradox (Hynes 1970; Waters 1988). However, the principal invertebrates in the smallmouth bass diet—corixids for small fish, and corixids and crayfish for larger fish—obviously were not assessed accurately by bottom sampling.

In future studies to assess the productivity of all food resources for smallmouth bass, improvements over past methodologies should be attempted. Previous assessments have mainly emphasized benthos production (Waters 1988, 1992b). Sampling of quiet-water bottom habitat should be included to assess corixids, which were important items in the diet of age-0 smallmouth bass in Bear Creek. Corixids may be similarly important in other low-gradient streams (e.g., Angermeier 1982). Other possible food sources that will require special sampling techniques include other nekton, crayfish, hyporheic organisms, drift of terrestrial origin, and small prey fish.

Sources of Error

Several outcomes in the present study suggest that the 278-m study reach selected was too short to achieve highly reliable results. For example, the inconsistency in strength of smallmouth bass yearclasses suggests either large variance, because of the few fish in the short study reach, or substantial seasonal movements of both young and older fish. Both factors may have been influential in the present study.

The mark–recapture method used to estimate smallmouth bass populations in this study is subject to various systematic errors, and the method can be relied upon for accuracy only if a set of assumptions, described by Ricker (1975), are met. If systematic errors resulting from violations of these assumptions exist in fish density estimates, then errors will occur also in standing stock and production estimates. Lyons and Kanehl (in press) noted a tendency for catches during recapture runs to be smaller than those during marking runs, and we recorded this pattern in six of eight of our density estimates. If such a phenomenon is due to a reduced vulnerability of the marked fish, an overestimate of density will result. However, if the reduced catch on the recapture run is due to mortality or emigration, but marked fish form the same proportion of fish removed as of fish remaining, then no assumption is violated and resulting estimates will be accurate. Further studies are needed, however, to identify potential sources of systematic error associated with mark–recapture estimates of smallmouth bass populations. Measures of variance (95% confidence intervals) associated with the estimates of smallmouth bass density, standing stock, and production (Tables 1, 2) represent sampling error and provide no indication of systematic error.

Published literature on smallmouth bass movements is equivocal, and broad conclusions depend upon spatial and temporal scales. Two classic early studies by Larimore (1952) and Gerking (1953) indicated that large smallmouth bass (means of 29.1 cm total length and 17.9 cm fork length, respectively) in streams established home ranges and were fairly sedentary within a season, provided that their habitat needs were met. However, Funk (1957), while classifying smallmouth bass as "sedentary," indicated that they were "mobile" during the spring, and Larimore (1952) reported that about one-third of a smallmouth bass population emigrated from their home ranges over a year's time. Recent studies also confirmed the sedentary nature of smallmouth bass, but noted distinct diel activity and seasonal movement patterns (Todd and Rabeni 1989; Langhurst and Schoenike 1990). The above reports suggest that fish size, season, water temperature and level, and habitat quality may influence smallmouth bass movements.

The appearance of high numbers of age-0 smallmouth bass in 1985 suggested that successful reproduction occurred within the study reach. The virtual absence of age-0 fish in 1987 suggested a weak year-class, but the 1987 year-class appeared later in good strength, suggesting that successful reproduction took place elsewhere in the stream. Smallmouth bass reproduction appeared to be extremely variable and unevenly distributed within the stream. Winemiller and Taylor (1982) found an average of 15 nests with spawn per kilometer of an Ohio stream, but fry were associated with only about 25% of the nests during one spawning season and with none of the nests in another season. Such variation in reproductive success and fry distribution is an additional compelling reason for selecting a large sampling area in future studies.

The low numbers of fish, particularly in the older age-groups, and the low precision of standing stock and production estimates (Table 2) further suggested an inadequate study reach. However, the potential problem of immigration and emigration theoretically should not have affected the accuracy of estimates of standing stock and production as long as marked fish did not emigrate in the interval (usually 2 d) between the two sampling runs of an estimate, and as long as the sizes of immigrating and emigrating fish of a given year-class were the same as the sizes of resident fish of the same year-class.

The results of the present study suggest a particular need for future population assessments to take into consideration the locations of smallmouth bass spawning and of young and adult growth, as well as movements between spawning and growth habitats.

Production of Smallmouth Bass and Trout: Management Implications

In streams of similar quality and fertility, annual production by smallmouth bass appears to be generally less than 50 kg/hectare (Table 5), whereas trout production is typically 100–200 kg/hectare (Waters 1977b; Chapman 1978; Mann and Penczak 1986; Waters et al. 1990). A possible explanation for this difference is that smallmouth bass share their habitat and food resources with many other fish species (Larimore 1952; Funk 1975a; 25 species in the present study), whereas trout are commonly found alone or with only one or two other fish species (e.g., Petrosky and Waters 1975). When total annual production for all fish species in a fertile smallmouth bass stream like

Bear Creek is compared with total production in trout streams, a greater similarity will probably appear.

Annual production by the other 25 fishes in Bear Creek was not estimated, but multiplying the total mean biomass (100 kg/hectare) by the $P/\bar{B}$ ratio of 1.6 observed for smallmouth bass in 1985–1986 yields an approximate annual production of 160 kg/hectare for the other fishes. Adding the annual production for smallmouth bass (44 kg/hectare) brings the total estimate to 204 kg/hectare, which compares favorably to values often found for trout in the similarly fertile streams in parts of the "driftless area" in Wisconsin and Minnesota (Hunt 1974: 258 kg/hectare; Avery and Hunt 1981: 152 kg/hectare; Waters 1983: 190 kg/hectare; Brynildson and Brynildson 1984: 360 kg/hectare; Newman and Waters 1989: 195 kg/hectare).

Several accounts in the literature stress the high vulnerability of smallmouth bass to heavy exploitation by angling (Fleener 1975; Paragamian 1984b; Paragamian and Coble 1975). These accounts are supported by other studies showing that regulations restricting size of creeled fish have been largely successful in improving smallmouth bass fisheries in streams (Paragamian 1984b; Austen and Orth 1988; Hayes 1990; Smith and Kauffman 1991). Thus, angler expectations of catch, and management programs designed to respond to these expectations, must be tempered by knowledge of not only the high vulnerability of smallmouth bass, but also of the species' inherently low production in streams that also support large populations of other fishes.

In view of the striking contrast in annual production by smallmouth bass and trout populations, equal regulations would not seem appropriate. Yet in much of Wisconsin and Minnesota, the daily creel limits for trout and smallmouth bass are about the same—five or six fish. An angler legally taking a limit from each type of fishery will remove a much higher proportion of the smallmouth bass population than of the trout population. The potential differences in production and harvest between trout and smallmouth bass suggest that different regulations should be applied to the two groups, and that smallmouth bass should receive the greater protection.

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