

**THE ROLES OF PREDATION, COMPETITION, AND
EXPLOITATION IN THE COMMUNITY DYNAMICS
OF THE NEW RIVER IN WEST VIRGINIA**

by

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(ABSTRACT)

A model of the trophic dynamics among key macroinvertebrate and fish populations in the New River, West Virginia, was developed to help define the roles of predation, competition, and fishery exploitation in the food web of this large, warmwater stream. The fates of production of the harvested crayfish (*Orconectes virilis*, *Orconectes sanbornii sanbornii*, and *Cambarus sciotensis*), hellgrammite (*Corydalus cornutus* larvae), smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and flathead catfish (*Pylodictis olivaris*) populations were quantified to evaluate the status of these stocks and to aid specification of the model. Analysis and application of the model were designed to address three research objectives, which were to (1) quantify the roles that predation, competition, and exploitation have in structuring the prey-predator assemblage, (2) evaluate through simulation the effects of multispecies exploitation, and (3) assess through simulation the impacts to the food web of reductions in aquatic insect production associated with the systematic control of black fly larvae in the New River.

The trophic basis of production of smallmouth bass, rock bass, and flathead catfish was primarily aquatic insects (in young fishes) and crayfish (in older fishes). Hellgrammites and prey fishes were inconsequential in that regard. Predation by these fishes (primarily smallmouth bass and rock bass) accounted for 76% of the production of ages-1 and -2 crayfish, and harvest by people was equivalent to 5% of

crayfish production. Fish predation (primarily by rock bass) and harvest accounted for 14% and 8%, respectively, of the annual production of ages-1 and -2 hellgrammites. Anglers harvested the equivalents of about 91% and 12% of the annual production of fully-recruited smallmouth bass and rock bass, respectively; the extent of flathead catfish harvest was unclear.

Error analysis of the model suggested that “bottom-up” (food-limitation) effects were more important than “top-down” (mortality from predation) effects, interspecific and intraspecific competition, and exploitation in maintaining the structure of the prey-predator assemblage in the New River. Exploitation was important in causing transitions in assemblage structure. Simulations of multispecies exploitation demonstrated that production and yield of populations are strongly dependent on food web interactions. Simulation of a 50% reduction in aquatic insect production, similar to that observed following poisoning of black fly larvae, predicted substantial declines in insectivores and their predators. Management of New River resources for maximum benefits to people will necessarily involve new approaches to addressing problems in a food web context.

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_____ helped make the sometimes-twisted roads of fish energetics a little less twisted through meaningful discussion and no small amount of idle banter.

The written word will not convey the meaning of the love and support I received from my parents _____, my sister _____, and my brothers _____ and _____ to whom I dedicate this work. Lastly, I thank my grandfather _____ and my great uncle _____ for placing rod and gun in my hands at an early age, thus planting the seed of a lifelong obsession.

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Introduction

Scientists studying aquatic ecosystems seek to predict system dynamics for three general purposes. The first purpose is to learn more about system structure and function. The second reason is to understand how human activities, such as fishery exploitation, affect the system. Apart from the inherent value of this knowledge, improved understanding of system dynamics can guide the development of appropriate management practices. The third purpose then is to recommend management approaches that are designed to maximize benefits to people from system resources. Improvements in the quality of fishery products are the most conspicuous benefits. Another benefit is the enhanced understanding of system structure and function once the effects of new management practices are assessed. Thus, fulfillment of one purpose necessarily involves re-evaluation of the other two purposes. This cycle of continued enhancement of system understanding is limited by numerous social, political, economic, and biological factors. Biological factors are ulti-

mately the major limitation to further understanding because aquatic systems, like most natural systems, are extremely complex.

System complexity in streams has thwarted previous attempts by ecologists to predict accurately the dynamics of abiotic and biotic phenomena. However, since Lindeman (1942) first proposed the trophic-level concept of ecosystem "organization" and Odum (1957) and Teal (1957) studied streams from a holistic viewpoint, ecologists have continually improved the technology and approach to studying system complexity. Thus, recent advances have been made in understanding the structural and functional relationships among populations in stream ecosystems (for example, Webster and Patten 1979; Vannote and Sweeney 1980; Vannote et al. 1980; Minshall et al. 1985; Bowlby and Roff 1986).

One approach to understanding the function of stream ecosystems or their components is to study energy dynamics. Energy is the common denominator of all organisms, and must be available for all life-sustaining processes. Therefore, the representation of organisms and their processes in terms of energy is appropriate. Although individuals in a community acquire, use, and store energy in different ways, knowledge of the flow of energy through a stream community provides insight into the functional relationships among constituent populations.

The effects of exploitation on the energy dynamics of stream communities have not been studied. Energy budgets have been developed for several stream communities (Odum 1957; Teal 1957; Margalef 1960; Warren et al. 1964; Fisher and Likens 1973; Hall 1972; Mann et al. 1972; Vannote and Ball 1972; Westlake et al. 1972), but none have been applied to fishery management problems.

My research goal was to assess the roles of predation, competition, and fishery exploitation in the structure and function of the prey-predator assemblage in the New River in West Virginia. The research strategy involved four basic steps. First, I at-

tempted to quantify the trophic dynamics of key prey and predator populations in this system, mostly from direct measurement in the field, but also from the work of other researchers. I then developed a mathematical model of energy flow among the key components. In the third phase, I evaluated the importance of predation, competition, and exploitation through analysis of the model. Lastly, I evaluated through simulation with the model the effects of simultaneous changes in exploitation at two trophic levels and assessed the effects of the control of black fly larvae on community structure.

The New River originates in the mountains of northwestern North Carolina and flows generally northward through Virginia and into West Virginia. In central West Virginia, it joins the Gauley River to form the Kanawha River, which is a major tributary of the Ohio River. My research was conducted on the New River in West Virginia from Bluestone Dam, near the town of Hinton, downstream to Sandstone Falls. This sixth-order river reach is about 16.4 km in length, and averages about 230 m in width. The river there consists of well-defined riffles and pools. The construction of Bluestone Dam was completed in 1949, and is operated by the United States Army Corps of Engineers. The dam is a flood-control structure that is operated as a run-of-the-river facility; that is, during non-flood periods, water is released from the reservoir at a rate similar to that entering the lake to maintain a constant pool elevation. The total watershed area above the dam is 11,919 km². The average daily discharge from the dam (54 years of discharge records; USGS 1984) was about 159 m³ • s⁻¹. The Greenbrier River, the largest tributary of the New River, enters about 1.2 km below the dam. The total watershed area of the two streams at this point is 16,203 km², and the average daily discharge (47 years of discharge records; USGS 1984) was about 225 m³ • s⁻¹. The majority of the study reach (lower 11.4 river kilometers) lies

within the 84 km-long New River Gorge National River, established in 1978 under Public Law 95-625 and administered by the United States National Park Service.

The New River below Bluestone Dam offers a variety of natural resources-related benefits to people. A sport fishery and a commercial bait fishery are just two of several benefits there. The river harbors one of the most productive and valuable warmwater fisheries in the state. Smallmouth bass (*Micropterus dolomieu*) is the target species of most anglers, but rock bass (*Ambloplites rupestris*) and flathead catfish (*Pylodictis olivaris*) are also relatively abundant (Lobb 1986); at least 11 other species are also caught (Pierce et al. 1981). Crayfish (Decapoda: Cambaridae) and hellgrammites (*Corydalus cornutus* larvae) are harvested extensively by commercial retailers for sale as bait and by anglers for personal use. This bait fishery harvests annually nearly one million animals, the majority of which are caught between Bluestone Dam and Sandstone Falls (Nielsen and Orth 1988). Crayfish and hellgrammites are also important prey to predatory fishes.

Two activities have become particularly controversial; commercial exploitation of resources within the boundaries of a National Park (the New River Gorge National River), and the application of a bacterial larvicide, *Bacillus thuringiensis israelensis* (BTI), to kill black fly (Simuliidae) larvae in the river and therefore control nuisance adult black flies in adjacent uplands. Black fly larvae are a functionally important component of the macroinvertebrate assemblage in the New River (Voshell 1985). A third action under consideration and certain to be controversial is the conversion of Bluestone Dam to a peaking-mode, hydroelectric facility. Therefore, given the importance of the New River to the State of West Virginia and to the citizens of the United States, informed management is clearly required if the biological integrity and productivity of this system are to be maintained.

The relevant biological knowledge of this system was limited to surveys of sport fish harvest (Pierce et al. 1981) and bait harvest (Nielsen and Orth 1988), trophic structure and production of aquatic macroinvertebrates (Voshell 1985; Voshell et al. 1987, 1988, 1989), and abundances of non-game fishes (Lobb 1986). Investigation of the dynamics of the prey and predator populations and their interactions was clearly warranted so that complex resource management issues could be addressed in a more holistic framework.

This dissertation is organized into three chapters. The first chapter summarizes my attempts to determine the production of crayfish and hellgrammites living between Bluestone Dam and Sandstone Falls in the New River, and then relate that production to the level of harvest of these groups. The second chapter characterizes the trophic basis of production of the principal predatory fishes there; namely, smallmouth bass, rock bass, and flathead catfish. The third chapter describes the development of the energy flow model, model analysis, simulation of changes in exploitation in the system, and simulation of reductions in black fly larvae on community structure.

Chapter 1

Production and Harvest of Crayfish and Hellgrammites in the New River, West Virginia

Introduction

Populations of wild crayfish are exploited for food and bait throughout the United States and Canada (Huner 1978); for example, more than 20,000 kg of crayfish are harvested annually in Wisconsin for bait, food, and scientific purposes. Harvesting of crayfish (*Orconectes virilis*, *Orconectes sanbornii sanbornii*, and *Cambarus sciotensis*) and hellgrammites (*Corydalus cornutus* larvae) for bait from the New River in West Virginia is a common activity of anglers and commercially-licensed bait catchers. The majority of bait harvest occurs in the 16.4-km river reach between Bluestone Dam and Sandstone Falls, where about 197,000 crayfish ($0.05 \text{ crayfish} \cdot \text{m}^{-2}$) and 743,000 hellgrammites ($0.18 \text{ larvae} \cdot \text{m}^{-2}$) were harvested in 1983 (Nielsen and Orth 1988).

Smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and flathead catfish (*Pylodictis olivaris*) are the principal predatory fishes there (Lobb 1986; Roell and Orth 1988), and are known to prey extensively on crayfish in other aquatic systems (Minckley and Deacon 1959; Turner and Summerfelt 1970; Vannote and Ball 1972; Scott and Crossman 1973; Edmundson 1974; Coble 1975; Miner 1978; Layher and Boles 1980; Probst et al. 1984; Austen and Orth 1988). Extensive predation on hellgrammites by fish has not been reported.

The New River between the dam and the falls harbors popular recreational fisheries for smallmouth bass and rock bass (Pierce et al. 1981). Because people and predatory fishes may compete for limited crayfish and hellgrammite resources there, the sport fisheries may be negatively affected by the exploitation of bait stocks. The degree of exploitative effects depends on the extent of total use of these invertebrates by people and predatory fishes in relation to invertebrate productivity. Investigation of the production of crayfish and hellgrammites in the New River and the magnitude of harvest by people was warranted. My objectives were to (1) evaluate the status and distribution of the crayfish and hellgrammite stocks; and (2) determine the extent of annual harvest of crayfish and hellgrammites with respect to their annual production in the New River between Bluestone Dam and Sandstone Falls.

Site Description

The crayfish and hellgrammite populations residing in the river reach between Bluestone Dam and Sandstone Falls were the focus of study. Crayfish and hellgrammites were sampled at six sites within this study reach (Figure 1). Sampling was conducted at three sites in 1983 during a pilot study (Roell and Orth 1988), and four sites were the focus of sampling in 1984 and 1985. The majority of sampling occurred immediately below Bluestone Dam and in the vicinity of Brooks Pool. The Bluestone Dam site included the area immediately below the dam downstream to the Route 3 bridge (about 1.1 km). The Longbottom site was located about eight river kilometers (RK) below the dam. The Upper and Lower Riffles were located about 12.3 RK and 14.8 RK, respectively, downstream from the dam, and bounded Brooks Pool. Sandstone Falls was 16.4 RK below the dam, and sampling at this site occurred immediately above the falls. All sites, except Brooks Pool, were shallow riffle areas averaging less than 0.5 m deep during normal summer discharge. The predominant streambed substrata at all sites, except Sandstone Falls and Brooks Pool, were gravel, cobble, boulder, and rock outcrops. Substrata at Sandstone Falls were primarily gravel, bedrock, and rock outcrops, and those in Brooks Pool were mostly sand, gravel, and bedrock.

Two species of aquatic macrophytes appeared to predominate. Patches of water willow (*Justicia americana*), an emergent plant, were present throughout this river

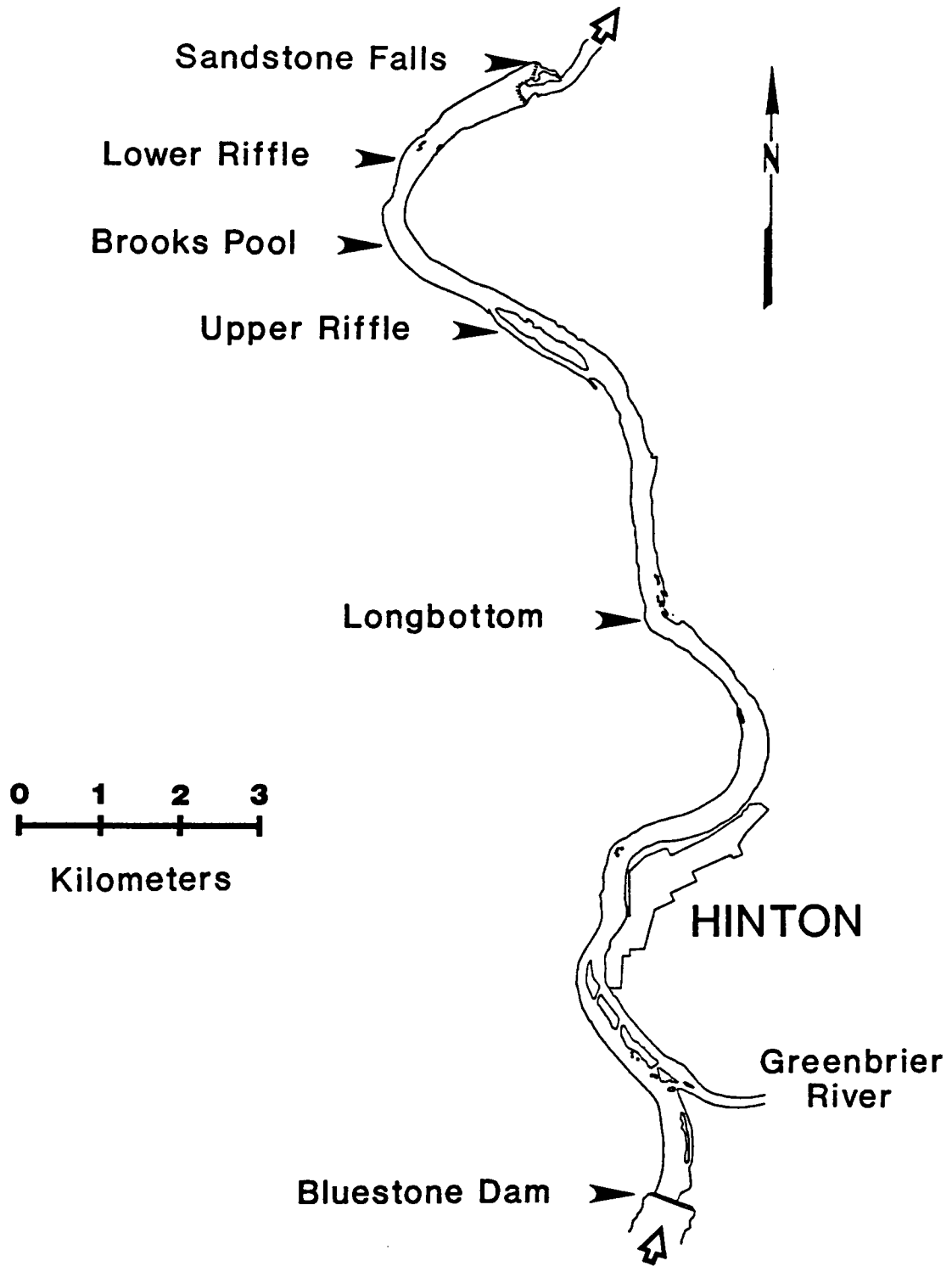


Figure 1. Map of the study reach showing the location (arrows) where crayfish and hellgrammites were sampled during 1983, 1984, and 1985 in the New River, West Virginia.

reach and were usually associated with the stream margins (including those of islands) and shallow, mid-stream areas having fine substrata. *Podostemum ceratophyllum*, a submergent plant, was widespread on the larger substrata in riffle-rapid areas. Two other species (*Elodea nuttallii* and *Heteranthera dubia*) occurred, but were not as widespread as *J. americana* and *P. ceratophyllum*.

Methods

Study Reach Characteristics

Riffles and pools within the study reach were delineated on topographic maps with the aid of aerial photographs and on-site inspection. Surface areas of riffles and pools were measured from the maps with a Tektronix digitizing instrument.

Water temperature data, collected below Bluestone Dam during all or part of eight years, were used to develop an annual profile of average daily temperatures. Continuously-recording thermographs measured temperature from June 1984 to December 1985 and from March to June 1986. In addition, published daily temperature data (USGS 1979, 1980, 1984) corresponding to 1977 - 1979 and 1982 - 1983 were used. A date-specific estimate of mean daily temperature was calculated for the first day of each of seven-day intervals, which in total represented a complete year. Total degree-days for the year were estimated from the date-specific estimates of mean daily temperature.

Abundance

The estimation of abundance of each crayfish population and the hellgrammite population was facilitated with two sampling techniques. In 1984 (except 9 and 14 October), a shock-kick method was employed. The gear consisted of a 2.44 X 1.22-m seine with either 0.8-mm or 1.6-mm mesh. The lead line of the seine was tied loosely to a 1.52-m diameter aluminum hoop that encompassed 1.815 m². The gear was held in place on the streambed by one person while another person thoroughly shocked within the hoop with a backpack electroshocker using either alternating-current or pulsed direct-current electricity. Immediately after shocking, the substrata were kicked to dislodge stunned crayfish and hellgrammites. The larger rocks were removed to facilitate this. The seine was then lifted into a canoe, and the crayfish and hellgrammites were collected. Each of these samples was preserved in a plastic bag with either 10% formalin or 100% 2-propanol and retained for laboratory analysis. At least 20 quadrats were sampled on each sampling date. A transect across the river was chosen arbitrarily, and a quadrat was sampled at each of about 5-m intervals along the transect. The gear was difficult to use in depths greater than about 0.75 m; therefore, a sampling site chosen there was ignored and a new one was selected until a workable site was encountered. A total of 70 quadrats were sampled with this technique on three dates at two sites in 1984.

The shock/kick technique worked well with hellgrammites, but crayfish often recovered quickly from electrical shock and escaped the gear. Two other problems limited the usefulness of this technique. Low stream flows in August, September, and October often failed to carry stunned animals into the seine. Also, the design of the gear precluded the collection of samples in deeper water (> 0.75 m). Consequently, on 9 and 14 October 1984 and all sampling dates in 1985, samples were collected by

hand while snorkeling or using SCUBA. The aluminum hoop alone was used to delimit quadrats. Two divers worked side-by-side starting at the downstream portion of the quadrat and working to the upstream portion. Rocks with a diameter greater than about 50 mm were slowly removed, and the crayfish and hellgrammites were captured by hand. Most crayfish and hellgrammites were caught, yet those few that escaped (virtually all crayfish) were counted and recorded. Escaping animals were pursued until caught or lost. Each sample was preserved in plastic bags with 100% 2-propanol. At least 15 quadrats were sampled on each sampling date, and quadrat sites were chosen as in the shock/kick technique. A total of 140 quadrats on seven dates at four sites were sampled with this technique in 1984 and 1985.

Crayfish and hellgrammite density estimates from a 1983 pilot study (Roell and Orth 1988) were also used to estimate abundances. The shock/kick technique was used in 1983 also. A total of 160 quadrats was sampled at three sites on eight dates in that year.

SCUBA was used to sample thirty quadrats on 9 October 1984 in Brooks Pool along a longitudinal, midstream transect. This information was used to facilitate the estimation of abundance of crayfish and hellgrammites in pools.

Qualitative sampling was conducted, in addition to quadrat sampling, in 1984 on 9 October (Brooks Pool site; depth of 1.5 m) and in 1985 on 5 May and 13 June (Bluestone Dam site), 14 June (Upper Riffle site), 30 July (Sandstone Falls site), 2 August (Brooks Pool site; depths < 1 m), 6 September (Longbottom site), and 10 and 11 September (Brooks Pool site; depths of 2 m and < 1 m, respectively). A team of two divers overturned streambed substrata and attempted to capture all crayfish and hellgrammites. The animals were preserved in 3.8-L plastic jugs with 100% 2-propanol and retained for laboratory analysis. These samples were used to help elucidate individual cohorts by length-frequency analysis.

Age-specific estimates of abundance (number • m²) were calculated for crayfish (each species) and hellgrammites at each site on each date. Cohorts (age groups) were identified from length-frequency distributions (method of Momot 1967) in the quantitative and qualitative collections.

Age-specific estimates of hellgrammite and crayfish abundance were highly variable within and among sample dates, thus preventing the direct estimation of annual mortality for all four species. A short life span and poor representation of age-0 animals in the catch precluded estimation of reliable instantaneous annual mortality rates from catch curves.

Identification and Measurements

Each crayfish was identified to the species level of classification, and its carapace length (CL - tip of the rostrum to the mid-posterior margin of the carapace; mm) was measured. Identification was made with the aid of a taxonomic key (Hobbs 1976), illustrations (Hobbs 1974), and a reference collection that was verified by Horton H. Hobbs, Jr. of the Smithsonian Institution in Washington, D.C. Females bearing eggs or young were noted. The head capsule width (HCW; mm) of each hellgrammite was measured. For the purpose of developing predictive equations, carapace length and the width (mm) of a non-regenerated chela were measured from each crayfish in a subsample of crayfish of each species. For the same purpose, the wet weight and carapace length of crayfish (head capsule width of hellgrammites) were measured. All length attributes were measured with vernier calipers to the nearest 0.05 mm, and wet weight was measured to the nearest 0.01 g.

Linear regression was used to develop predictive equations (Appendix Table 1) of wet weight versus carapace length for each of the three crayfish species and wet weight versus head capsule width for hellgrammites. Log_{10} transformations were performed on the values of the dependent and independent variables before the regression procedure was conducted. Predictive equations were also developed for carapace length versus chela width (no transformations) of each crayfish species.

Production

Estimates of annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; live weight) of crayfish and hellgrammites were calculated for ages-1 and -2 animals residing in riffles. An assessment of the sizes of crayfish and hellgrammites sold by four bait retailers (see "Exploitation" below) in Hinton, West Virginia, suggested that primarily ages-1 and -2 animals of all four species comprised the bait harvest from the New River. Age-0 animals were not fully recruited to the capture gear, thus precluding reasonable estimates of their production. *O. virilis* and *C. sciotensis* can live to age 3, but no *O. virilis* and only 16 *C. sciotensis* of that age were caught during quantitative sampling. Age-3 crayfish of these species probably contribute little to the total annual production of their populations due to low abundances and slow growth rates.

Production was calculated by the instantaneous growth method (Ricker 1975), where, for a given time interval, production was the product of instantaneous growth (in weight) and mean biomass. Growth was estimated using length-frequency information. Carapace lengths of crayfish and head capsule widths of hellgrammites were used as the length attributes. Crayfish and hellgrammites caught during quantitative and qualitative sampling served as the source of length data.

Inspection of the length-frequency distributions of crayfish (each species) caught at all sites and hellgrammites caught in riffles near Brooks Pool revealed that each age group of each population exhibited similar growth rates through the year and among years. Thus, length data from crayfish and hellgrammites collected at the same general time within the year and among years at these sites were pooled. Length-frequency distributions were then developed (2-mm CL intervals for crayfish; 0.75-mm HCW intervals for hellgrammites), and age groups were identified (Momot 1967). For each age group, a wet weight that corresponded to the midpoint of each length interval was estimated with a length-weight equation (Appendix Table 1). These wet weights, each weighted by the frequency of animals represented in the corresponding length interval, were used to calculate a mean weight for the age group. The instantaneous growth rate for a time interval was the natural logarithm of the ratio of the mean weight on the last day of the interval and the mean weight on the first day of the interval. The mean biomass during a time interval was calculated from the corresponding abundance and mean weight estimates for the interval.

Production was estimated only for the growing season (22 March to 22 November), which was assumed to be the time of year when water temperatures equaled or exceeded 10 °C. Production intervals within the growing season were determined by the availability of abundance and/or mean weight estimates. When only one estimate was available, the other estimate was approximated under certain assumptions (see below). Estimates of both abundance and mean weight were approximated for each species for the dates of 22 March and 22 November only, but at least one of the required estimates was available for all other dates.

For each crayfish species, length-frequency distributions were similar among all sample areas during the year. Consequently, for each age group of each popu-

lation, mean abundance estimates and length-frequency data (used to estimate mean weights) from all sample sites were pooled for production computations.

Site-specific estimates of abundance of age-1 and age-2 crayfish were used to calculate age-specific estimates that were representative of abundance in the study reach. For a given day of the year, each site-specific estimate was weighted by its corresponding number of quadrats and then used to calculate an estimate of mean abundance. Because crayfish samples were collected on different days in the same year and in different years, equivalent dates were assigned to each estimate of mean abundance. Equivalent dates corresponded to the following pooled samples: 24 June (26 June 1983 and 22 and 23 June 1985), 29 July (26 July 1983 and 31 July 1985), 12 August (15 and 16 August 1983 and 7 and 8 August 1984), 5 September (4 and 5 September 1985), and 14 October (13 and 14 October 1984). Abundance estimates for 22 March, 5 May, and 22 November were linearly interpolated from proximate estimates, if such estimates declined with time, or were assumed equal to a proximate estimate, if such estimates did not decline with time.

Equivalent dates for crayfish mean weights corresponded to the following pooled samples: 24 June (26 June 1983 and 13, 14, 22, and 23 June 1985), 29 July (26 July 1983, 30 and 31 July 1985, 1 August 1983, 7 and 8 August 1984, and 2 August 1985), 5 September (29 August 1983 and 4, 5, 6, 10, and 11 September 1985), and 14 October (9, 13, and 14 October 1984). Mean weight estimates on 22 March, 12 August, and 22 November were either linearly interpolated from proximate estimates (assuming no weight loss or growth during the winter period) or assumed equal to the previous estimate.

Two factors complicated the estimation of hellgrammite production. First, larval abundance immediately below Bluestone Dam seemed unusually low in 1985 compared to that in 1983 and 1984. Abundance was "normal" again beginning at ap-

proximately 1 km below the dam. Second, the growth rate of hellgrammites residing immediately below the dam was greater than that of larvae elsewhere in the reach. Growth at the Longbottom site, the midpoint in the study reach, was similar to that in riffles near Brooks Pool (Upper Riffle, Lower Riffle, and Sandstone Falls sites) at the downstream end of the reach. Hence, I assumed that abundance and growth rate of hellgrammites in riffles throughout the study reach were similar at any one time, and used abundance estimates and length-frequency distributions of larvae in riffles near Brooks Pool to estimate production of larvae in riffles in the study reach.

Estimates of age-1 hellgrammite abundance on 8 August 1984, 4 September 1985, and 14 October 1984, when assumed representative of abundances on those dates in any one year, were used to calculate an instantaneous daily mortality rate using linear regression. This rate was used to estimate the abundances of age-1 larvae on 22 March, 19 June, and 30 July. Similarly, the abundances of age-1 larvae on 22 November and age-2 larvae on 22 March and 1 August were estimated with an instantaneous daily mortality rate, which was calculated from the abundances of age-1 larvae on 14 October 1984 and age-2 larvae on 23 June 1985. Emergence from the river by 1 August was assumed for all age-2 larvae.

Mean weight of age-0 hellgrammites on 22 November was assumed equal to the mean weight of age-1 larvae on 22 March, further assuming that no weight was lost during the winter period (temperatures $< 10^{\circ}\text{C}$). The November estimate was calculated by linear extrapolation from estimates of mean weight of age-0 larvae on 1 September (data of 29 August 1983 and 4 September 1985 samples pooled) and 14 October 1984. Mean weights of age-1 larvae on 22 November and that of age-2 larvae on 22 March were linearly interpolated from the mean weights of age-1 larvae on 14 October 1984 and that of age-2 larvae on 23 June 1985, again assuming no weight loss during the winter period.

Estimates of annual production of age-1 and age-2 crayfish and hellgrammites, representative of the study reach, were calculated. First, production in pools was calculated. Then mean production was calculated by weighting the estimates of production in riffles and in pools by the total surface area in riffles and pools, respectively, and averaging the weighted values. Production in pools was estimated for each age group by multiplying production in riffles by a scalar, which was the ratio of abundance in Brooks Pool on 9 October 1984 and the mean of abundances at the Bluestone Dam and Lower Riffle sites on 13 and 14 October 1984, respectively (only abundance at the Lower Riffle site on 14 October 1984 was used for hellgrammites). I assumed that the growth rates of crayfish and hellgrammites living in pools was equal to that in riffles. Annual mean biomass, which was required for the calculation of turnover rates (annual production divided by annual mean biomass), was estimated for ages-1 and -2 animals (combined) from the abundance and mean weight information that was used to calculate production.

Exploitation

A qualitative survey of four bait sellers in Hinton, West Virginia, was conducted to determine the minimum sizes of hellgrammites and crayfish that were acceptable for sale. Then, for each species, length-frequency distributions were examined to determine the time of year when particular age groups were vulnerable to harvest. Abundance and mean weight information, used to estimate the annual production of the riffle-dwelling portion of each population, was also used to estimate the annual mean abundance of marketable-sized members of each population in the study reach.

Hellgrammites first achieved marketable size as age-1 larvae on about 1 August. Annual mean abundance (number \cdot m²) of marketable-sized hellgrammites in riffles was thus computed as the mean of abundances of age-1 larvae on 30 July (a date represented in production computations) and later dates and age-2 larvae. The ratio of the abundance of age-1 larvae in Brooks Pool on 9 October 1984 and the abundance of age-1 larvae in the Lower Riffle on 14 October 1984 (no age-2 larvae were present in October) was multiplied by the estimate of annual mean abundance of larvae in riffles to gain an estimate of pool-dwelling hellgrammites of marketable size. These estimates of larval abundance in riffles and pools were multiplied by their corresponding estimates of area of each macrohabitat to obtain an estimate of absolute abundance of marketable-sized larvae in the study reach.

Similar computations of annual mean abundance of marketable-sized crayfish were made for each crayfish population. All age-1 *C. sciotensis* greater than or equal to their mean individual weight on 29 July (approximate day of the year when minimum marketable size was attained) were considered marketable, as were all age-2 *C. sciotensis*. All age-1 and age-2 *O. virilis* and *O. s. sanbornii* were considered so. The species-specific estimates were combined to obtain estimates representative of the crayfish assemblage.

The proportion of the annual production of ages-1 and -2 hellgrammites that was harvested was computed. The annual harvest in 1983 was about 742,980 larvae (Nielsen and Orth 1988) and was multiplied by the annual mean weight of the average marketable-sized larva (1.30 g; calculated from mean weights used to calculate production) to gain an estimate of total biomass harvested from the study reach. The annual harvest of crayfish in 1983 (197,424 crayfish; Nielsen and Orth 1988) was multiplied by 7.44 g (annual mean weight of the average marketable-sized crayfish) to obtain an estimate of total crayfish biomass harvested from the study reach.

Results

Study Reach Characteristics

The total area of the study reach between Bluestone Dam and Sandstone Falls was about 408 ha. The areas of riffles and pools were about 197 ha and 211 ha, respectively (Figure 2; Table 1). Average daily water temperatures ranged from about 2 °C in mid-February to about 27 °C in early August (Figure 3). The growing season of crayfish and hellgrammites was considered to be the time of year when water temperature equaled or exceeded 10 °C. Water temperature rose above 10 °C on about 22 March and fell below 10 °C on about 23 November.

Species Life Histories

Four crayfish species were caught, three species of the genus *Orconectes* (*O. virilis*, *O. sanbornii sanbornii*, and *O. spinosus*) and one species of *Cambarus* (*C. sciotensis*). *O. virilis*, *O. s. sanbornii*, and *C. sciotensis* were caught regularly and were the focus of study. Members of the *O. spinosus* population represented < 1% of the total crayfish catch, and were not considered further.

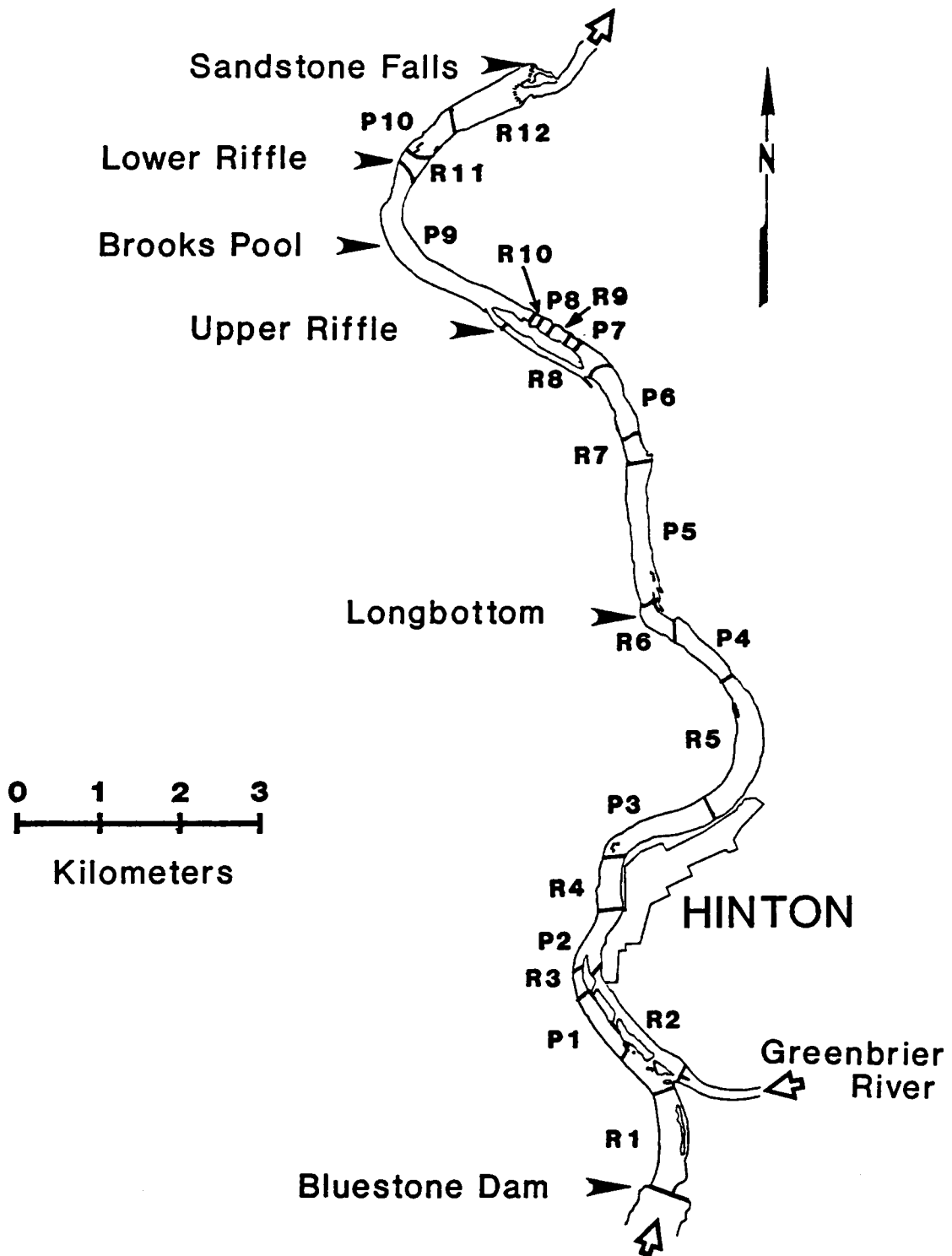


Figure 2. Locations of riffles (R1 - R12) and pools (P1 - P10) in the study reach of the New River, West Virginia.

Table 1. Surface areas (ha) of riffles and pools within the study reach of the New River, West Virginia.

<u>Riffle</u>	<u>Surface Area</u>	<u>Pool</u>	<u>Surface Area</u>
R1	30.6	P1	14.3
R2	34.4	P2	17.2
R3	4.4	P3	31.7
R4	15.4	P4	15.7
R5	41.9	P5	37.0
R6	8.7	P6	19.5
R7	6.4	P7	1.1
R8	13.7	P8	2.3
R9	3.3	P9	56.4
R10	0.9	P10	15.9
R11	5.5		
<u>R12</u>	<u>31.8</u>		<u> </u>
Total	197.0		211.1

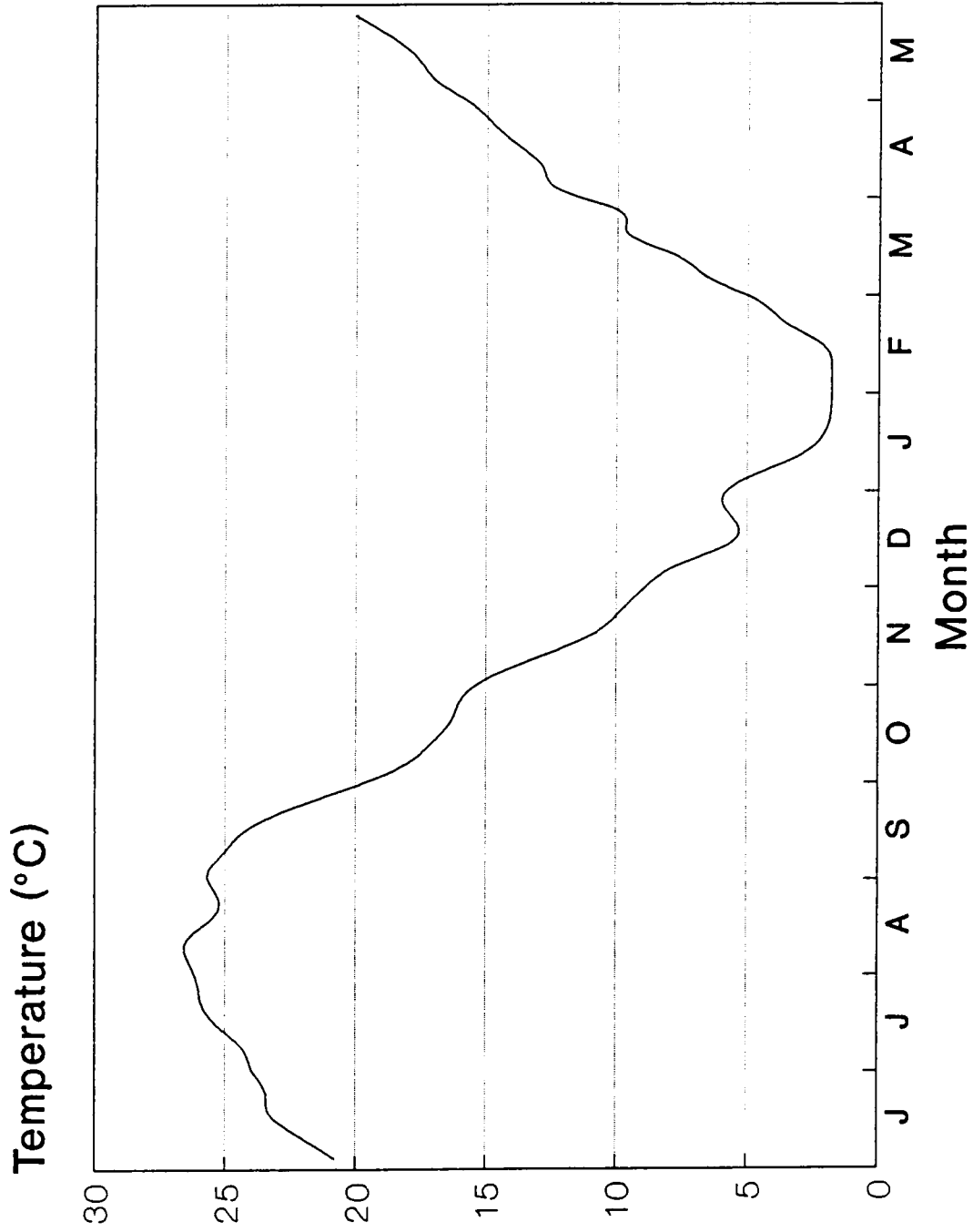


Figure 3. Annual temperature (°C) profile of the New River, West Virginia, immediately below Bluestone Dam.

O. virilis and *O. s. sanbornii* had three- and two-year life cycles, respectively (Appendix Tables 2 and 3). Young of both species hatched in about May, and adults died of senescence in late spring of their fourth and third year of life, respectively. *C. sciotensis* also had a three-year life cycle (Appendix Table 4), but the young hatched in early autumn and the senescent adults died in mid-summer of their fourth year.

Larval corydalids of two species were caught. The larvae (hellgrammites) of the dobsonfly *Corydalus cornutus* were numerous and the focus of study. *Nigronia* sp. larvae were also found, but were ignored because they were rarely caught and were too small to interest bait harvesters.

C. cornutus exhibited a two-year life cycle (semivoltine; Appendix Table 5) in the study reach. The "typical" surviving larva hatched from the egg in about late July, and then emerged from the river to pupate the spring of its third growing season. Emergence was asynchronous, occurring from about late May to late July, as judged from the occurrence of adults and their egg masses in mid-June and the absence of age-2 larvae in riffles in early August. Pupation was assumed to require one week (Brown and Fitzpatrick 1978).

Abundance

Crayfish (all species and ages) were more abundant than hellgrammites. Crayfish mean abundance, derived from date-specific estimates (Tables 2 - 4), was 2.9 crayfish • m⁻² in riffles and 0.4 crayfish • m⁻² in Brooks Pool (on 9 October 1984). Densities were slightly higher in riffles near Brooks Pool (3.5 crayfish • m⁻²) than at the Bluestone Dam site (2.7 crayfish • m⁻²). Abundance at the Longbottom site (on

Table 2. Site-specific estimates of abundance of ages-0, -1, and -2 *Orconectes virilis* living in the study reach of the New River, West Virginia, in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Bluestone Dam	26 Jun 83	20	0	48	2.400	1.323
			1	1	0.050	0.028
			2	1	0.050	0.028
	26 Jul 83	20	0	29	1.450	0.799
			1	7	0.350	0.193
			2	4	0.200	0.110
	15 Aug 83	20	0	2	0.100	0.055
			1	3	0.150	0.083
			2	1	0.050	0.028
	7 Aug 84	25	0	6	0.240	0.132
			1	4	0.160	0.088
			2	5	0.200	0.110
	13 Oct 84	25	0	1	0.040	0.022
			1	0	0	0
			2	1	0.040	0.022
22 Jun 85	15	0	7	0.467	0.257	
		1	4	0.267	0.147	
		2	3	0.200	0.110	
31 Jul 85	15	0	29	1.933	1.065	
		1	9	0.600	0.331	
		2	8	0.533	0.294	
5 Sep 85	20	0	0	0	0	
		1	0	0	0	
		2	1	0.050	0.028	
Longbottom	16 Aug 83	20	0	0	0	0
			1	2	0.100	0.055
			2	0	0	0
Upper Riffle	23 Jun 85	15	0	0	0	0
			1	1	0.067	0.037
			2	0	0	0
4 Sep 85	20	0	0	0	0	
		1	0	0	0	
		2	0	0	0	
Brooks Pool	9 Oct 84	30	0	2	0.067	0.037
			1	1	0.033	0.018
			2	0	0	0

Table 2. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Lower Riffle	8 Aug 84	20	0	25	1.250	0.689
			1	1	0.050	0.028
			2	0	0	0
	14 Oct 84	25	0	9	0.360	0.198
			1	39	1.560	0.860
			2	2	0.080	0.044
Sandstone Falls	18 Jul 83	20	0	157	7.850	4.326
			1	49	2.450	1.350
			2	1	0.050	0.028
	1 Aug 83	20	0	29	1.450	0.799
			1	6	0.300	0.165
			2	0	0	0
	29 Aug 83	20	0	83	4.150	2.287
			1	161	8.050	4.436
			2	0	0	0

Table 3. Site-specific estimates of abundance of ages-0, -1, -2, and -3 *Cambarus sciotoensis* living in the study reach of the New River, West Virginia, in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Bluestone Dam	26 Jun 83	20	0	0	0	0
			1	14	0.700	0.386
			2	2	0.100	0.055
			3	2	0.100	0.055
	26 Jul 83	20	0	0	0	0
			1	5	0.250	0.138
			2	0	0	0
			3	0	0	0
	15 Aug 83	20	0	0	0	0
			1	0	0	0
			2	1	0.050	0.028
			3	0	0	0
	7 Aug 84	25	0	0	0	0
			1	0	0	0
			2	2	0.080	0.044
			3	0	0	0
	13 Oct 84	25	0	5	0.200	0.110
			1	0	0	0
			2	9	0.360	0.198
			3	0	0	0
	22 Jun 85	15	0	0	0	0
			1	24	1.600	0.882
			2	1	0.067	0.037
			3	2	0.133	0.073
31 Jul 85	15	0	0	0	0	
		1	13	0.867	0.478	
		2	4	0.267	0.147	
		3	7	0.467	0.257	
5 Sep 85	20	0	0	0	0	
		1	14	0.700	0.386	
		2	4	0.200	0.110	
		3	0	0	0	
Longbottom	16 Aug 83	20	0	0	0	0
			1	2	0.100	0.055
			2	0	0	0
			3	0	0	0

Table 3. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Upper Riffle	23 Jun 85	15	0	0	0	0
			1	72	4.800	2.645
			2	22	1.467	0.808
			3	4	0.267	0.147
	4 Sep 85	20	0	0	0	0
			1	55	2.750	1.515
			2	13	0.650	0.358
Brooks Pool	9 Oct 84	30	0	10	0.333	0.184
			1	4	0.133	0.073
			2	5	0.167	0.092
			3	0	0	0
Lower Riffle	8 Aug 84	20	0	0	0	0
			1	8	0.400	0.220
			2	3	0.150	0.083
			3	0	0	0
	14 Oct 84	25	0	31	1.240	0.683
			1	17	0.680	0.375
			2	22	0.880	0.485
Sandstone Falls	18 Jul 83	20	0	0	0	0
			1	5	0.250	0.138
			2	0	0	0
			3	0	0	0
	1 Aug 83	20	0	0	0	0
			1	5	0.250	0.138
			2	0	0	0
	29 Aug 83	20	0	0	0	0
			1	7	0.350	0.193
2			1	0.050	0.028	
			3	0	0	0

Table 4. Site-specific estimates of abundance of ages-0, -1, and -2 *Orconectes sanbornii* living in the study reach of the New River, West Virginia, in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Bluestone Dam	26 Jun 83	20	0	28	1.400	0.772
			1	13	0.650	0.358
			2	2	0.100	0.055
	26 Jul 83	20	0	27	1.350	0.744
			1	8	0.400	0.220
			2	1	0.050	0.028
	15 Aug 83	20	0	16	0.800	0.441
			1	5	0.250	0.138
			2	1	0.050	0.028
	7 Aug 84	25	0	96	3.840	2.116
			1	14	0.560	0.309
			2	0	0	0
	13 Oct 84	25	0	34	1.360	0.749
			1	4	0.160	0.088
			2	0	0	0
22 Jun 85	15	0	34	2.267	1.249	
		1	93	6.200	3.417	
		2	2	0.133	0.073	
31 Jul 85	15	0	93	6.200	3.417	
		1	29	1.933	1.065	
		2	0	0	0	
5 Sep 85	20	0	7	0.350	0.193	
		1	2	0.100	0.055	
		2	0	0	0	
Longbottom	16 Aug 83	20	0	0	0	0
			1	0	0	0
			2	0	0	0
Upper Riffle	23 Jun 85	15	0	0	0	0
			1	3	0.200	0.110
			2	0	0	0
4 Sep 85	20	0	2	0.100	0.055	
		1	6	0.300	0.165	
		2	0	0	0	
Brooks Pool	9 Oct 84	30	0	0	0	0
			1	0	0	0
			2	0	0	0

Table 4. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Lower Riffle	8 Aug 84	20	0	20	1.000	0.551
			1	0	0	0
			2	0	0	0
	14 Oct 84	25	0	9	0.360	0.198
			1	1	0.040	0.022
			2	0	0	0
Sandstone Falls	18 Jul 83	20	0	13	0.650	0.358
			1	3	0.150	0.083
			2	0	0	0
	1 Aug 83	20	0	2	0.100	0.055
			1	0	0	0
			2	0	0	0
	29 Aug 83	20	0	1	0.050	0.028
			1	2	0.100	0.055
			2	0	0	0

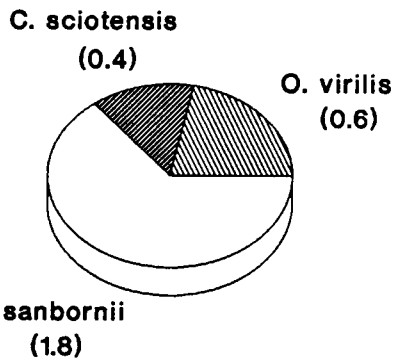
16 August 1983) was 0.1 crayfish • m⁻². *O. virilis* was the most abundant crayfish (1.2 crayfish • m⁻² overall and 1.3 crayfish • m⁻² in riffles), followed by *O. s. sanbornii* (0.9 crayfish • m⁻² overall and 0.9 crayfish • m⁻² in riffles) and *C. sciotensis* (0.7 crayfish • m⁻² overall and 0.6 crayfish • m⁻² in riffles).

Crayfish abundance was variable among species at each site (Figure 4). *O. s. sanbornii* was the most abundant crayfish (1.8 crayfish • m⁻²) in riffles immediately below Bluestone Dam, and was the least abundant crayfish (0.2 crayfish • m⁻²) in riffles near Brooks Pool. *C. sciotensis* was the least abundant crayfish (0.4 crayfish • m⁻²) in riffles at Bluestone Dam, and was intermediate in abundance (1.0 crayfish • m⁻²) in riffles near Brooks Pool. *O. virilis* was intermediate in abundance (0.6 crayfish • m⁻²) in riffles at Bluestone Dam, and was the most abundant crayfish (2.2 crayfish • m⁻²) in riffles near Brooks Pool. *C. sciotensis* and *O. virilis* had equal estimates of abundance (0.1 crayfish • m⁻²) at the Longbottom site, where *O. s. sanbornii* was not captured. *C. sciotensis* was more abundant (0.3 crayfish • m⁻²) than *O. virilis* (0.1 crayfish • m⁻²) or *O. s. sanbornii* (none caught) in Brooks Pool (Figure 4).

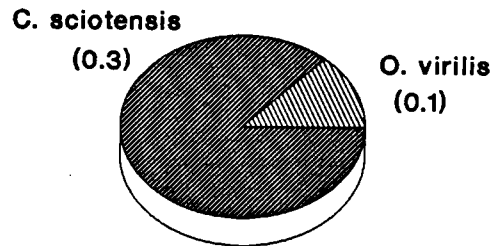
The variation in crayfish density among quadrat samples was substantial for each species. Coefficients of variation of date-specific density estimates (all ages groups combined) averaged 250% (range of 86 - 500%) for *O. virilis*, 156% (range of 52 - 346%) for *C. sciotensis*, and 135% (range of 39 - 280%) for *O. s. sanbornii*.

Age-0 crayfish were apparently under-represented in samples collected when young crayfish were present. Age-1 and older crayfish were assumed to be fully recruited to the sampling gear.

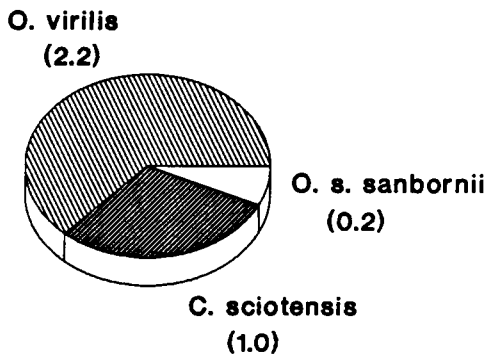
The relative abundance of each species in the four qualitative collections from Brooks Pool was 18% *O. virilis*, 65% *C. sciotensis*, and 17% *O. s. sanbornii*. *C. sciotensis* dominated two collections from deeper locations (1.5-m and 2-m depths) in the pool (7% *O. virilis*, 86% *C. sciotensis*, and 7% *O. s. sanbornii*; N = 116), but rela-



Bluestone Dam Riffles



Brooks Pool



Brooks Riffles

Figure 4. Mean crayfish abundance (number · m⁻²) by species in Bluestone Dam-area riffles, Brooks Pool, and Brooks Pool-area riffles of the New River, West Virginia.

tive abundance was more evenly distributed in two collections from shallower (< 1-m depth) locations (23% *O. virilis*, 55% *C. sciotensis*, and 22% *O. s. sanbornii*; N = 232).

Mean abundance (all ages) of hellgrammites, calculated from date-specific estimates (Table 5), was 1.3 larvae \cdot m⁻². As expected, abundance in riffles (1.4 larvae \cdot m⁻²) was greater than in Brooks Pool (0.1 larvae \cdot m⁻² on 9 October 1984). Hellgrammites were more abundant in riffles near Brooks Pool (2.0 larvae \cdot m⁻²) than in riffles near Bluestone Dam (1.0 larvae \cdot m⁻²). At the Longbottom site, larval abundance was 1.3 larvae \cdot m⁻² (on 16 August 1983). Age-0 larvae were apparently under-represented in samples collected at times of the year when age-0 larvae were present (August to December; Table 5). Age-1 and older larvae were assumed to be fully recruited to the sampling gear.

The variation in hellgrammite density (all age groups) among quadrat samples was considerable. Coefficients of variation of date-specific density estimates averaged 139% and ranged from 58 - 291%.

Production

The annual production in riffles of ages-1 and -2 crayfish (a total of 12.68 g \cdot m⁻² \cdot year⁻¹) was more than double that of ages-1 and -2 hellgrammites (6.04 g \cdot m⁻² \cdot year⁻¹). Annual production of any one crayfish species (Tables 6 - 8) was less than that of hellgrammites (Table 9). In riffles, *C. sciotensis* had the greatest estimate of annual production (4.92 g \cdot m⁻² \cdot year⁻¹), followed by that of *O. s. sanbornii* (4.48 g \cdot m⁻² \cdot year⁻¹) and *O. virilis* (3.29 g \cdot m⁻² \cdot year⁻¹). The production estimate for age-1 *O. virilis* (0.81 g \cdot m⁻² \cdot year⁻¹) appeared low, and was probably due to underestimation of abundance. In Brooks Pool, the annual production of *C. sciotensis* (1.61

Table 5. Site-specific estimates of abundance of ages-0, -1, and -2 *Corydalis cornutus* larvae living in the study reach of the New River, West Virginia, in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Bluestone Dam	26 Jun 83	20	0	0	0	0
			1	28	1.400	0.772
			2	6	0.300	0.165
	25 Jul 83	20	0	0	0	0
			1	29	1.450	0.799
			2	21	1.050	0.579
	15 Aug 83	20	0	15	0.750	0.413
			1	50	2.500	1.378
			2	0	0	0
	7 Aug 84	25	0	3	0.120	0.066
			1	6	0.240	0.132
			2	0	0	0
	13 Oct 84	25	0	5	0.200	0.110
			1	39	1.560	0.860
			2	0	0	0
22 Jun 85	15	0	0	0	0	
		1	1	0.067	0.037	
		2	2	0.133	0.073	
31 Jul 85	15	0	0	0	0	
		1	23	1.533	0.845	
		2	11	0.733	0.404	
5 Sep 85	20	0	5	0.250	0.138	
		1	49	2.450	1.350	
		2	0	0	0	
Longbottom	16 Aug 83	20	0	2	0.100	0.055
			1	32	1.600	0.882
			2	13	0.650	0.358
Upper Riffle	23 Jun 85	15	0	0	0	0
			1	37	2.467	1.359
			2	42	2.800	1.543
	4 Sep 85	20	0	1	0.050	0.028
			1	99	4.950	2.728
Brooks Pool	9 Oct 84	30	0	1	0.033	0.018
			1	6	0.200	0.110
			2	0	0	0

Table 5. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number per Quadrat	Mean N • m ⁻²
Lower Riffle	8 Aug 84	20	0	0	0	0
			1	115	5.750	3.169
			2	3	0.150	0.083
	14 Oct 84	25	0	33	1.320	0.727
			1	88	3.520	1.940
			2	0	0	0
Sandstone Falls	18 Jul 83	20	0	0	0	0
			1	8	0.400	0.220
			2	0	0	0
	1 Aug 83	20	0	0	0	0
			1	23	1.150	0.634
			2	4	0.200	0.110
	29 Aug 83	20	0	21	1.050	0.579
			1	35	1.750	0.964
			2	0	0	0

Table 6. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of ages-1 and -2 *Orconectes virilis* living in riffles in the study reach of the New River, West Virginia.

Date *	Mean $\text{N} \cdot \text{m}^{-2}$	Mean Weight (g)	Biomass $(\text{g} \cdot \text{m}^{-2})$	Mean Biomass $(\text{g} \cdot \text{m}^{-2})$	Growth Rate	Production $(\text{g} \cdot \text{m}^{-2})$
Age 1						
22 Mar	0.082 ^b	2.219 [•]	0.182			
5 May	0.075 ^b	2.744	0.206	0.194	0.212	0.041
24 Jun	0.066 ^c	4.977 ^f	0.328	0.267	0.595	0.159
29 Jul	0.252 ^c	7.771 ^f	1.958	1.143	0.446	0.510
12 Aug	0.065 ^c	7.844 [•]	0.510	1.234	0.009	0.011
5 Sep	0 ^c	7.970 ^f	0	0.255	0.016	0.004
14 Oct	0.430 ^c	7.191 ^f	3.092	1.546	-0.103	-0.159
22 Nov	0.370 ^b	7.803 [•]	2.887	2.990	0.082	0.245
				Age 1 Annual Production = 0.811		
Age 2						
22 Mar	0.187 ^b	7.803 [•]	1.459			
5 May	0.120 ^b	8.493	1.019	1.239	0.085	0.105
24 Jun	0.044 ^c	16.846 ^f	0.741	0.880	0.685	0.603
29 Jul	0.189 ^c	26.461 ^f	5.001	2.871	0.452	1.298
12 Aug	0.039 ^c	30.600 [•]	1.193	3.097	0.145	0.449
5 Sep	0.014 ^c	37.695 ^f	0.528	0.861	0.209	0.180
14 Oct	0.033 ^c	27.198 ^f	0.898	0.713	-0.326	-0.232
22 Nov	0.033 ^d	29.398 [•]	0.970	0.934	0.078	0.073
				Age 2 Annual Production = 2.476		
				Total Production = 3.287		

* 22 March and 22 November are the first and last days, respectively, of the growing season (temperatures ≥ 10 °C).

^b Linearly interpolated from 14 October and 24 June abundances.

Table 6. Concluded.

^c Abundances on the following dates were calculated from pooled information: 24 June (22, 23, and 26 June), 29 July (26 and 31 July), 12 August (7, 8, 15, and 16 August), 5 September (4 and 5 September), and 14 October (13 and 14 October).

^d Assumed to be the same as the previous abundance estimate.

^e Linearly interpolated from 14 October and 5 May mean weights, assuming no growth or weight loss during temperatures < °10 C.

^f Mean weights on the following dates were calculated from pooled information: 24 June (13, 14, 22, 23, and 26 June), 29 July (26, 30, and 31 July, and 1, 2, 7, and 8 August), 5 September (29 August, and 4, 5, 6, 10, and 11 September), and 14 October (9, 13, and 14 October).

^g Linearly interpolated from 29 July and 5 September mean weights.

Table 7. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of ages-1 and -2 *Cambarus sciotensis* living in riffles in the study reach of the New River, West Virginia.

Date ^a	Mean N \cdot m ⁻²	Mean Weight (g)	Biomass ($\text{g} \cdot \text{m}^{-2}$)	Mean Biomass ($\text{g} \cdot \text{m}^{-2}$)	Growth Rate	Production ($\text{g} \cdot \text{m}^{-2}$)
Age 1						
22 Mar	1.213 ^b	0.314 ^f	0.381			
24 Jun	1.213 ^c	0.998 ^g	1.211	0.796	1.156	0.920
29 Jul	0.284 ^c	1.936 ^g	0.550	0.881	0.663	0.584
12 Aug	0.065 ^c	2.401 ^h	0.156	0.353	0.215	0.076
5 Sep	0.951 ^c	3.199 ^g	3.042	1.599	0.287	0.459
14 Oct	0.188 ^c	3.518 ^g	0.661	1.852	0.095	0.176
22 Nov	0.188 ^d	4.360 ^f	0.820	0.741	0.215	0.159
				Age 1 Annual Production = 2.374		
Age 2						
22 Mar	0.276 ^b	4.360 ^f	1.203			
24 Jun	0.276 ^c	6.388 ^g	1.763	1.483	0.382	0.567
29 Jul	0.063 ^c	9.535 ^g	0.601	2.364	0.401	0.948
12 Aug	0.039 ^c	11.278 ^h	0.440	0.521	0.168	0.088
5 Sep	0.234 ^c	14.267 ^g	3.338	1.889	0.235	0.444
14 Oct	0.342 ^c	14.903 ^g	5.097	4.218	0.044	0.186
22 Nov	0.303 ^e	15.381 ^f	4.660	9.757	0.032	0.312
				Age 2 Annual Production = 2.545		
				Total Production = 4.919		

^a 22 March and 22 November are the first and last days, respectively, of the growing season (temperatures ≥ 10 °C).

^b Assumed to be the same as the subsequent abundance estimate.

^c Abundances on the following dates were calculated from pooled information: 24 June (22, 23, and 26 June), 29 July (26 and 31 July), 12 August (7, 8, 15, and 16 August), 5 September (4 and 5 September), and 14 October (13 and 14 October).

^d Assumed to be the same as the previous abundance estimate.

Table 7. Concluded.

- Linearly interpolated from 14 October and 24 June abundance estimates of age 2 and age 3 crayfish, respectively.
- † Linearly interpolated from 14 October and 24 June mean weights, assuming no growth or weight loss during temperatures < 10 °C.
- ‡ Mean weights on the following dates were calculated from pooled information: 24 June (13, 14, 22, 23, and 26 June), 29 July (30 and 31 July, and 2, 7, and 8 August), 5 September (4, 5, 6, 10, and 11 September), and 14 October (9, 13, and 14 October).
- ‡ Linearly interpolated from 29 July and 5 September mean weights.

Table 8. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of ages-1 and -2 *Orconectes sanbornii sanbornii* living in riffles in the study reach of the New River, West Virginia.

Date ^a	Mean N \cdot m ⁻²	Mean Weight (g)	Biomass ($\text{g} \cdot \text{m}^{-2}$)	Mean Biomass ($\text{g} \cdot \text{m}^{-2}$)	Growth Rate	Production ($\text{g} \cdot \text{m}^{-2}$)
Age 1						
22 Mar	1.201 ^b	2.156 ^c	2.589			
5 May	1.201 ^b	3.007	3.611	3.100	0.333	1.032
24 Jun	1.201 ^c	4.794 ^f	5.758	4.685	0.466	2.183
29 Jul	0.582 ^c	5.620 ^f	3.271	4.515	0.159	0.718
12 Aug	0.123 ^c	5.969 ^g	0.734	2.003	0.060	0.120
5 Sep	0.110 ^c	6.566 ^f	0.722	0.728	0.095	0.069
14 Oct	0.055 ^c	4.438 ^f	0.244	0.483	-0.392	-0.189
22 Nov	0.053 ^d	7.011 ^e	0.372	0.308	0.457	0.141
				Age 1 Annual Production = 4.074		
Age 2						
22 Mar	0.053 ^d	7.011 ^e	0.372			
5 May	0.046 ^d	9.913	0.456	0.414	0.346	0.143
24 Jun	0.044 ^c	12.913 ^f	0.568	0.512	0.264	0.135
29 Jul	0.016 ^c	17.395 ^f	0.278	0.423	0.298	0.126
12 Aug	0.007 ^c	17.395 ^h	0.122	0.200	0	0
				Age 2 Annual Production = 0.404		
				Total Production = 4.478		

^a 22 March and 22 November are the first and last days, respectively, of the growing season (temperatures ≥ 10 °C); 12 August assumed to be the date when all living age 2 crayfish died.

^b Assumed to be the same as the subsequent abundance estimate.

^c Abundances on the following dates were calculated from pooled information: 24 June (22, 23, and 26 June), 29 July (26 and 31 July), 12 August (7, 8, 15, and 16 August), 5 September (4 and 5 September), and 14 October (13 and 14 October).

^d Linearly interpolated from 14 October and 24 June abundance estimates of age 1 and age 2 crayfish, respectively.

^e Linearly interpolated from 14 October and 5 May mean weights, assuming no growth or weight loss during temperatures < 10 C.

Table 8. Concluded.

^f Mean weights on the following dates were calculated from pooled information: 24 June (13, 14, 22, 23, and 26 June), 29 July (26, 30, and 31 July, and 2, 7, and 8 August), 5 September (4, 5, 6, 10, and 11 September), and 14 October (9, 13, and 14 October).

^g Linearly interpolated from 29 July and 5 September mean weights.

^h Assumed to be the same as the previous mean weight estimate.

Table 9. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of ages-1 and -2 *Corydalus cornutus* larvae living in riffles near Brooks Pool of the New River, West Virginia.

Date ^a	Mean N \cdot m ⁻²	Mean Weight (g)	Biomass ($\text{g} \cdot \text{m}^{-2}$)	Mean Biomass ($\text{g} \cdot \text{m}^{-2}$)	Growth Rate	Production ($\text{g} \cdot \text{m}^{-2}$)
Age 1						
22 Mar	8.528 ^b	0.109 ^d	0.930			
19 Jun	4.598 ^b	0.229 ^e	1.053	0.992	0.742	0.736
30 Jul	3.389 ^b	0.585	1.983	1.518	0.938	1.424
8 Aug	3.169	0.819	2.595	2.289	0.336	0.769
4 Sep	2.728	1.712 ^f	4.670	3.633	0.737	2.678
14 Oct	1.940	1.321	2.563	3.617	-0.259	-0.937
22 Nov	1.872 ^c	1.470 ^g	2.752	2.658	0.107	0.284
				Age 1 Annual Production = 4.954		
Age 2						
22 Mar	1.679 ^c	1.470 ^g	2.468			
23 Jun	1.543	1.825 ^e	2.816	2.642	0.216	0.571
1 Aug	1.489 ^c	2.162 ^h	3.219	3.018	0.169	0.510
				Age 2 Annual Production = 1.081		
				Total Production = 6.035		

^a 22 March and 22 November are the first and last days, respectively, of the growing season (temperatures ≥ 10 °C); 1 August was assumed to be the date of complete emergence from the river.

^b Estimated with the instantaneous mortality rate calculated from the abundances on 8 August, 4 September, and 14 October using least squares regression (see text for details).

^c Estimated with the instantaneous mortality rate calculated from the abundances on 14 October and 23 June.

^d Assumed equal to the 22 November mean weight of age 0 hellgrammites, which was calculated by linear extrapolation from the mean weights on 1 September and 14 October.

^e Calculated from a pooling of the 14 June and 23 June samples.

^f Calculated from a pooling of the 29 August and 4 September samples.

^g Linearly interpolated from 14 October and 23 June mean weights, assuming no growth or weight loss during temperatures < 10 °C.

^h Calculated from the 30 July sample.

$\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was greater than that of *O. virilis* ($0.03 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$); *O. s. sanbornii* were not caught there, so their annual production was assumed to be zero. The annual production of hellgrammites in Brooks Pool was $0.34 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$.

Estimates of annual production of each crayfish population (age groups 1 and 2 combined), representative of the study reach, were $1.61 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ for *O. virilis*, $3.21 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ for *C. sciotensis*, and $2.16 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ for *O. s. sanbornii*. A total of $6.98 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ was produced by the three crayfish species. Estimates of annual mean biomass in the study reach were $1.29 \text{ g} \cdot \text{m}^{-2}$ for *O. virilis*, $2.19 \text{ g} \cdot \text{m}^{-2}$ for *C. sciotensis*, and $1.15 \text{ g} \cdot \text{m}^{-2}$ for *O. s. sanbornii*. The respective turnover rates of the three species were 1.2, 1.5, and $1.9 \cdot \text{year}^{-1}$.

Annual production of hellgrammites (age groups 1 and 2 combined) representative of the study reach was $3.09 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. Annual mean biomass in the study reach was $1.83 \text{ g} \cdot \text{m}^{-2}$, so the turnover rate was about $1.7 \cdot \text{year}^{-1}$.

Exploitation

The qualitative survey of four bait sellers in Hinton, West Virginia, revealed that the crayfish harvest corresponded primarily to ages-1 and -2 animals. Crayfish with carapace lengths of about 20 mm or greater were marketable. Thus, ages-1 and -2 *O. virilis* and *O. s. sanbornii* were assumed marketable throughout the harvest season, and age-1 *C. sciotensis* caught on about 1 August and thereafter and age-2 animals caught any time were deemed marketable.

Annual mean abundance of marketable-sized ages-1 and -2 crayfish (all three species) in riffles was $1.2 \text{ crayfish} \cdot \text{m}^{-2}$ and that in pools was $0.2 \text{ crayfish} \cdot \text{m}^{-2}$. The annual mean abundance of marketable-sized crayfish in the study reach was

2,786,000 crayfish (2,364,000 crayfish in riffles and 422,000 crayfish in pools). In 1983, the total annual harvest of crayfish in the study reach was about 197,424 crayfish (1,469 kg). About 129,744 crayfish (965 kg) were caught by commercial harvesters and 67,680 crayfish (504 kg) were caught by anglers (Nielsen and Orth 1988). Thus, the instantaneous rate of annual fishing mortality of marketable-sized crayfish was about $0.07 \cdot \text{year}^{-1}$. The total annual crayfish harvest in the study reach ($0.36 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was equivalent to about 5% of the annual production of ages-1 and -2 crayfish.

The hellgrammite harvest corresponded primarily to ages-1 and -2 animals also. Larvae with head capsule widths (HCW) of about 6 mm or greater were marketable. Therefore, age-1 larvae caught on about 1 August and thereafter were assumed marketable, and all age-2 animals caught were marketable. In any single year, hellgrammite harvest in the spring and early summer (March through July) consisted of age-2 larvae, and subsequent harvest in the year (from August through October) consisted of age-1 larvae.

The annual mean abundance of marketable-sized ages-1 and -2 hellgrammites in riffles was $2.5 \text{ larvae} \cdot \text{m}^{-2}$ and that in pools was $0.1 \text{ larvae} \cdot \text{m}^{-2}$. Thus, the abundance of marketable-sized larvae in the study reach was about 5,136,000 larvae (4,925,000 larvae in riffles and 211,000 larvae in pools). In 1983, the total annual harvest of larvae between Bluestone Dam and Sandstone Falls was about 742,980 larvae (966 kg). About 633,144 larvae (823 kg) were caught by commercial harvesters and 109,836 larvae (143 kg) were caught by anglers (Nielsen and Orth 1988). Therefore, the instantaneous rate of annual fishing mortality of marketable-sized hellgrammites was about $0.14 \cdot \text{year}^{-1}$. The total annual harvest of hellgrammite biomass ($0.24 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was equivalent to about 8% of the annual production of ages-1 and -2 hellgrammites.

Discussion

Crayfish

The crayfish assemblage in the New River, West Virginia, has changed in recent years. Markham et al. (1980) found four species in 1979 in a survey of five sites located between Bluestone Dam and Sandstone Falls. *O. virilis* was the only relatively abundant species (52 animals caught), having expanded its range from Bluestone Lake, where it was introduced prior to 1972 (as judged from Edmundson 1974); the occurrences of *C. sciotensis* (3), *O. spinosus* (1), and *O. obscurus* (2) were rare. I did not find *O. obscurus* in the study reach. Markham et al. (1980) used a 1.3-m deep seine and presumably sampled in riffles; therefore, *O. s. sanbornii* and a relatively greater number of *C. sciotensis* should have been caught if the crayfish assemblage in 1979 resembled that found in this study. This information suggests that *O. virilis* was well-established before the arrival of *O. s. sanbornii* from its former range, tributaries of the Ohio River in West Virginia, Ohio, and northeast Kentucky (Hobbs 1976). *O. virilis* and *O. s. sanbornii* were probably introduced unintentionally by anglers and/or bait dealers.

The life histories of *O. virilis* and *O. s. sanbornii* in the New River accord with life histories reported by Momot (1967), Fielder (1972), Momot and Gowing (1977a, 1977b, 1983), and Momot (1978). I did not find published life history information for *C.*

sciotensis. I found published accounts of the population dynamics of *O. virilis* only. Thus, first accounts of the population dynamics of *C. sciotensis* and *O. s. sanbornii* are reported here.

Momot (1967, 1978) and Momot and Gowing (1977a) quantified the population dynamics of lake-resident populations of *O. virilis* in three northern Michigan lakes and two northern Ontario lakes. Estimates of the abundances of ages-1 and -2 crayfish in the Michigan lakes were greater than those for the New River population, while those from the Ontario lakes were slightly lower than found in this study. However, given the substantial variance of the crayfish densities reported here, valid comparisons among the four studies were precluded. A crayfish population may, in general, attain greater biomass in lentic versus lotic systems (Hopkins 1967a, 1967b; Momot et al. 1978). Jones and Momot (1983) suggested that food availability (and presumably quality) may be the primary limiting factor of crayfish abundance in most aquatic environments, because crayfish must process substantial quantities of food to acquire sufficient energy for tissue maintenance and growth. Several other factors (predation, competition, exploitation, habitat quality, and others) probably have roles in limiting the abundance of a crayfish population.

The species composition of crayfish in different locations in Brooks Pool suggested that habitat partitioning among the three species was occurring. *C. sciotensis* clearly dominated deeper (1 - 3 m), mid-stream locations (87% by number), but relative abundances in shallower (< 1 m) locations were more evenly distributed among the three species (23% *O. virilis*, 55% *C. sciotensis*, and 22% *O. s. sanbornii*). All three species appeared to coexist in riffle areas, although species associations in both habitats may not yet be "stabilized" as a result of the introduction of *O. virilis* and *O. s. sanbornii*.

Estimation of annual mortality rates was not possible. Momot and Gowing (1977a) estimated *O. virilis* yearling and adult annual mortality rates, which ranged from 0 - 0.94% and 0.01 - 0.89%, respectively. They concluded that mortality for adult crayfish was density-dependent, but yearling mortality showed little response to population fluctuations. In addition, the abundance of adults had no noticeable effect on the mortality rate of age-0 crayfish. Extrinsic factors such as availability of nursery area and food for young can regulate subsequent numbers of adults, regardless of the initial size of a cohort (Jones and Momot 1981; Momot and Gowing 1983), through changes in age-specific mortality rates (Momot 1984).

Comparison of length-frequency distributions between the New River *O. virilis* population and each of three Michigan (Momot 1967; Momot and Gowing 1977a) and two Ontario *O. virilis* populations (Momot 1978) indicated similar growth rates for age-0 and age-1 crayfish, but somewhat higher rates for age-2 crayfish in the New River population. Given the subjective nature of age assignment from length-frequency data (the method used in this research and in the Michigan and Ontario research), growth in the New River population may not be significantly different from that of the northern populations, but faster growth could be expected in more southern populations due to warmer temperature regimes and longer growing seasons. The length-frequency distributions (and assigned ages) of New River *O. s. sanbornii* accord with those of a stream population of *O. s. sanbornii* described by Fielder (1972). Momot et al. (1978) considered abundance to be an important factor in controlling growth of *O. virilis*, and they supported their argument with information from Hopkins (1966, 1967a, 1967b), who assessed growth and reproduction of *Paranephrops planifrons* in New Zealand.

Accounts of production of *O. virilis* were found in the literature, but no accounts were found for *C. sciotensis* or *O. s. sanbornii*. Estimates of the annual production of

ages-1 and -2 *O. virilis* in three Michigan lakes (7.27 - 17.35 g • m⁻² • year⁻¹ ; Momot and Gowing 1977a) and two Ontario lakes (2.04 and 2.75 g • m⁻² • year⁻¹ ; Momot 1978) were greater than that of New River *O. virilis* (1.61 g • m⁻² • year⁻¹). However, the variance of density estimates used to calculate production precluded valid comparisons among estimates of production from these studies.

Crayfish production is highly variable among different stream populations, reflecting site-specific differences in crayfish standing stock, survivorship, and growth. Annual production of *C. bartonii*, the only crayfish species in a North Carolina mountain stream, was about 6.4 g • m⁻² • year⁻¹ (assuming 83% water content as recommended by Waters 1977; Huryn and Wallace 1987). Mason (1975) estimated the annual production of *Pacifastacus leniusculus trowbridgii*, the only crayfish species living in a small stream in western Oregon; six age classes contributed to the production of 13.3 g • m⁻² • year⁻¹. Estimates of 235.8 and 241.7 g • m⁻² • year⁻¹ (from two different methods) were reported by Shimizu and Goldman (1983) for *P. leniusculus* residing in a rip-rap area in the Sacramento River, California. Charles F. Rabeni (research results presented at the 117th Annual American Fisheries Society meeting) reported a total crayfish production of 48 g • m⁻² • year⁻¹ (assuming 83% water content; Waters 1977) for two species (25.8 g • m⁻² • year⁻¹ by *O. luteus*; 22.2 g • m⁻² • year⁻¹ by *O. punctimanus*) living in a small stream in south-central Missouri. The production of *O. propinquus*, a species closely related to *O. virilis* (Momot et al. 1978), in an enriched warmwater stream in Michigan was 41.5 g • m⁻² • year⁻¹ (Vannote and Ball 1972). Production of ages-1 and -2 crayfish there was 33.7 g • m⁻² • year⁻¹.

The annual turnover rate (the ratio of annual production to annual mean biomass) of ages-1 and -2 *O. virilis* in the New River (1.2 • year⁻¹) was similar to turnover rates of *O. virilis* in three Michigan lakes and two Ontario lakes (1.0 - 1.4 • year⁻¹; calculated from Momot and Gowing 1977a and Momot 1978); the turnover rates

of *C. sciotensis* and *O. s. sanbornii* in the New River were about 1.5 and 1.9 • year⁻¹, respectively. The turnover rate of New River *O. virilis* should be slightly greater on average than that of their more northern counterparts, because growth of crayfish in West Virginia should be greater as a result of a warmer temperature regime and a longer growing season. However, Momot et al. (1978) noted remarkably similar turnover rates for four species (representing three genera) in four different environments, suggesting that knowledge of biomass and turnover rate could facilitate the estimation of crayfish production.

Few studies have evaluated the effect of harvest on crayfish populations. Brandt and Schreck (1975) evaluated qualitatively the effect of harvest of *O. spinosus* and *C. bartonii* populations in a West Virginia stream, and concluded that these stocks were relatively resilient to moderate exploitation. Momot and Gowing (1977b, 1977c) exploited *O. virilis* populations in two Michigan lakes, harvesting from 25 - 57% of the annual production of age-1 to age-3 crayfish during three years of trapping. Harvest, which targeted male crayfish, led indirectly to an increase in the survival rate of female crayfish, but decreases in the fecundity of females (through density-dependent effects) led to population stability.

The total harvest of New River crayfish by people (0.2 million crayfish in 1983; Nielsen and Orth 1988) was a small proportion of crayfish production. Only about 5% of the annual production of ages-1 and -2 crayfish was harvested annually. Furthermore, the instantaneous rate of fishing mortality (0.07 • year⁻¹) was only 5% of the annual turnover rate (1.5 • year⁻¹) of the three crayfish populations (combined). This suggests that greater exploitation of crayfish by people may be sustainable, but the demands for crayfish by predatory fishes and other predators must also be considered before substantial increases in harvest rate are justified.

River cooters (*Pseudemys concinna*) and queen snakes (*Regina septemvittata*) are among other vertebrates known to feed on crayfish in the New River (Buhlmann 1986; Buhlmann and Vaughan 1986), and others which likely do so are other reptiles, various waterfowl and wading birds, raccoon, mink, and muskrat. The extent of crayfish use by these animals is unknown.

Hellgrammites

Corydalus cornutus occurs throughout North America east of the continental divide (Chandler 1956; Merritt and Cummins 1984), but the few detailed studies reported in the literature are of southern (Georgia and Texas), univoltine populations (Brown and Fitzpatrick 1978; Benke et al. 1984; Short et al. 1987). Dobsonflies in more northern regions (Michigan) have two- or three-year life cycles (Chandler 1956; Knight and Simmons 1975), and those in the New River have a two-year life cycle. This suggests that the *C. cornutus* life span is governed by latitude-associated temperature effects. Vannote and Sweeney (1980) hypothesized that members of at least some aquatic insect species attain a maximum adult body size and fecundity (desireable attributes in terms of species success) as a result of an optimum thermal regime experienced during the immature stage. Suboptimal (warmer or cooler) thermal regimes result in less fecund, smaller adults. For a given species, maximum larval size (and subsequent adult size) is associated with an intermediate generation time, which is controlled by the temperature regime (in this case, optimal). Larger larvae have lower weight-specific respiration costs, and therefore higher individual adult fecundity. Warmer/cooler thermal regimes shorten/lengthen generation time. Associated larval (and adult) size and, therefore, fecundity are lower. New River

hellgrammites may experience a near-optimal thermal regime, because generation time is intermediate between that reported in the literature for other populations (see above).

Brown and Fitzpatrick (1978) investigated an univoltine population of *C. cornutus* residing in and around a north-central Texas stream. The "typical" Texas hellgrammite hatched in mid-June, grew until November, resumed growth in March, and emerged from the river to pupate in early June. Similar life histories were reported by Benke et al. (1984) in Georgia and Short et al. (1987) in Texas. New River hellgrammites apparently experience a shorter growing season, and are thus unable to emerge to pupate in their second summer. Prey organisms were extremely abundant (Voshell 1985) and were not considered a limitation to growth.

Hellgrammite abundance in the New River (2.5 larvae \cdot m⁻² in riffles) was about equal to or less than that reported for five Texas streams (Brown and Fitzpatrick 1978; Short et al. 1987). However, the substantial variation of estimates of larval density in the New River (variance was not reported in the other studies) forestalled valid comparisons of abundance among these populations. The New River is 5 - 30 times wider than the streams in Texas; therefore, the absolute abundance per unit stream length is much greater in the New River and supports a substantial bait fishery. In addition, a two-year life cycle facilitates the capture of marketable-sized hellgrammites throughout the sport fishing season. Univoltine populations, such as those in Texas, would not necessarily provide the same benefit to bait harvesters.

The annual production of New River hellgrammites (3.09 g \cdot m⁻² \cdot year⁻¹) was less than that of hellgrammites studied in four Texas streams (Brown and Fitzpatrick 1978; Short et al. 1987). However, the substantial variance of the density estimates used to calculate production of New River hellgrammites precluded valid comparisons with production estimates from other populations. Two causes for true differ-

ences between production of New River larvae and that of Texas hellgrammites relate to underrepresentation of age-0 larvae in the catch of New River hellgrammites (Table 5) and a slower growth rate of New River larvae. Young larvae contribute substantially to the total production of a population (Brown and Fitzpatrick 1978). Differences in growth rates are probably due to differences in thermal regimes between the New River and the Texas streams. Degree-days ($> 0^{\circ}\text{C}$) in the four Texas streams ranged from 7,499 to 8,107 (Short et al. 1987); degree-days in the New River were about 5,389. Short et al. (1987) attributed the variation in hellgrammite production in four Texas streams to differences in thermal regimes. Hellgrammite production in these streams varied from 9.72 to $79.14 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (assuming 83% water content; Waters 1977).

The annual turnover rates of the hellgrammite populations in Texas also reflect the inclusion of young larvae in the production computations and the faster growth rates there. The turnover rates ranged from 8.6 to $11.9 \cdot \text{year}^{-1}$ (Brown and Fitzpatrick 1978; Short et al. 1987). The turnover rate of ages-1 and -2 larvae in the New River was about $1.7 \cdot \text{year}^{-1}$; this value would be somewhat greater if fast-growing age-0 larvae had been included. Nevertheless, compared to the Texas populations, the turnover rate in the New River population should be less, reflecting a lower standing crop and a slower growth rate there.

The annual harvest of New River hellgrammites in 1983 was substantial (0.8 million larvae) in an absolute sense, but was only about 8% of the annual production of ages-1 and -2 larvae. The instantaneous rate of fishing mortality ($0.14 \cdot \text{year}^{-1}$) was only 8% of the annual turnover rate ($1.7 \cdot \text{year}^{-1}$). This suggests that the population could sustain greater exploitation by people. However, as recommended for crayfish harvest, the demand for hellgrammites by predatory fishes and other predators deserves consideration before the expansion of hellgrammite harvest can be proposed.

The demand for crayfish and hellgrammites by the principal predatory fishes in the New River is addressed in the next chapter.

Chapter 2

Trophic Basis of Production of Predatory Fishes in the New River, West Virginia

Introduction

Research and management of warmwater streams have lagged behind that of coldwater streams primarily because fishery biologists strongly emphasized the management of salmonids prior to the 1980's (Winger 1981). Such a focus may have engendered a poor perception, in the minds of the public and other resource managers, of the value of warmwater streams (Stroud 1981). Another contributing factor to this delay in warmwater stream research was that the typically greater size and complexity of warmwater streams precluded the use of sampling methods employed in coldwater streams (Cleary and Greenbank 1954; Stroud 1981).

The scientific, economic, and recreational values of warmwater streams have received greater recognition in the 1980's, and several avenues of research have been rigorously investigated (for example, see Krumholz 1981 and Matthews and

Heins 1987). Naturally, the focus of research was initially on small streams, which facilitated the use of conventional sampling methods. Larger streams tend to be deeper and more open systems and are thus inherently more difficult to sample than smaller streams. Therefore, less is known about the community dynamics of larger warmwater streams compared to smaller ones.

Larger streams meet the needs of people in several ways. Recreational and commercial fishing, canoeing and boating, water supply (for agricultural, industrial, and municipal uses), and generation of electricity are some examples. Because society's demand for resources in large warmwater streams is or may become substantial, investigation of the community dynamics in these systems is warranted. This is particularly true if resource managers are to cope with such demands and their attendant management problems.

One approach to investigating a stream community is to quantify the trophic basis of production of the populations of interest. The productivity of a population is a measure of the population's ability to sustain predation, exploitation, and other sources of mortality, and thus perpetuate the population. Production is directly related to food intake, and consumption of food is directly related to the availability of food resources. Thus, from the perspective of a population, the production of its food resources and the fate of such production affect the biomass that the population can sustain.

The New River from Bluestone Dam downstream to Sandstone Falls harbors one of the most popular sport fisheries in West Virginia. The principal sport fish there is the smallmouth bass (*Micropterus dolomieu*), but rock bass (*Ambloplites rupestris*) and flathead catfish (*Pylodictis olivaris*) are also numerous (Lobb 1986). Other sport fishes comprise a much lower proportion of the total biomass of predatory fishes. Smallmouth bass, rock bass, and flathead catfish feed extensively

on crayfish (Decapoda: Cambaridae) in other waters (Minckley and Deacon 1959; Turner and Summerfelt 1970; Vannote and Ball 1972; Scott and Crossman 1973; Edmundson 1974; Coble 1975; Miner 1978; Layher and Boles 1980; Probst et al. 1984; Austen and Orth 1988). The popularity of hellgrammites (*Corydalis cornutus* larvae) among anglers on the New River (Nielsen and Orth 1988) suggests that hellgrammites are a preferred prey of some predatory fishes. A bait fishery harvested about one million crayfish and hellgrammites there in 1983 (Nielsen and Orth 1988).

Substantial exploitation of crayfish and hellgrammites could limit the principal food resources of these predatory fishes, and could indirectly cause substantial losses in predator production. The extent of exploitation effects depends critically on the magnitude of consumption of crayfish and hellgrammites by the predator populations. Because predatory fishes and bait harvesters may compete for limited crayfish and hellgrammite resources, quantitative evaluation of the dynamics of these key predator populations and their consumption of prey was warranted as a first step to determining the supply of prey and its demand by predatory fishes and bait harvesters. When this research was initiated in 1984, the status and dynamics of the fish stocks in the New River were unknown. I therefore examined the trophic basis of production of smallmouth bass, rock bass, and flathead catfish in the New River to: (1) quantify the proportion of production of predatory fishes harvested by people; and (2) evaluate the potential for competition among these predatory fishes and people for limited prey stocks, specifically crayfish and hellgrammites. Furthermore, this work embodies new information about the dynamics of rock bass and flathead catfish populations in a warmwater stream.

Site Description

Population parameters of smallmouth bass, rock bass, and flathead catfish were estimated in the second pool (hereafter called Brooks Pool) upstream from Sandstone Falls (Figure 2 in Chapter 1). This pool, which represented about 15% of the area between the dam and the falls, was selected on the basis of access and clear definition by riffles. Brooks Island partially extended into the upper portion of the pool. The left bank (when facing upstream) was overhung by deciduous trees and was virtually undeveloped except for a railroad track approximately 30 - 50 m from the river. The right bank was moderately developed by private-land owners and was dominated by beds of emergent hydrophytes (primarily *Justicia americana*). Length, surface area, and maximum, minimum, and mean widths of the pool, estimated from 1:25,000 topographic maps, were 2.7 km, 61.65 ha, 287 m, 154 m, and 228 m, respectively. Maximum and mean depths were approximately 4 m and 2 m, respectively, during the summer. Streambed substrata were predominately sand, gravel, and bedrock. Boulders, submerged ledges (or outcrops), and depositional areas occurred throughout the pool.

Lobb (1986) inventoried the fish fauna in Brooks Pool in August and September of 1985. He identified and counted fishes along 45 transects in the daytime using SCUBA. Nearly 70% of the fish counted were age-0 smallmouth bass (31.8%), shiners (*Notropis* spp.; 23.9%), and age-0 and juvenile sunfish (*Lepomis* spp.; 13.8%).

The other sport fishes observed were rock bass, spotted bass (*Micropterus punctulatus*), flathead catfish, channel catfish (*Ictalurus punctatus*), muskellunge (*Esox masquinongy*), white crappie (*Pomoxis annularis*), and common carp (*Cyprinus carpio*). The other common non-game fishes included central stoneroller (*Campostoma anomalum*), bigmouth chub (*Nocomis platyrhynchus*), logperch (*Percina caprodes*), sharpnose darter (*Percina oxyrhyncha*), greenside darter (*Etheostoma blennioides*), rainbow darter (*Etheostoma caeruleum*), bluntnose minnow (*Pimephales notatus*), and northern hogsucker (*Hypentelium nigricans*).

Methods

Simulations of the bioenergetics of smallmouth bass, rock bass, and flathead catfish enabled estimation of cohort-specific estimates of the annual consumption and annual production of these predators. Several groups of information about each predator population were required. Fish physiology parameters, abundance and mortality rate, age and growth statistics, energy densities, and diet composition were estimated for each cohort of each population. Fish physiology parameters and energy densities were either taken directly from the literature or were derived from information there. All other parameters were estimated directly from populations in the New River. Diet overlap among the three predator populations was evaluated with a diet overlap index, length-frequency distributions of prey types, and statistical analyses.

Consumption

Bioenergetics simulations (Hewett and Johnson 1987) were used to estimate the annual consumption of prey by smallmouth bass, rock bass, and flathead catfish. Six groups of information about each predator population were required; the last five

groups are site-specific information and were required for each of three time intervals, which together represented a complete year. The six groups are:

- 1) a mass balance equation, and algorithms and parameter estimates therewith, representing fish energetics and physiology,
- 2) estimates of abundance and daily mortality rates (for cohort-level modeling),
- 3) estimates of initial and final live weights that correspond to the beginning and ending, respectively, of each time interval,
- 4) energy densities ($J \cdot g^{-1}$ wet weight) of the predator and each prey type,
- 5) diet composition by prey type (proportions by wet weight), and
- 6) water temperatures.

Cohort-specific estimates of consumption quantified the dependence of each age group on each prey type. The time of annulus formation on scales or spines (subjectively determined from age and growth data) was used to separate age groups. For smallmouth bass and rock bass, 1 June was recognized as the date of annulus formation on scales. For flathead catfish, 15 June was recognized as the date of annulus formation on pectoral spines. Furthermore, a growing season (water temperatures ≥ 10 °C; 22 March to 22 November) and a winter period (temperatures < 10 °C; 23 November to 21 March) were defined, because activity ceases or is minimal below temperatures of 10 °C for smallmouth bass (Webster 1954; Bennett and Childers 1957), rock bass (Keast 1968), crayfish (Momot 1967; Fast and Momot 1973; Momot and Gowing 1977a; Momot 1978), and hellgrammites (Brown and Fitzpatrick 1978). Inactivity below 10 °C was also assumed for flathead catfish.

The simulation year for all cohorts was thus segregated into three time intervals. The first interval was from the time of annulus formation (simulation day 1) to

the end of the growing season (day 175 for the basses; day 161 for flathead catfish). The second interval represented the winter period (days 176 - 294 for the basses; days 162 - 280 for flathead catfish). The last interval was from the start of the growing season to the day before the next annulus was formed (days 295 - 365 for the basses; days 281 - 365 for flathead catfish). Simulations were conducted for age-0 to age-6 cohorts of smallmouth bass, age-0 to age-5 cohorts of rock bass, and age-0 to age-8 cohorts of flathead catfish. For each species, the last cohort for which consumption was estimated was arbitrarily determined on the basis of abundance estimates.

The Mass Balance Equation, Algorithms, and Parameter Estimates

Ingested energy has five general fates: 1) respiration, 2) egestion, 3) excretion, 4) accumulation as eggs or sperm, and 5) accumulation as somatic tissue. The ability to estimate these fates allows estimation of consumption by

$$C = G + R + S + F + U + E \quad , \quad [1]$$

where

C = Consumption,

G = Somatic tissue growth,

R = Metabolism or respiration,

S = Apparent specific dynamic action,

F = Egestion,

U = Excretion, and

E = Eggs or sperm.

Each component of this mass balance equation is calculated as a daily specific rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$), enabling calculation of absolute estimates of each component for a fish through multiplication by fish weight. For this research, each component was estimated with algorithms from the fish energetics literature. Reproductive energy storage (E) was ignored, because the energy dynamics of reproductive tissues in fishes are not well understood (Ursin 1979). The energy equivalent of eggs spawned by female fishes is in the range of 1 - 13% of their annual consumption (Ursin 1979; Wootton 1979); sperm shed by male fishes probably corresponds to a much lower percentage. The error associated with omission of reproductive energy storage from the consumption estimation procedure was considered acceptable with respect to my objectives. Estimates of the physiology-related parameters used in the bioenergetics procedure to estimate consumption for smallmouth bass, rock bass, and flathead catfish are listed in Table 10.

Consumption

The specific rate of consumption (C) was modeled as a function of three sub-components as follows:

$$C = C_{\max} \cdot C_{\text{adj}}(T) \cdot P \quad [2]$$

C_{\max} is the maximum weight-specific consumption rate of a fish feeding at the optimal temperature for consumption. It was calculated as

$$C_{\max} = a_1 \cdot W^{b_1} \quad [3]$$

where

Table 10. Parameter estimates used in the bioenergetics models to estimate consumption by smallmouth bass (SB), rock bass (RB), and flathead catfish (FC) living in Brooks Pool of the New River, West Virginia.

Symbol	Parameter Description	Parameter Estimate		
		SB	RB	FC
Consumption				
a_1	Intercept for maximum consumption ($g \cdot g^{-1} \cdot day^{-1}$)	0.33	0.25	0.25
b_1	Slope for maximum consumption dependence on weight	-0.325	-0.27	-0.20
θ_1	Temperature for K_1 ($^{\circ}C$):	10	10	10
θ_2	Temperature for K_2 ($^{\circ}C$): Age 0 fish	29	29	33
	Age 1 and older fish	26	27	31
θ_3	Temperature for K_3 ($^{\circ}C$): Age 0 fish	31	31	34
	Age 1 and older fish	28	29	32
θ_4	Temperature for K_4 ($^{\circ}C$): Age 0 fish	35	35	37
	Age 1 and older fish	33	33	35
K_1	Proportion of maximum consumption at θ_1	0.10	0.10	0.10
K_2, K_3	Proportion of maximum consumption at θ_2, θ_3	0.98	0.98	0.98
K_4	Proportion of maximum consumption at θ_4	0.01	0.01	0.01
Respiration				
a_2	Intercept for maximum standard respiration ($g O_2 \cdot g^{-1} \cdot day^{-1}$)	0.008352	0.0108	0.01
b_2	Slope for maximum standard respiration dependence on weight	-0.355	-0.20	-0.36
Q	Slope for standard respiration dependence on temperature	2.1	2.1	2.1
T_{opt}	Optimum temperature for standard respiration: Age 0 fish	35	35	37
	Age 1 and older fish	33	33	35
T_{max}	Maximum temperature for standard respiration: Age 0 fish	39	39	40
	Age 1 and older fish	38	37	38
SDA	Proportion of assimilated energy lost to SDA	0.17	0.17	0.17

Table 10. Concluded.

Symbol	Parameter Description	Parameter Estimate		
		SB	RB	FC
A	Activity multiple of standard respiration for:			
	Temperatures < 10 °C			
	Young-of-year	1.10	1.05	1.05
	Juveniles and adults	1.05	1.025	1.025
	Temperatures ≥ 10 °C			
	Age 0 fish	1.60	1.3	1.3
	Age 1 and older fish	1.30	1.15	1.15
	Egestion			
	Proportion of consumed energy egested for the following prey:			
IP ₁	Crayfish	0.180	0.180	0.180
IP ₂	Hellgrammites	0.150	0.150	0.150
IP ₃	Other insects	0.150	0.150	0.150
IP ₄	Fish	0.104	0.104	0.104
	Excretion			
UP	Proportion of assimilated energy excreted (all prey)	0.088	0.088	0.088

- a_1 = the intercept for maximum consumption ($g \cdot g^{-1} \cdot day^{-1}$),
- b_1 = the slope for maximum consumption dependence on weight, and
- W = fish weight (g).

The $C_{adj}(T)$ function is a temperature-dependent adjuster of C_{max} , and determines the maximum consumption rate of a fish experiencing a given temperature. The algorithm chosen to represent $C_{adj}(T)$ was the Thornton and Lessem (1978) function, which employs the logistic equation to approximate biological rates that behave in a sigmoid manner. The adjuster function was calculated as

$$C_{adj}(T) = K_A(T) \cdot K_B(T) \quad , \quad [4]$$

where

$$K_A(T) = \frac{K_1 \cdot (e^{\gamma_1(T-\theta_1)})}{1 + K_1 \cdot (e^{\gamma_1(T-\theta_1)} - 1)} \quad ,$$

$$K_B(T) = \frac{K_4 \cdot (e^{\gamma_2(\theta_4-T)})}{1 + K_4 \cdot (e^{\gamma_2(\theta_4-T)} - 1)} \quad ,$$

$K_A(T)$ = the rate multiplier when temperatures are less than or equal to the lower maximum-rate temperature,

$K_B(T)$ = the rate multiplier when temperatures are equal to or greater than the upper maximum-rate temperature,

T = the water temperature,

K_1 = the rate multiplier at the lower minimum-rate temperature,

$K_2, K_3 = 0.98$, the rate multipliers at the lower and upper maximum-rate temperatures,

K_4 = the rate multiplier at the upper minimum-rate temperature,

θ_1 = the lower minimum-rate temperature,

θ_2, θ_3 = the lower and upper maximum-rate temperatures,

θ_4 = the upper minimum-rate temperature, and

γ_1, γ_2 = the specific rate coefficients,

where

$$\gamma_1 = \frac{1}{\theta_2 - \theta_1} \cdot \log_e \left(\frac{(K_2 \cdot (1 - K_1))}{(K_1 \cdot (1 - K_2))} \right), \text{ and}$$

$$\gamma_2 = \frac{1}{\theta_4 - \theta_3} \cdot \log_e \left(\frac{(K_3 \cdot (1 - K_4))}{(K_4 \cdot (1 - K_3))} \right).$$

P is a proportionality constant that represents prey availability and the predator's prey-search efficiency. P can range from zero to one and is used to fit the model estimates of consumption to observed growth patterns. Values of P were iteratively chosen until the initial and final fish weights, corresponding to the beginning and ending of a time interval, conformed with the solution of the mass balance equation (see "Estimating Consumption with Energetics" below).

Values of a_i and b_i were not available in the bioenergetics literature for smallmouth bass, rock bass, and flathead catfish. The values of these parameters for smallmouth bass were assumed equal to those of the largemouth bass (*Micropterus salmoides*) model derived by Rice et al. (1983). A different approach was used in selecting the parameter values for the rock bass and flathead catfish models, because values for closely-related species were not available. Parameter estimates of a_i and b_i (summarized by Hewett and Johnson 1987) of six species were reviewed as potential surrogates for those parameters of the rock bass model. The six species were largemouth bass, yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), bluegill (*Lepomis macrochirus*), northern pike (*Esox lucius*), and muskellunge. I assumed that the maximum consumption rate (C_{max}) was directly related to the stomach capacity per unit body weight (the ability to supply energy; Cuenco et al. 1985). In this regard, rock bass were considered to be most similar to yellow perch for which estimates were derived by Kitchell et al. (1977); therefore, the

parameter estimates of a_1 and b_1 for yellow perch were used for rock bass. For flathead catfish, I concluded that none of the six species sufficed as surrogates with respect to the C_{max} assumption. Because the values of a_1 for the six species ranged from 0.18 to 0.33, a midpoint value of 0.25 was arbitrarily chosen for flathead catfish. Values of b_1 for the six species ranged from -0.33 to -0.18. This parameter defines the negatively-exponential relationship between the specific feeding rate of the fish (grams of food eaten per gram of fish per day) and fish weight, so the value of b_1 was chosen on the basis of values used for larger fish (-0.18; northern pike and muskellunge). Thus, a value of b_1 of -0.20 was used for flathead catfish.

Values for K_1 to K_4 were the same for the three predator species. K_1 was arbitrarily assumed to be 0.10 (10% of the maximum rate). K_2 and K_3 are restricted to values less than 1.0 due to the asymptotic nature of the logistic equation, therefore 0.98 was used as suggested by Thornton and Lessem (1978). A value of 0.01 was assumed for K_4 as suggested by Hewett and Johnson (1987), and as used by Stewart and Binkowski (1986) for Lake Michigan alewives. A value of 10 °C was chosen as the lower minimum-rate temperature (θ_1) for all three predators. θ_2 and θ_3 delimit the range of "optimal" temperatures at which maximum consumption occurs, and may be equal in some species. The final temperature preference of a fish closely corresponds with the optimum temperature for growth and consumption (Brett 1956; Kitchell et al. 1977; Jobling 1981). Reports of temperature preference of smallmouth bass (Fry 1950 as cited by Ferguson 1958; Peek 1965; Barans and Tubb 1973; Horning and Pearson 1973; Reutter and Herdendorf 1974; Cherry et al. 1975; Coutant 1975; Stauffer et al. 1976; Cherry et al. 1977; Mathur et al. 1981) were reviewed, and respective estimates for θ_2 and θ_3 of 29 °C and 31 °C for age-0 smallmouth bass, and 26 °C and 28 °C for age-1 and older bass were chosen. A similar review of temperature preferenda of rock bass (Neill and Magnuson 1974; Reutter and Herdendorf

1974; Cherry et al. 1977) led to respective estimates for θ_2 and θ_3 of 29 °C and 31 °C for age-0 rock bass and 27 °C and 29 °C for age-1 and older rock bass. Gammon (1973) hypothesized that the final temperature preference of flathead catfish adults ranged from 31.5 °C to 33.5 °C. Thus, values of 31 °C and 32 °C were assumed for θ_2 and θ_3 , respectively, for age-1 and older flathead catfish; 33 °C and 34 °C were assumed for age-0 catfish. The upper avoidance temperature was used to approximate θ_4 for each species. Review of upper avoidance temperatures reported in Cherry et al. (1975), Stauffer et al. (1976), and Cherry et al. (1977) led to θ_4 estimates of 35 °C for age-0 smallmouth bass and rock bass and 33 °C for age-1 and older members of these species. For flathead catfish, values of 37 °C and 35 °C were assumed for age-0 fish and older fish, respectively.

Respiration

The specific rate of respiration (R) was modeled as a function of three sub-components as follows:

$$R = R_{\max} \cdot R_{\text{adj}}(T) \cdot A \quad . \quad [5]$$

R_{\max} is the maximum weight-specific standard respiration rate for a fish experiencing the "optimum" temperature for respiration. The general equation is

$$R_{\max} = a_2 \cdot W^{b_2} \quad , \quad [6]$$

where

a_2 = the intercept for maximum standard respiration ($\text{g O}_2 \cdot \text{g}^{-1} \cdot \text{day}^{-1}$),

b_2 = the slope for maximum standard respiration dependence on weight, and

W = fish weight (g).

The $R_{adj}(T)$ function, similar to $C_{adj}(T)$ for consumption, is a temperature-dependent adjuster of R_{max} . The algorithm of O'Neill et al. (1972; adapted by Kitchell et al. 1974, 1977) was used for $R_{adj}(T)$, and is as follows:

$$R_{adj}(T) = V \cdot e^{(X \cdot (1 - V))} \quad , \quad [7]$$

where

$$V = \frac{T_{max} - T}{T_{max} - T_{opt}} \quad ,$$

$$X = \frac{W^2 \cdot \left(1 + \sqrt{1 + 40 / Y}\right)^2}{400} \quad ,$$

$$W = \log_e(Q) \cdot (T_{max} - T_{opt}) \quad ,$$

$$Y = \log_e(Q) \cdot (T_{max} - T_{opt} + 2) \quad ,$$

T = the water temperature,

T_{opt} = the optimum temperature for standard respiration,

T_{max} = the maximum temperature for standard respiration, and

Q = the slope for standard respiration dependence on temperature (approximates a Q_{10}).

A is a multiplier (≥ 1) of standard respiration, and represents metabolic demands above standard respiration that were a result of activity.

Values of a_2 and b_2 were not available in the bioenergetics literature for smallmouth bass, rock bass, and flathead catfish. The values of these parameters for smallmouth bass were assumed equal to those of the largemouth bass model derived by Rice et al. (1983). A different approach was used in selecting the parameter values for the rock bass and flathead catfish models, because values for closely-related

species were not available. Parameter estimates of a_2 and b_2 (summarized by Hewett and Johnson 1987) of six species were reviewed as potential surrogates for those parameters of the rock bass model. The six species were largemouth bass, yellow perch, walleye, bluegill, northern pike, and muskellunge. I assumed that the maximum respiration rate (R_{max}) was directly related to the gill surface area per unit body weight (ability to supply oxygen), which is correlated to maximum adult body size (Pauly 1981). In this regard, rock bass were considered to be most similar to yellow perch for which estimates were derived by Kitchell et al. (1977); therefore, the parameter estimates of a_2 and b_2 for yellow perch were used for rock bass. For flathead catfish, I concluded that none of the six species sufficed as surrogates with respect to the R_{max} assumption. Because the values of a_2 for the six species ranged from 0.002 to 0.015, a compromise value of 0.01 was arbitrarily chosen for flathead catfish. Values of b_2 for the six species ranged from -0.36 to -0.18. This parameter defines the negatively-exponential relationship between the specific respiration rate of the fish (grams of oxygen per gram of fish per day) and fish weight, so the value of b_2 was chosen on the basis of values used for the largest warmwater species (largemouth bass). Thus, a value of b_2 of -0.36 was used for flathead catfish.

A value of 2.1 for Q has been used by Kitchell et al. (1974, 1977) and Kitchell and Breck (1980); this estimate was also applied here to the three sport fish. Optimum and maximum temperatures for respiration were derived by the method of Kitchell et al. (1977).

Activity (A) above standard respiration was derived for adult smallmouth bass from activity data in Klauda (1975). He quantified the time-activity budgets of nine wild smallmouth bass (ranging from 2 to 5 years of age) living in a small stream. Activity was apportioned into non-movement-related activities, which I assumed corresponded to standard metabolism, and movement-related activities, which corre-

sponded to standard metabolism plus activity metabolism. Position-changing behavior represented 95% of the time that the bass engaged in movement-related activity; feeding and agonistic behavior represented 5% of that time. Thus, swimming speeds during upstream position changes were used to estimate activity metabolism. I assumed that no energy was expended for activity metabolism during downstream changes in position. Mean swimming speeds (velocity of fish plus water velocity) of 29.1, 32.9, and 15.3 cm • s⁻¹ during summer, fall, and winter, respectively, were applied to the activity algorithm

$$A = e^{0.0198 \cdot s}$$

where

s = swimming speed (cm • s⁻¹).

This algorithm was developed by Rice et al. (1983) for the activity metabolism of largemouth bass. Values of A of 1.77 (summer), 1.91 (fall), and 1.35 (winter) were the result. The values corresponded only to the time that bass engaged in position-changing behavior. Activity metabolism is represented in the bioenergetics model by the decimal portion of A, so this portion was adjusted with the percentage of total time that bass engaged in position-changing behavior during the three seasons (summer - 19.2%; fall - 18.1%; winter - 8.3%). The adjusted values of A were 1.15 (summer), 1.16 (fall), and 1.03 (winter). Finally, because Klauda (1975) attempted to ensure that the smallmouth bass were not food-limited (by stocking forage fish) and because the above derivation of A did not consider that portion of activity metabolism associated with foraging and agonistic behaviors, values of A were arbitrarily doubled for use in the simulations of smallmouth bass bioenergetics. Thus, A was 1.30 for age-1 and older smallmouth bass experiencing temperatures greater than or equal to 10 °C, and 1.05 for bass experiencing temperatures less than 10 °C. Based on my own

qualitative observations, I assumed that age-0 smallmouth bass engaged in twice as much activity as older smallmouth bass at all times of year, and that rock bass and flathead catfish activity was half that of smallmouth bass for all ages and times of year.

Apparent Specific Dynamic Action

Apparent specific dynamic action is the energy used in absorption, digestion, transportation, and deposition of ingested energy (Beamish 1974). The specific rate (S) was modeled as a function of assimilated energy as follows:

$$S = SDA \cdot (C - F) \quad , \quad [8]$$

where

SDA = the proportion of assimilated energy lost to apparent specific dynamic action,

F = the specific rate of egestion (see below).

Pierce and Wissing (1974) reported an SDA value of 0.127 as a fraction of total consumption for bluegills fed mayfly nymphs. Because egestion was 27% of total consumption, SDA as a fraction of assimilated energy was 0.174. Thus, a value of 0.17 was used for the three sport fish, which had an invertebrate-dominated diet.

Egestion

The specific rate of egestion was modeled as a function of consumption, prey digestibility, and proportion by weight of each prey type in the diet as follows:

$$F = FP \cdot C \quad , \quad [9]$$

where

$$FP = \sum_{i=1} (P_i \cdot IP_i) \quad ,$$

P_i = the proportion of the i^{th} prey in the diet (preserved wet weight), and

IP_i = the indigestible proportion of the i^{th} prey.

For all three species, the proportion of consumed energy egested for each prey type was 0.18 for crayfish, 0.15 for hellgrammites, 0.15 for other insects, and 0.104 for fish. The value for crayfish was derived from Stein and Murphy (1976), and agrees with that of Kelso (1972). The estimate for hellgrammites and aquatic insects was based on the work by Elliott (1976), who fed brown trout (*Salmo trutta*) insects of different ration sizes over a range of temperatures. The estimate for fish was reported by Beamish (1972).

Excretion

The specific rate of excretion was modeled as a proportion of assimilated food as follows:

$$U = UP \cdot (C - F) \quad , \quad [10]$$

where

UP = the proportion of assimilated food that is excreted (all prey).

An estimate of 0.088 for the proportion of assimilated energy excreted (UP) was derived from Rice et al. (1983).

Abundance and Mortality

The modified Schnabel abundance estimator (Ricker 1975) was used to estimate age-specific abundances of smallmouth bass, rock bass, and flathead catfish residing in Brooks Pool in 1984 and 1985. Fish were captured during four consecutive mark-recapture periods in 1984 with a 4.9-m electrofishing boat equipped with a Wisconsin hoop anode array and pulsed-DC electricity. Electrical failure of the boat during mid-July (beginning of the fifth mark-recapture period) precluded further mark-recapture sampling in 1984. In 1985, fish were caught during four consecutive mark-recapture periods with a 5.5-m electrofishing boat similarly equipped.

Approximately four days were required to thoroughly electrofish the area of Brooks Pool. Each four-day period was regarded as a mark-recapture period. About eight hours of electrofishing and marking were conducted each day. Fishing proceeded from the lower riffle up the right ascending bank, across the upper riffle, and downstream to the end of Brooks Island. Fishing continued in the same fashion for the left ascending bank, upper riffle, and left side of Brooks Island. Finally, relatively shallow areas not associated with the stream margins (mid-pool habitat) were fished to complete the mark-recapture period. Fish were retained in a live well within the boat until approximately 100 - 150 fish were caught. Batches of about 25 - 30 fish were lightly anesthetized with tricaine methanesulfonate (MS-222) in a 19-L bucket to lessen the stress of handling. All anesthetized fish were fin-clipped, and their total lengths (mm) were measured. During the first two marking periods in 1984, fish were fin-clipped and tagged with metal, individually-numbered strap tags affixed to the edge of the opercle. High tag loss ensued, so tagging was abandoned in favor of fin-clipping only. In 1985, fish were fin-clipped only. Scales (from smallmouth bass and rock bass) and pectoral spines (from flathead catfish) were collected, and live weights (g) were measured from a subsample of fish for age and growth analyses.

The fish were then released alive into shallow areas where recovery could be monitored. Virtually no immediate mortality was observed, but fish that did die were eliminated from the procedure.

Estimates of age-specific abundances and mortality rates of each age group (Appendix Tables 6 - 8) were needed to estimate consumption. Acceptable estimates from the Schnabel method were possible for only particular age groups of smallmouth bass, rock bass, and flathead catfish. Abundance estimates for other cohorts of smallmouth bass and rock bass were calculated from the acceptable estimates using an appropriate mortality rate. For example, acceptable estimates were achieved for smallmouth bass only at ages 2 and 3 in 1984 and 1985. These estimates corresponded to the middle of the estimation period in each year (27 June in 1984 and 2 July in 1985), so the mean of abundances from both years was considered applicable to 30 June of the year. The annual mortality rate from age 2 to age 3 was estimated from these age-specific mean abundances, and was converted to an instantaneous daily mortality rate (Ricker 1975). Abundance on 1 June (the recognized time of annulus formation in smallmouth bass) was then estimated by back-calculation using the daily rate. Lobb (1986) enumerated age-0 smallmouth bass along underwater transects in Brooks Pool. Abundance was about 61,650 age-0 fish on about 1 September. This estimate was used to back-calculate age-0 smallmouth bass abundance on 1 June. Abundances of ages-1, -4, -5, and -6 smallmouth bass were estimated from the abundances of age-2 and age-3 bass with a 70% annual mortality rate, which was the rate from age 2 to age 3.

Acceptable abundance estimates were obtained for rock bass only at ages 2, 3, and 4 in 1984 and 1985. Mean abundances were calculated for these age groups, and the same procedure as with smallmouth bass was used to estimate abundances of ages-0, -1, and -5 rock bass. A 95% annual mortality rate was assumed for age-0

fish. The annual mortality rate from age 2 to age 3 was used to estimate abundance of age-1 rock bass, and that from age 3 to age 4 was used to estimate abundances of age-4 and age-5 rock bass.

Reliable age-specific abundance estimates were not obtained for flathead catfish in Brooks Pool in 1984 and 1985. Flathead catfish that were recaptured ranged in age from 2 to 4, so all mark-recapture information was pooled for each year, and the resulting estimates were assumed applicable to age-2 and older fish. Estimates of 2,094 fish and 1,329 fish were calculated for 1984 and 1985, respectively. The average, 1,712 fish, and a 56% annual mortality rate, calculated from a catch curve of age-2 to age-9 fish, was used to approximate abundances for fish of these ages. Age-1 and age-0 flathead catfish abundances were estimated by back-calculation assuming annual mortality rates of 56% and 95%, respectively.

Cohort-specific annual mortality for smallmouth bass and rock bass was estimated from age-specific abundance estimates from the two consecutive years. Pooled catch-at-age data (from 1984 and 1985) and catch curve analysis (least-squares regression procedure; Ricker 1975) were also used to estimate the annual mortality rate in each of the three fish populations.

Age and Growth

Ages were directly estimated from scales or spines and lengths-at-annulus were back-calculated for 661 smallmouth bass (505 in 1984 and 156 in 1985), 825 rock bass (586 in 1984 and 239 in 1985), and 374 flathead catfish (232 in 1984 and 142 in 1985) captured in the two years. Impressions of scales collected from smallmouth bass and rock bass were made on acetate slides using a roller press. Catfish

pectoral spines were thin-sectioned with a diamond-blade saw. An age was assigned to each fish by identifying annuli from enlarged projections of the scale impressions and spine sections. Scale (or spine) radius and annular measurements were made for determination of mean lengths-at-annulus using the Fraser-Lee method of back calculation. One technician and I each assigned ages to 426 smallmouth bass scales and 490 rock bass scales from 1984 with nearly 100% agreement (most fish were age 3 or younger); therefore, I assigned ages to all remaining scales and spines. This age information was used in the calculation of age-specific abundances and mortality estimates. The age and growth information was used to derive seasonal growth equations for smallmouth bass and rock bass. Mean lengths-at-annulus (Appendix Tables 9 - 11) were compared to the average of those of other stream-dwelling populations of each species reported in Carlander (1977) and Turner (1977).

A method of assigning age from length using a probability matrix was used to estimate the ages of several smallmouth bass and rock bass due to the large number of bass caught in the two years. A modification of the procedure presented by Bartoo and Parker (1983) was used, where an age-length key was coupled with a seasonal von Bertalanffy growth model (Appendix Table 12) to estimate the age of a fish from its length. The seasonal growth model (Moreau 1987)

$$L_t = L_{\infty} \cdot (1 - e^{-K \cdot (t - t_0) + A \cdot \sin(2\pi \cdot (t - t_0))})$$

was fit to age-specific estimates of mean length of the two bass species (Appendix Tables 9 and 10) using a computer-implemented nonlinear regression procedure (Ihnen and Goodnight 1985). Ages were assigned to 1,398 smallmouth bass (611 in 1984 and 787 in 1985) and 3,608 rock bass (911 in 1984 and 2,697 in 1985). This information was used in the calculation of age-specific abundances.

Log₁₀ transformations of live weights and total lengths were used to develop length-weight equations (Appendix Table 12) for each species using linear regression. Lengths and weights were collected from 731 smallmouth bass (566 in 1984 and 165 in 1985), 922 rock bass (659 in 1984 and 263 in 1985), and 416 flathead catfish (271 in 1984 and 145 in 1985).

Four estimates of live weight (g) were required for the estimation of consumption of each cohort (Appendix Tables 6 - 8). They corresponded, in chronological order, to the day of annulus formation, the last day of the growing season (and the first day of the winter period), the last day of the winter period (and the first day of the next growing season), and the day before the next annulus was formed. Mean lengths-at-annulus for each cohort were used in the appropriate length-weight equation (Appendix Table 12) to estimate live weight on the day of annulus formation. Each of these cohort-specific live weights was also the weight for the previous cohort on the day before annulus formation and the first day of the previous winter period. Fish weight on the day of annulus formation was assumed equal to fish weight at the end of the previous growing season. A weight of 1 g was used for age-0 smallmouth bass on the first day of simulation, and corresponded to the day of annulus formation of older smallmouth bass. A weight of 1 g was used for age-0 rock bass and age-0 flathead catfish on the first day of simulation, and corresponded to 29 days and 50 days, respectively, after annulus formation of older members of those species. These weights were estimated on the basis of weight-frequency information collected in June and July of both years. Consumption was not estimated for age-0 rock bass and age-0 flathead catfish prior to those times.

The assumed level of activity (A) of these fish was less in the winter period than in the growing season; therefore, separate bioenergetics simulations were required for each period. Direct estimates of live weight were not available for the first day

of the growing season for cohorts of the three species. Thus, these weights were approximated with the following procedure. A weighted value of A was calculated for each cohort using the estimates of A from the previous and subsequent periods, and weighting each estimate by the corresponding number of days in each period. The iterative fitting procedure (adjusting consumption with P to fit observed growth) was performed with the weighted value of A and the live weights corresponding to the first day of the winter period and the next day of annulus formation. The resulting value of P was then used as a constant (not an iteratively-fit parameter) in an additional bioenergetics simulation, which predicted the weight on the first day of the growing season (see “Estimating Consumption with Energetics” below for simulation details).

Energy Densities

Energy density estimates were chosen on the basis of bomb calorimetry of crayfish and hellgrammites (Roell and Orth 1988) and energy density information reported in Cummins and Wuycheck (1971), Kelso (1972), Vannote and Ball (1972), and Brown and Fitzpatrick (1978). Energy densities of 3,766, 6,565, 5,648, and 4,184 $J \cdot g^{-1}$ wet weight represented crayfish, hellgrammites, aquatic insects, and all other fish, respectively. A constant energy density through the year was assumed for all groups.

Diet Composition

Stomach contents were collected from smallmouth bass, rock bass, and flathead catfish on 28 dates in 1984 and 1985 to estimate the proportion by wet weight of each prey type in the diet. Fish were captured with an electrofishing boat (see "Abundance and Mortality" above for details on boat configuration and operation). Smallmouth bass and rock bass were caught at approximately 0800 hours to collect diet items ingested during the presumed peak feeding periods of the previous evening and early morning (Reynolds and Casterlin 1976). Nearly all flathead catfish that were captured were sampled for diet items due to a low catch rate. Four prey types were recognized: crayfish, hellgrammites, all other aquatic insects, and fish. Stomach contents were removed by inserting an acrylic tube of appropriate diameter through the esophagus and into the stomach, and then withdrawing the tube with the stomach contents (Van Den Avyle and Roussel 1980). A clawed retriever (Dimond 1985) inserted through the tube was often used to extract crayfish. Following the removal of their stomach contents, the fish were released alive. The contents were preserved in plastic bags with either 10% formalin or 100% 2-propanol. The stomach contents of age-0 smallmouth bass and rock bass were qualitatively examined throughout the 1985 field season (starting in mid-June), because these cohorts were expected to feed exclusively on aquatic insects. An all-insect diet was assumed for age-0 flathead catfish (Minckley and Deacon 1959), because only two were caught in the two years. The 1985 diet data for flathead catfish were used, because only seven of 36 flathead catfish caught in 1984 contained food items.

In the laboratory, stomach contents were segregated into the four prey types, placed on paper towels to absorb excess moisture, and weighed to the nearest 0.01 g. The proportion by preserved wet weight of each prey type in the diet was estimated for each cohort of each predator species (Appendix Tables 13 - 15). Small

sample sizes for older fish necessitated pooling of diet information for age-3 and older smallmouth bass, age-3 and older rock bass, and age-5 and older flathead catfish.

Activity is known to be greatly reduced below temperatures near 10 °C for crayfish (Momot 1967; Fast and Momot 1973; Momot and Gowing 1977a; Momot 1978) and hellgrammites (Brown and Fitzpatrick 1978). During this time, these animals were assumed to be unavailable to predators. Therefore, during the winter period, fish and aquatic insects other than hellgrammites were assumed to be the only available prey. Diet proportions were calculated relative to those used during the growing season. For example, if aquatic insects and fish each contributed 25% during the growing season, then in winter each group comprised 50% of the diet.

Water Temperatures

Water temperature data, collected below Bluestone Dam during all or part of eight years, were used to develop an average annual temperature profile (Figure 3 in Chapter 1). The computer software (Hewett and Johnson 1987) used to simulate fish bioenergetics allowed input of temperatures for 36 dates within the year, and temperatures on days between each input date were linearly interpolated. Thus, input dates and corresponding temperatures (Appendix Table 16) were chosen accordingly. For flathead catfish, a constant temperature of 6.4 °C was assumed for 87 days during the winter period due to computing problems. This introduced error was not expected to significantly affect consumption estimates for flathead catfish, because low consumption rates are predicted at temperatures below 10 °C.

Estimating Consumption with Energetics

The consumption by each cohort was predicted with the bioenergetics computer software of Hewett and Johnson (1987). A cohort was defined as a group of fish of the same age having the same beginning and ending points in weight for a given interval of time. Therefore, the *average* individual in a cohort was modeled, and then cohort abundance was multiplied to the result for cohort-level estimates of consumption. Three simulation time intervals were necessary to represent a year of life, partly because activity and prey availability differ between the growing season and the winter period (see introduction to "Consumption" above). A daily time step was used in each simulation.

Consumption estimation was a two-step simulation process. First, P was iteratively chosen to allow predicted growth to match observed growth in a particular time interval; therefore, P was implicitly assumed to be constant during a time interval. Because the consumption subcomponent is adjusted by P , the food required to produce observed growth was estimated. On each simulation day, a growth equivalent was calculated in terms of grams of food per gram of fish per day. The absolute growth increment is the product of this specific rate and the weight of the fish on that day. The weight of the fish on the next day was calculated by converting the absolute growth increment to energy equivalents with the energy density of the prey (because the prey supplies the energy), and then adding this absolute energy equivalent to the total energy content of the fish on that day. The new total energy content of the fish was then divided by the energy density of the fish on the next day, thus calculating the new weight of the fish. This procedure was thus performed through the last day of the time interval. If the predicted weight was not within plus or minus 0.05% of the observed end point in weight, a new P was estimated and the procedure was repeated one or more times until the condition was met. In the second step, the esti-

mate of P (Appendix Tables 6 - 8) was entered as a constant in the bioenergetics model, and the simulation was run a final time to estimate consumption by prey type on each day.

Production and Biomass

The bioenergetics procedure involved the calculation of age-specific daily abundances and daily specific growth in weight, thus enabling the estimation of age-specific production on a daily basis. Daily production was summed for each of the three time intervals. Annual production was the sum of production from the three periods.

The gross growth efficiency of each age group of each population was calculated as the ratio of annual production to annual consumption. Because the energy density of the predator and its prey differed, predator production and the consumption of each prey type were converted to energy equivalents prior to calculation of gross growth efficiency.

Age-specific daily biomass was also calculated in the bioenergetics procedure from abundance and mean weight. The annual mean biomass of each cohort was calculated from daily biomass values recorded at each of 7-day intervals over the simulation year.

The annual harvests of smallmouth bass, rock bass, and flathead catfish were estimated to determine the proportion of production of each population that is utilized by people. Annual harvests were estimated from Pierce et al. (1981), who conducted an angler survey on the New River, West Virginia, from April to November 1980. This survey was conducted within three river reaches, the first two of which corresponded

to the reach between Bluestone Dam and Sandstone Falls. The estimated total harvest of each of the three species from April to November from this reach was assumed to be the total annual harvest by anglers. These species are generally inactive at other times, when water temperatures are less than 10 °C. The annual harvest of each population was calculated as the product of age-specific harvest (numbers of fish) and mean individual fish weight (g), summed over all recruited age groups. Age-2 and older smallmouth bass and rock bass and age-4 and older flathead catfish were assumed to be fully recruited to the recreational fishery. The age composition of fish in the harvest was assumed to be directly proportional to the abundances of the fully-recruited age groups. Abundances on 1 June of age-2 to age-6 smallmouth bass (Appendix Table 6) and age-2 to age-5 rock bass (Appendix Table 7) and abundances on 15 June of age-4 to age-8 flathead catfish (Appendix Table 8) were used to represent age composition. The average of mean individual fish weights on 1 June and 22 November for smallmouth bass and rock bass (Appendix Tables 6 and 7) and on 15 June and 22 November for flathead catfish (Appendix Table 8) were used as an estimate of mean individual fish weight of each age group in the harvest.

Further Diet and Consumption Analysis

A more detailed analysis of the stomach contents of the three predatory fishes was conducted in addition to that done for consumption estimation. Crayfish were identified to species when possible (see “Species Identification and Measurements” in Chapter 1 for details concerning identification of species). Carapace length (CL; mm) was measured on relatively intact crayfish, but on those exhibiting advanced

digestion, the width (mm) of a non-regenerated chela was measured. The length of the medial margin of the palm of a regenerated chela is noticeably shorter (compared to the total length of the chela) than that of an original chela. Carapace length was then estimated from chela width using predictive equations (Appendix Table 1). Head capsule widths (HCW; mm) on hellgrammites were measured. Chela of crayfish and head capsules of hellgrammites were very resistant to digestion and persisted in the gut longer than most other body parts. Chi-square analyses were used to detect differences in crayfish species composition in the diet of the three predatory fishes.

The index of Schoener (1970) was used to quantify energy resource overlap between two populations as follows:

$$\alpha = 1 - 0.5 \cdot \left(\sum_{i=1}^n |P_{xi} - P_{yi}| \right) ,$$

where

α = the measure of overlap ranging from 0 to 1,

n = the number of prey types,

P_{xi} = the proportion of annual energy intake by species x from prey type i , and

P_{yi} = the proportion of annual energy intake by species y from prey type i .

Energy resource overlap (α) is a continuum of values from 0 (no overlap) to 1 (complete overlap).

Results

Abundance and Mortality

A total of 5,945 smallmouth bass, rock bass, and flathead catfish were marked during this study, 2,392 in 1984 and 3,553 in 1985. Nine hundred thirteen and 859 smallmouth bass, 1,307 and 2,561 rock bass, and 172 and 133 flathead catfish were marked in 1984 and 1985, respectively.

Schnabel estimates of age-specific abundances were possible for age-1 to age-3 smallmouth bass in 1984 and 1985, age-1 to age-4 rock bass in 1984, and age-1 to age-5 rock bass in 1985 (Table 11; see Appendix Tables 17 - 20 for mark-recapture calculations). A low recapture rate for flathead catfish precluded the estimation of age-specific abundances with the Schnabel estimator. Only three and four catfish were recaptured in 1984 and 1985, respectively, all of which were ages 2 - 4 in both years (Appendix Tables 21 and 22, respectively). Thus, respective estimates of abundance in 1984 and 1985 for these age groups combined were 2,094 fish and 1,329 fish.

Rock bass appeared to be the most abundant predatory fish in Brooks Pool in 1984 and 1985 compared to smallmouth bass and flathead catfish (Table 11). More

Table 11. Modified Schnabel estimates of age-specific abundances of smallmouth bass and rock bass in Brooks Pool of the New River, West Virginia, in 1984 and 1985. The estimates are applicable to 15 June of the year. Each estimate (N) and its corresponding number of recaptures (R) and 95% confidence interval (CI) are shown.

<u>Year</u>	<u>Age Group</u>	<u>Smallmouth bass</u>			<u>Rock bass</u>		
		<u>\hat{N}</u>	<u>R</u>	<u>95% CI</u>	<u>\hat{N}</u>	<u>R</u>	<u>95% CI</u>
1984	1	4144	28	2903 - 6132	3917	2	1433 - 9793
	2	3868	5	1827 - 8927	4924	45	3701 - 6701
	3	959	4	428 - 2397	1753	23	1188 - 2697
	4				90	2	33 - 225
1985	1	2314	29	1629 - 3403	2179	112	1813 - 2616
	2	2063	24	1409 - 3145	4085	195	3553 - 4696
	3	796	2	291 - 1990	1072	60	836 - 1373
	4				418	15	259 - 711
	5				21	3	8 - 51

precise estimates of smallmouth bass and rock bass abundance occurred when the number of recaptures was high. Thus, more precise estimates of abundance in 1985 were possible as a result of higher recapture rates.

The total annual mortality rate of the 1982 cohort of smallmouth bass, judged from Schnabel estimates of abundance, was an estimated 79% from age 2 to age 3. Estimates of total annual mortality for the 1980, 1981, and 1982 cohorts of rock bass were 77% from age 4 to age 5, 76% from age 3 to age 4, and 78% from age 2 to age 3, respectively. Total annual mortality estimates, calculated by least squares regression from catch-at-age data (Appendix Table 23; data from both years were pooled), were 80% for smallmouth bass (ages 2 - 5; $R^2 = 0.98$), 77% for rock bass (ages 2 - 5; $R^2 = 0.98$), and 56% for flathead catfish (ages 4 - 9; $R^2 = 0.95$).

Age and Growth

Estimates of mean lengths-at-annulus were the most precise for rock bass (Appendix Table 10; standard deviations ranging 9 - 16 mm), followed by those of smallmouth bass (Appendix Table 9; standard deviations ranging 16 - 42 mm) and then those of flathead catfish (Appendix Table 11; standard deviations ranging 17 - 69 mm). Mean square errors were relatively low for the seasonal von Bertalanffy growth equations (Appendix Table 12). Coefficients of determination (R^2) were 0.99 for the length-weight equations of all three species (Appendix Table 12), which indicated precise predictability of weight from length.

The growth rate of smallmouth bass in the New River was greater than the average of twenty seven other stream-dwelling populations of smallmouth bass (Figure 5). Rock bass growth rate was greater than the average of thirteen other populations

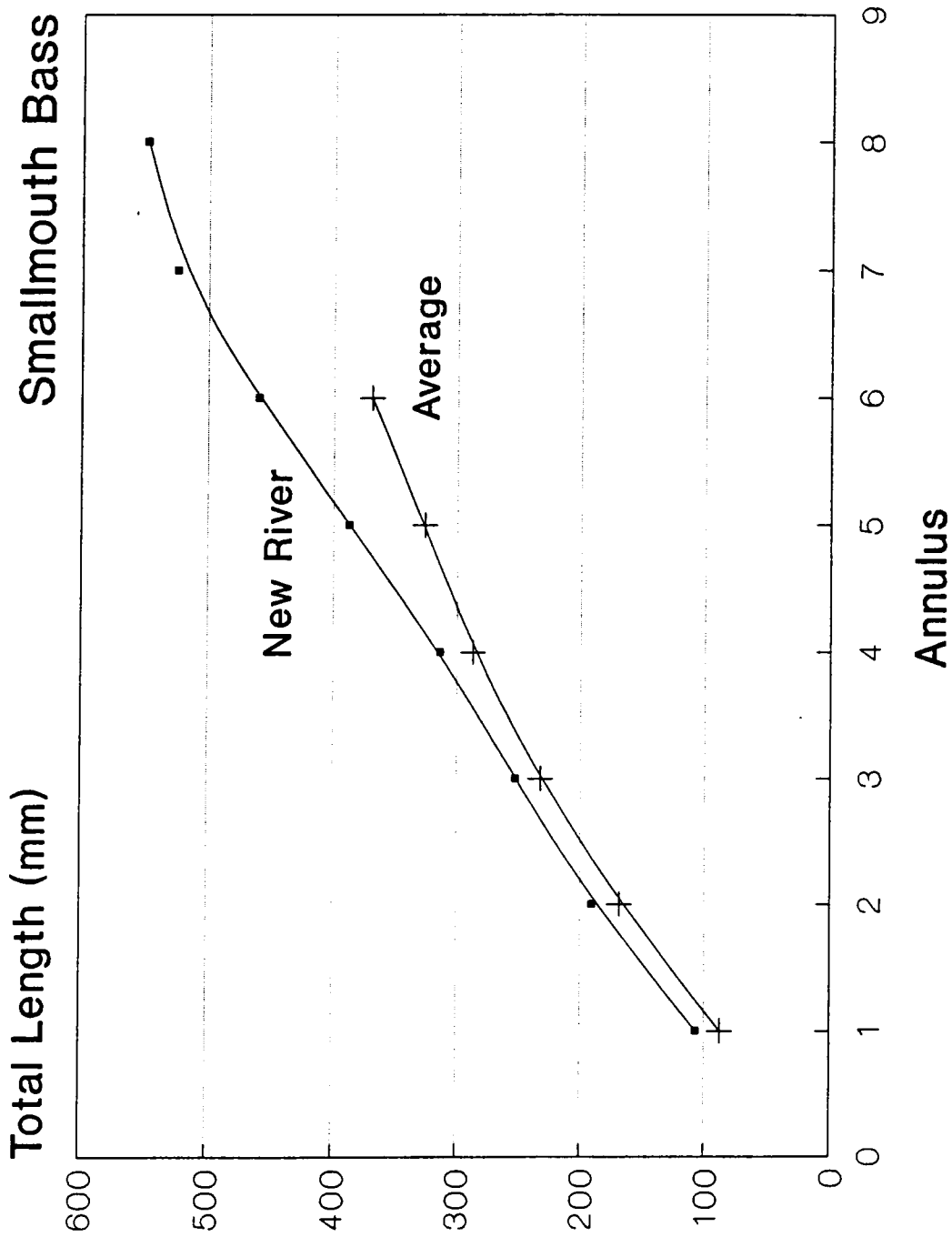


Figure 5. Comparison between mean total lengths-at-annulus (mm) of smallmouth bass from the New River, West Virginia, and the average of mean total lengths-at-annulus reported by Carlander (1977) for 27 stream-resident smallmouth bass populations in 11 states.

in streams (Figure 6). The growth rate of New River flathead catfish was less than the average in two other stream-dwelling populations (Figure 7).

Diet Composition and Analysis

The diet by preserved wet weight of the three predatory fishes (Tables 12 - 14) was dominated by aquatic insects (other than hellgrammites) and crayfish. Aquatic insects were generally most prevalent in the stomachs of age-1 fish, and became progressively less so with increasing age of fish. In 1985, qualitative observations of the diet of about 40 each of age-0 smallmouth bass and rock bass suggested an aquatic insect-dominated diet, which was also observed by George and Hadley (1979). Crayfish in the diet became more prevalent with increasing age of the fish. Hellgrammites were most notable in the diet of rock bass, but were less so in the diet of smallmouth bass and flathead catfish. Fish were secondary in importance to crayfish in the diet of older smallmouth bass and flathead catfish. Fish were most prevalent in the diet of smallmouth bass late in the growing season (August - October). Fish were virtually absent in the diet of rock bass. The percentage of empty stomachs was 19% for smallmouth bass (65 of 336 fish examined), 36% for rock bass (136 of 383 examined), and 45% for flathead catfish (65 of 210 examined).

Orconectes virilis, *Cambarus sciotensis*, and *Orconectes sanbornii sanbornii* were the three crayfish species found in the stomachs of the three predatory fishes. Identifiable crayfish in the diet of smallmouth bass (both years pooled) were comprised of 37% *O. virilis*, 51% *C. sciotensis*, and 12% *O. s. sanbornii*. The crayfish species composition in the rock bass diet (both years pooled) was 41% *O. virilis*, 48% *C. sciotensis*, and 11% *O. s. sanbornii*. Species composition of crayfish in the flathead

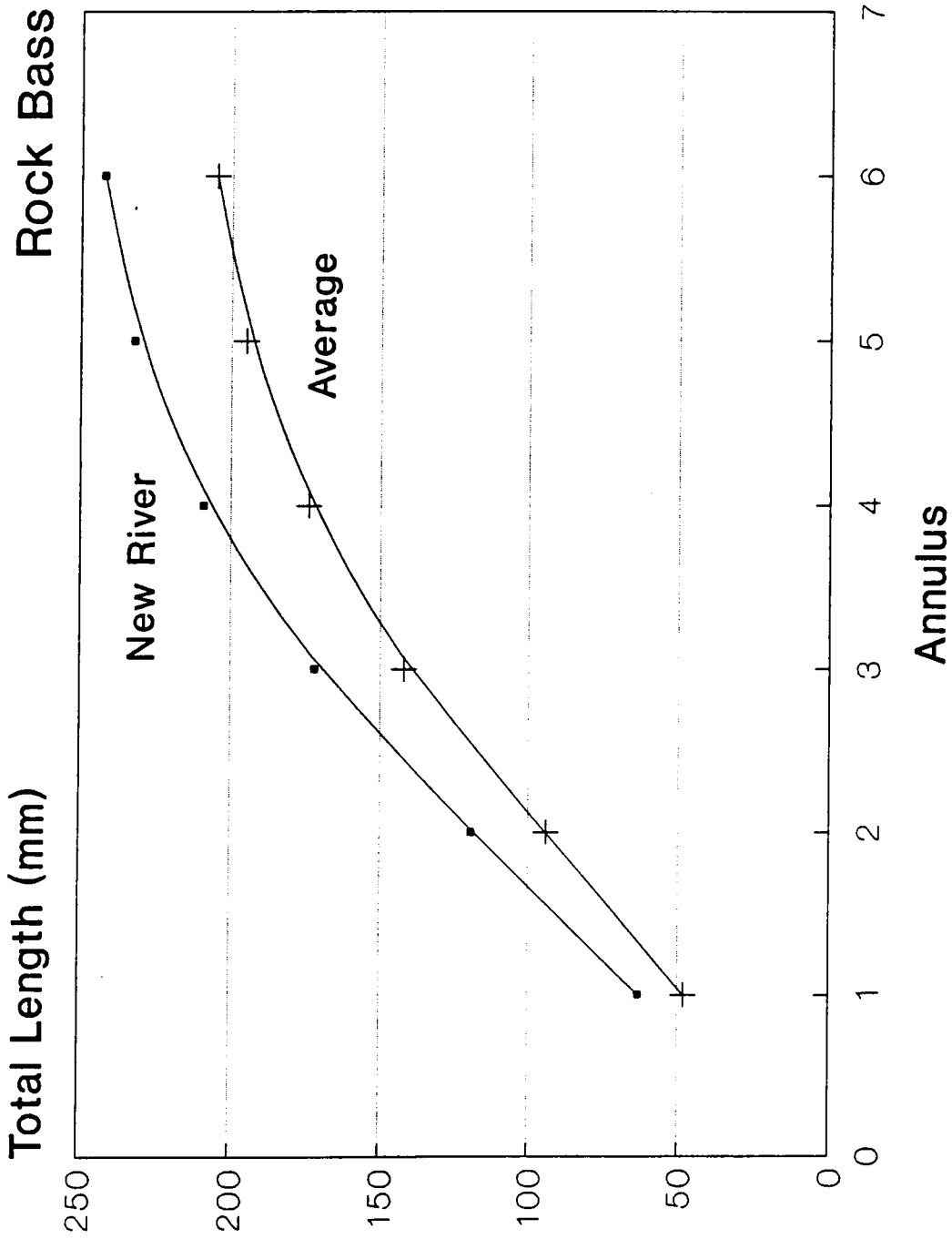


Figure 6. Comparison between mean total lengths-at-annulus (mm) of rock bass from the New River, West Virginia, and the average of mean total lengths-at-annulus reported by Carlander (1977) for 13 stream-resident rock bass populations in six states.

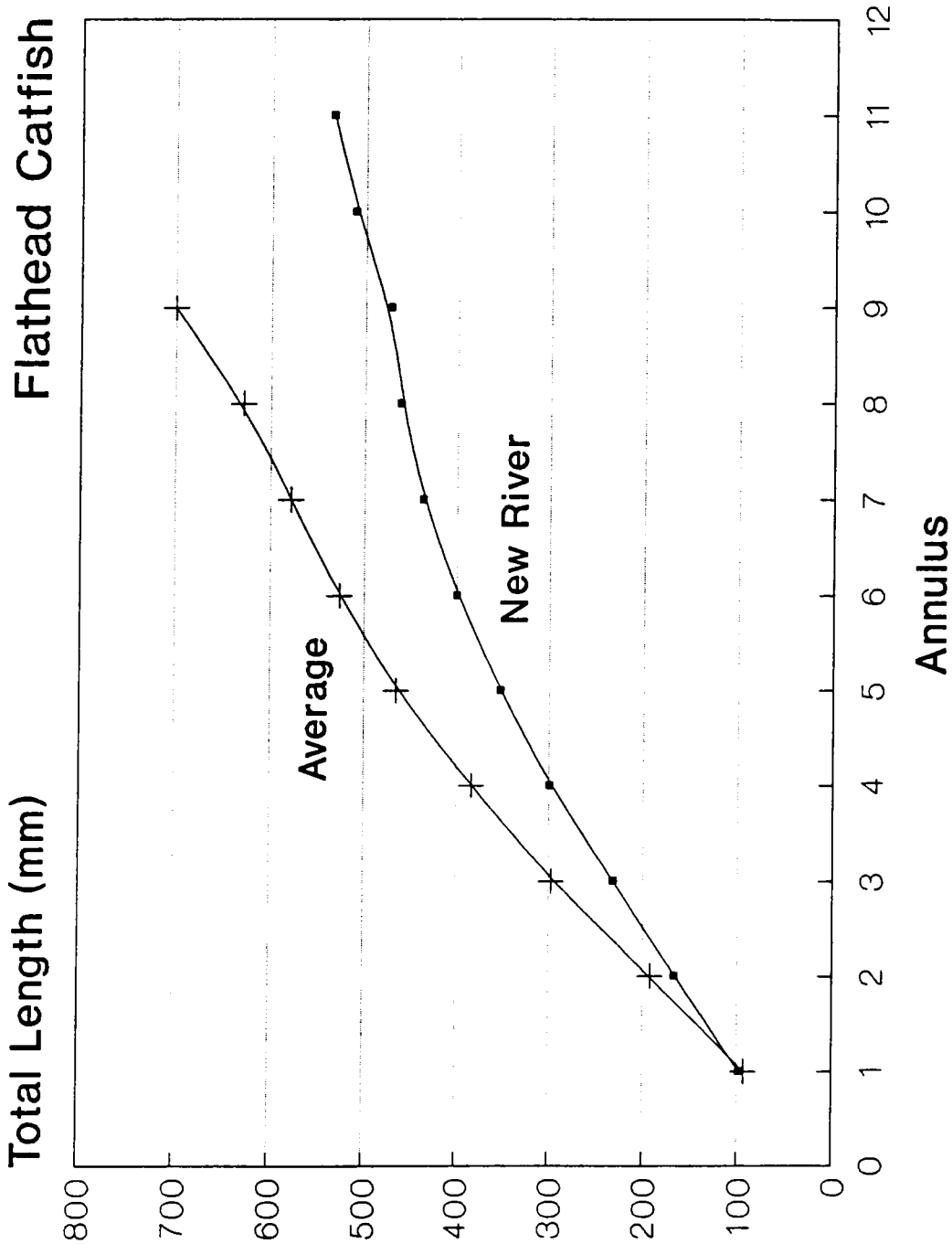


Figure 7. Comparison between mean total lengths-at-annulus (mm) of flathead catfish from the New River, West Virginia, and the average of mean total lengths-at-annulus reported by Turner (1977) for 2 stream-resident flathead catfish populations in 2 states.

Table 12. Diet composition (percentage of preserved wet weight) of age groups of smallmouth bass that were caught in Brooks Pool of the New River, West Virginia, in 1984 and 1985. N is the number of fish with diet items.

Date	Age Group	N	Prey Types			
			Crayfish	Helgram- mites	Aquatic Insects	Prey Fish
Sept 1984 ^a	1	43	7	0	92	1
	2	30	46	1	45	8
	3	10	95	0	5	0
	4	2	100	0	0	0
	6	1	100	0	0	0
	7	1	50	0	0	50
June 1985 ^b	1	3	0	0	100	0
	2	18	42	1	57	0
	3	5	74	2	16	8
	4	4	98	0	2	0
	5	2	100	0	0	0
July 1985 ^c	4	4	100	0	0	0
	5	3	100	0	0	0
	6	1	100	0	0	0
1 Aug 1985	1	11	37	0	63	0
	2	21	71	0	9	20
	3	1	100	0	0	0
29, 30 Aug 1985	1	19	55	0	32	13
	2	22	53	0	2	45
	3	3	0	0	15	85

Table 12. Concluded.

Date	Age Group	N	Prey Types			
			Crayfish	Hellgram- mites	Aquatic Insects	Prey Fish
17, 18 Sept 1985	1	15	5	0	36	59
	2	23	77	0	3	20
	3	3	100	0	0	0
7 Oct 1985	1	6	38	0	3	59
	2	14	73	0	1	26
	4	1	100	0	0	0
	5	1	100	0	0	0

• 11 - 13 September 1984

• 18 - 20 and 24 - 27 June 1985

• 3, 10, 11, 13, 14, and 16 July 1985

Table 13. Diet composition (percentage of preserved wet weight) of age groups of rock bass that were caught in Brooks Pool of the New River, West Virginia, in 1984 and 1985. N is the number of fish with diet items.

Date	Age Group	N	Prey Types			
			Crayfish	Hellgram- mites	Aquatic Insects	Prey Fish
Sept 1984 ^a	1	1	100	0	0	0
	2	39	41	8	51	0
	3	8	95	0	5	0
	4	1	0	96	4	0
June 1985 ^b	2	21	14	51	35	0
	3	5	34	64	2	0
	4	1	100	0	0	0
	5	2	28	72	0	0
	6	1	0	100	0	0
3, 10 July 1985	5	1	100	0	0	0
	6	1	100	0	0	0
1 Aug 1985	1	1	0	0	100	0
	2	16	44	25	31	0
	3	10	61	14	25	0
	4	5	89	0	11	0
29, 30 Aug 1985	1	6	0	0	100	0
	2	20	81	10	9	0
	3	3	100	0	0	0
	4	1	100	0	0	0

Table 13. Concluded.

Date	Age Group	N	Prey Types			
			Crayfish	Hellgram-mites	Aquatic Insects	Prey Fish
17, 18 Sept 1985	1	7	0	0	100	0
	2	44	63	1	36	0
	3	8	90	0	10	0
	4	7	95	5	0	0
7 Oct 1985	1	5	0	0	100	0
	2	23	94	0	6	<1
	3	6	100	0	0	0
	4	2	100	0	0	0
	5	1	100	0	0	0

^a 11 - 13 September 1984

^b 18 - 20 and 27 June 1985

Table 14. Diet composition (percentage of preserved wet weight) of age groups of flathead catfish that were caught in Brooks Pool of the New River, West Virginia, in 1984 and 1985. N is the number of fish with diet items.

Date	Age Group	N	Prey Types			
			Crayfish	Hellgram- mites	Aquatic Insects	Prey Fish
Sept 1984 ^a	1	1	100	0	0	0
	2	2	94	0	6	0
	4	1	100	0	0	0
	5	1	0	100	0	0
	10	1	0	0	0	100
June 1985 ^b	2	5	95	0	0	5
	3	10	76	21	3	0
	4	10	87	0	0	13
	5	2	100	0	0	0
July 1985 ^c	2	25	84	5	1	10
	3	20	69	3	1	27
	4	18	74	1	25	0
	5	7	100	0	0	0
	6	3	4	0	0	96
	7	4	100	0	0	0
1 Aug 1985	1	1	100	0	0	0
	4	1	100	0	0	0

Table 14. Concluded.

Date	Age Group	N	Prey Types			
			Crayfish	Hellgrammites	Aquatic Insects	Prey Fish
29, 30 Aug 1985	2	2	13	0	0	87
17, 18 Sept 1985	3	1	0	0	100	0

^a 11 - 13 September 1984

^b 18, 20, 21, and 24 - 27 June 1985

^c 2 - 4 and 9 - 16 July 1985

catfish diet (both years pooled) was comprised of 66% *O. virilis*, 29% *C. sciotensis*, and 5% *O. s. sanbornii*. Chi-square analysis of the crayfish species composition in the diets of smallmouth bass and rock bass suggested that these species foraged on crayfish resources similarly ($P > 0.05$). Significant differences in crayfish species composition in the diet were indicated between smallmouth bass and flathead catfish ($P < 0.01$) and between rock bass and flathead catfish ($P < 0.05$).

The size-frequency distributions of carapace lengths (CL) of crayfish in the fish diets (Figure 8) suggested a minimum threshold size of vulnerability to predation of about 15mm CL. In the rock bass diet, a maximum threshold size of 35 mm CL was also indicated. Therefore, judging from the length-frequency distributions of each crayfish species (Appendix Tables 2 - 4), the three predatory fishes consumed primarily age-1 and age-2 members of the three crayfish populations. Age-0 *O. virilis* and *O. s. sanbornii* became vulnerable to predation in about early August. The size-frequency distributions of head capsule widths (HCW) of hellgrammites in the fish diets (Figure 9) suggested a minimum threshold size to predation of 5.6 mm HCW. Judging from the length-frequency distribution of hellgrammites in riffles near Brooks Pool (Appendix Table 5), predation was on age-1 and age-2 hellgrammites.

Fish in the smallmouth bass diet were six shiners (*Notropis* spp.), five age-0 smallmouth bass, four darters (*Percina* spp., *Etheostoma* spp.), two age-0 rock bass, one age-0 flathead catfish, and 24 unidentified fish. Fish were virtually absent in the rock bass diet. Fish in the flathead catfish diet were five shiners, three age-0 smallmouth bass, two age-0 rock bass, two age-0 flathead catfish, and 11 unidentifiable fish.

Considerable overlap in energy resources occurred among the three fish populations. Overlap was the highest (Schoener's index of 0.93) between the smallmouth bass and rock bass populations. Overlap between smallmouth bass and flathead

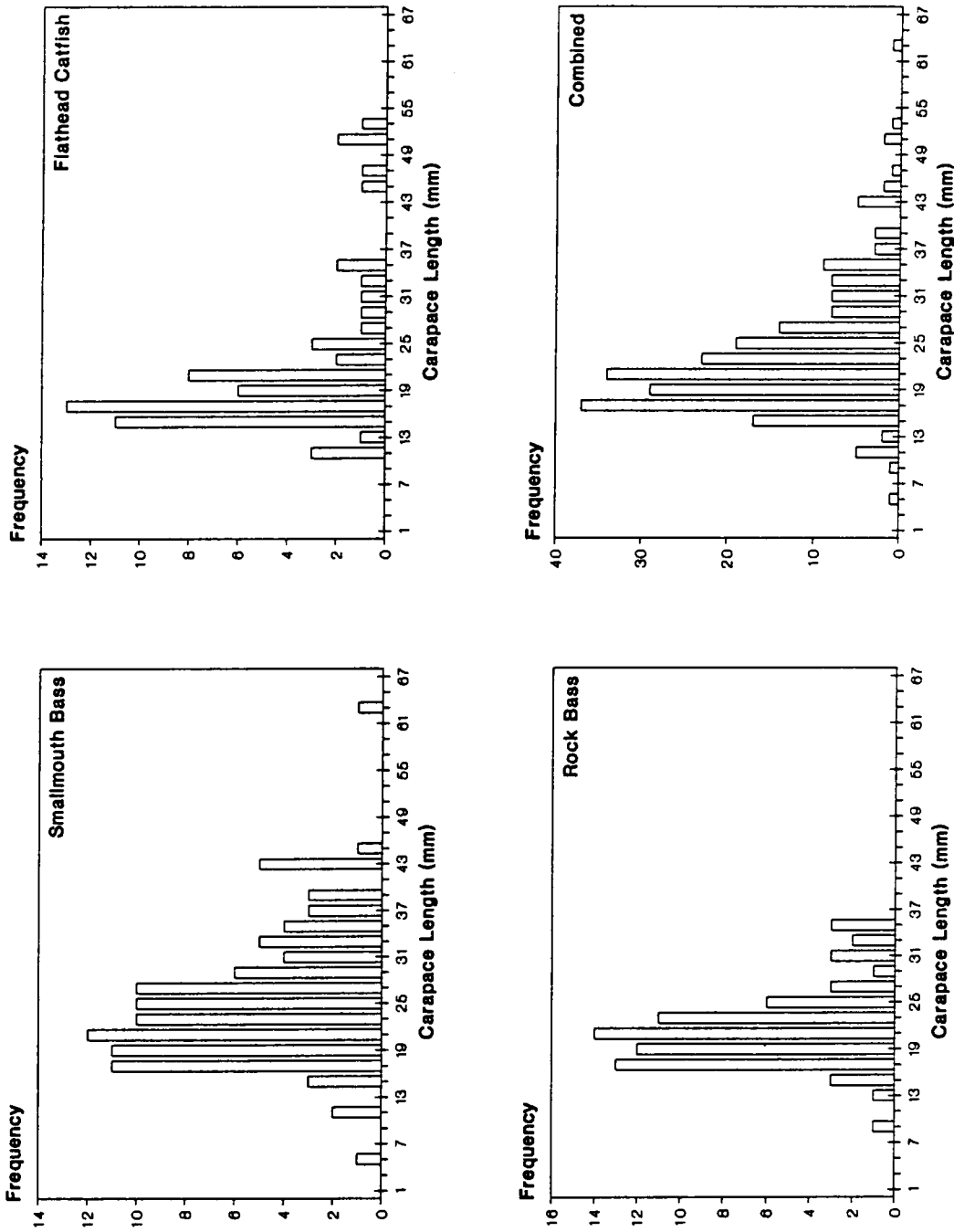


Figure 8. Frequency distribution of carapace lengths of crayfish removed from the stomachs of smallmouth bass (N = 102), rock bass (N = 73), and flathead catfish (N = 58) from Brooks Pool of the New River, West Virginia, in 1984 and 1985 (data pooled). The distribution representing all such crayfish combined is also shown.

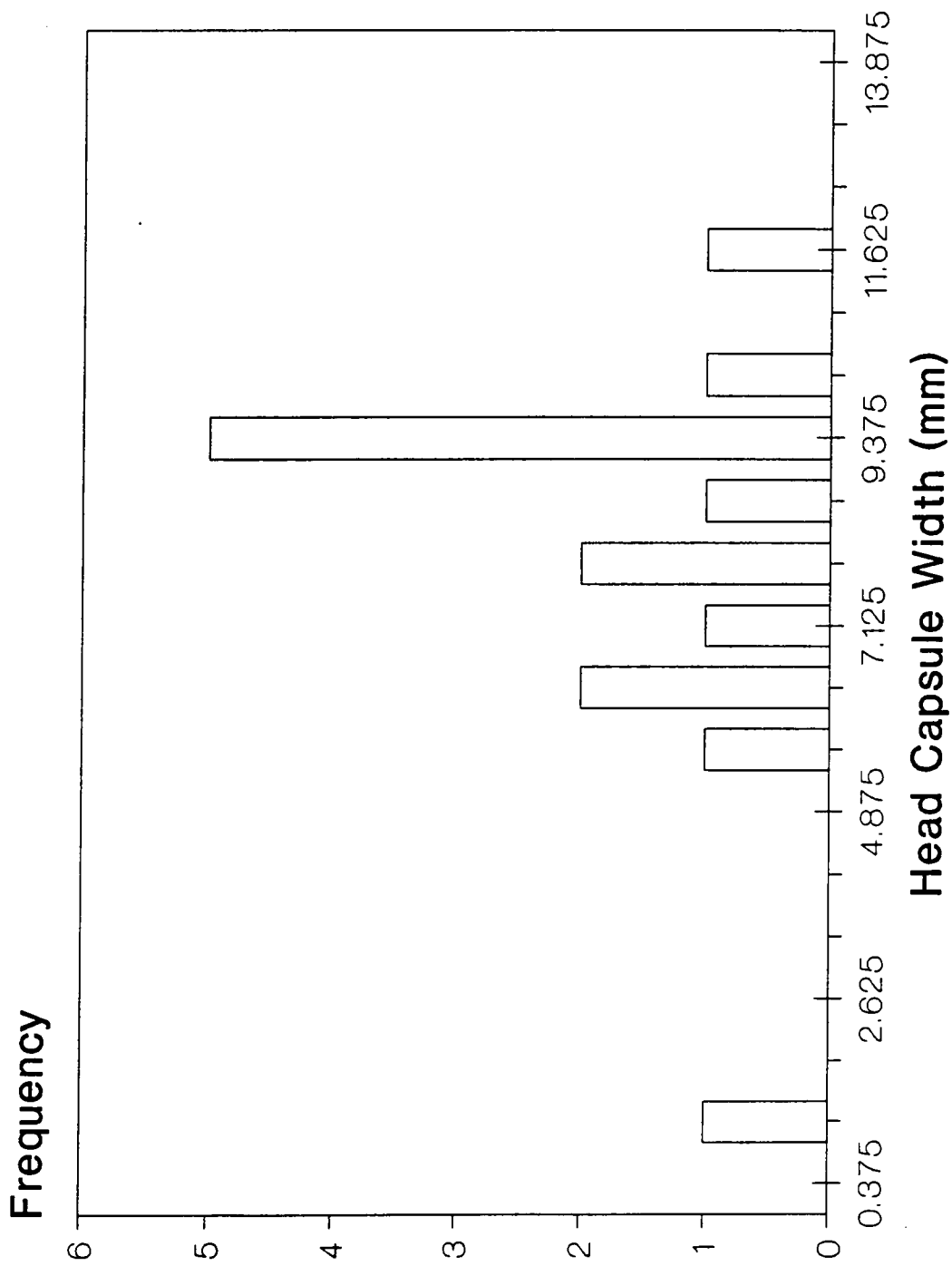


Figure 9. Frequency distribution of head capsule widths of all hellgrammites removed from the stomachs of smallmouth bass, rock bass, and flathead catfish from Brooks Pool of the New River, West Virginia, in 1984 and 1985 (data pooled); N = 15.

catfish was 0.76, and that between rock bass and flathead catfish was 0.74. The sizes of crayfish eaten by fish (Figure 8) indicated a high degree of overlap for that resource.

Production and Biomass

The total annual production of smallmouth bass, rock bass, and flathead catfish in Brooks Pool was $5.77 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. The smallmouth bass population exhibited the highest production ($3.21 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Table 15), double that by rock bass ($2.00 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Table 16) and more than seven times that by flathead catfish ($0.56 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Table 17). Estimates for each of the three species were highest for age-0 fish with progressively less production for older age groups.

The sum of the annual mean biomasses of the three fish populations in Brooks Pool was $4.15 \text{ g} \cdot \text{m}^{-2}$. Annual mean biomasses (Table 18) were greatest for smallmouth bass (total of $2.23 \text{ g} \cdot \text{m}^{-2}$), followed by that of rock bass (total of $1.37 \text{ g} \cdot \text{m}^{-2}$) and flathead catfish (total of $0.55 \text{ g} \cdot \text{m}^{-2}$). Age-1 smallmouth bass, age-0 rock bass, and age-2 and age-3 flathead catfish exhibited the highest estimates of annual mean biomass in their respective populations.

Production and biomass of each cohort of each species varied seasonally (Figure 10; shown for age-0 and age-2 smallmouth bass only) as modeled in bioenergetics simulations. The majority of production occurred June through September, achieving a maximum rate in late September. Negative production as a result of simulated weight loss by individual fish occurred from mid-November to early April, when water temperatures were usually less than $10 \text{ }^{\circ}\text{C}$. Maximum cohort biomasses occurred in October and coincided with maximum production rates.

Table 15. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each age group of smallmouth bass living in Brooks Pool of the New River, West Virginia.

Age Group	Season ¹			Total
	Summer-Fall	Winter	Spring	
0	1.46	- 0.08	0.04	1.42
1	0.95	- 0.06	0.04	0.93
2	0.47	- 0.03	0.02	0.46
3	0.22	- 0.01	0.01	0.22
4	0.12	- 0.01	< 0.01	0.11
5	0.05	> - 0.01	< 0.01	0.05
6	0.02	> - 0.01	< 0.01	0.02
Total	3.29	- 0.19	0.11	3.21

¹ Summer-fall is 1 June to 22 November, winter is 23 November to 21 March, and spring is 22 March to 31 May.

Table 16. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each age group of rock bass living in Brooks Pool of the New River, West Virginia.

<u>Age Group</u>	<u>Season¹</u>			<u>Total</u>
	<u>Summer-Fall</u>	<u>Winter</u>	<u>Spring</u>	
0	0.97	- 0.11	0.04	0.90
1	0.56	- 0.10	0.07	0.53
2	0.44	- 0.08	0.05	0.41
3	0.16	- 0.03	0.02	0.15
4	0.02	- 0.01	< 0.01	0.01
5	< 0.01	> - 0.01	< 0.01	< 0.01
<u>Total</u>	<u>2.15</u>	<u>- 0.33</u>	<u>0.18</u>	<u>2.00</u>

¹ Summer-fall is 1 June to 22 November, winter is 23 November to 21 March, and spring is 22 March to 31 May.

Table 17. Annual production ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each age group of flathead catfish living in Brooks Pool of the New River, West Virginia.

<u>Age Group</u>	<u>Season¹</u>			<u>Total</u>
	<u>Summer-Fall</u>	<u>Winter</u>	<u>Spring</u>	
0	0.22	- 0.02	0.01	0.21
1	0.10	- 0.01	0.01	0.10
2	0.10	- 0.01	0.01	0.10
3	0.08	- 0.01	0.01	0.08
4	0.04	> - 0.01	< 0.01	0.04
5	0.02	> - 0.01	< 0.01	0.02
6	0.01	< - 0.01	< 0.01	0.01
7	< 0.01	> - 0.01	< 0.01	< 0.01
8	< 0.01	> - 0.01	< 0.01	< 0.01
<u>Total</u>	<u>0.57</u>	<u>- 0.05</u>	<u>0.04</u>	<u>0.56</u>

¹ Summer-fall is 1 June to 22 November, winter is 23 November to 21 March, and spring is 22 March to 31 May.

Table 18. Annual mean biomass ($\text{g} \cdot \text{m}^{-2}$) of each age group of smallmouth bass, rock bass, and flathead catfish living in Brooks Pool of the New River, West Virginia.

<u>Age Group</u>	<u>Smallmouth bass</u>	<u>Rock bass</u>	<u>Flathead catfish</u>
0	0.57	0.42	0.09
1	0.60	0.33	0.07
2	0.49	0.37	0.10
3	0.29	0.19	0.10
4	0.16	0.05	0.08
5	0.08	0.01	0.05
6	0.04	-	0.03
7	-	-	0.02
8	-	-	0.01
Total	2.23	1.37	0.55

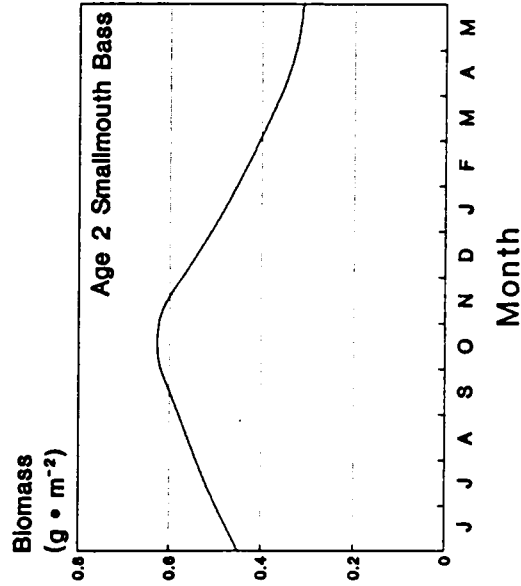
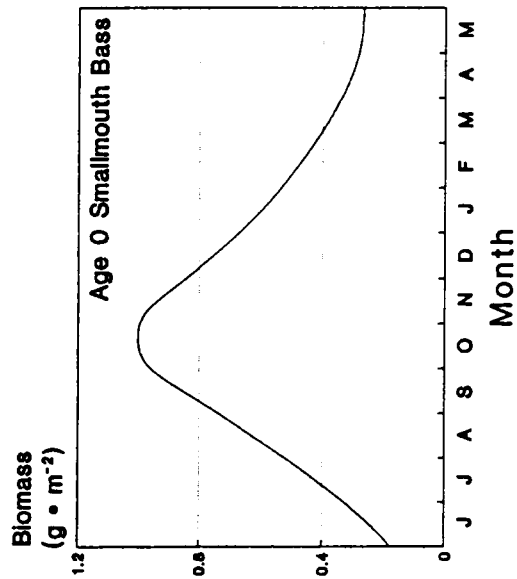
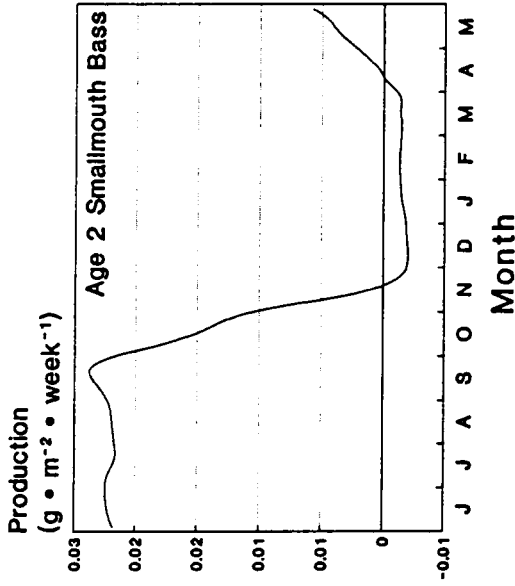
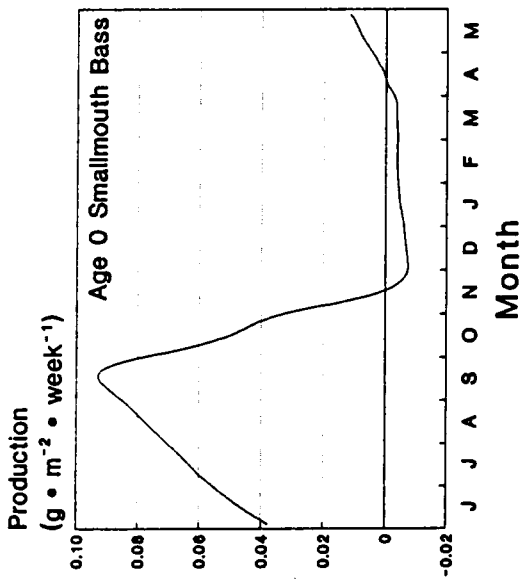


Figure 10. Production ($\text{g} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$) and biomass ($\text{g} \cdot \text{m}^{-2}$) of age-0 and age-2 smallmouth bass predicted with bioenergetics simulations.

The estimates of the annual harvests of age-2 to age-6 smallmouth bass, age-2 to age-5 rock bass, and age-4 to age-8 flathead catfish were 0.78, 0.07, and 0.25 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, respectively. Assuming that the annual production of each of the three fish populations in Brooks Pool was applicable to the entire study reach, the equivalent of about 91%, 12%, and 357% of the total annual production of the fully-recruited age groups of smallmouth bass, rock bass, and flathead catfish, respectively, were harvested.

Consumption

Crayfish and aquatic insects were the principal energy sources of smallmouth bass, rock bass, and flathead catfish in the New River. The total annual consumption of crayfish, hellgrammites, aquatic insects, and prey fish by the three predator populations in Brooks Pool was 5.31, 0.44, 11.51, and 0.87 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Tables 19 - 21), respectively, a total of 18.13 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. The smallmouth bass population consumed the most crayfish (2.43 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) and prey fish (0.70 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), while the rock bass population ate the most hellgrammites (0.40 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) and aquatic insects (5.79 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$). Aquatic insects were the single most important prey to the smallmouth bass population (62% of total consumption) and the rock bass population (69%). Aquatic insects and crayfish were equivalently the most important prey to the flathead catfish population, representing 43% and 45%, respectively, of total consumption.

The smallmouth bass population (ages 0 - 6) in Brooks Pool consumed about 8.17 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ of prey (Table 19). Gross growth efficiency ranged from 32% for age-0 and age-3 bass to 36% for age-1 bass. This indicated an incorrect specification

Table 19. Annual consumption ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each prey type by each age group of smallmouth bass living in Brooks Pool of the New River, West Virginia.

Age Group	Prey Type				Total
	Crayfish	Hellgrammites	Aquatic Insects	Prey Fish	
0	-	-	3.35	-	3.35
1	0.45	-	1.34	0.34	2.13
2	0.81	0.01	0.29	0.27	1.38
3	0.65	< 0.01	0.03	0.05	0.73
4	0.33	< 0.01	0.01	0.03	0.37
5	0.14	< 0.01	0.01	0.01	0.16
6	0.05	< 0.01	< 0.01	< 0.01	0.05
Total	2.43	0.01	5.03	0.70	8.17

Table 20. Annual consumption ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each prey type by each age group of rock bass living in Brooks Pool of the New River, West Virginia.

Age Group	Prey Type				Total
	Crayfish	Hellgram- mites	Aquatic Insects	Prey Fish	
0	-	-	3.34	-	3.34
1	0.09	-	1.72	-	1.81
2	1.07	0.24	0.63	< 0.01	1.94
3	0.79	0.12	0.08	-	0.99
4	0.18	0.03	0.02	-	0.23
5	0.03	0.01	< 0.01	-	0.04
Total	2.16	0.40	5.79	< 0.01	8.35

Table 21. Annual consumption ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each prey type by each age group of flathead catfish living in Brooks Pool of the New River, West Virginia.

Age Group	Prey Type				Total
	Crayfish	Hellgram- mites	Aquatic Insects	Prey Fish	
0	-	-	0.47	-	0.47
1	0.05	-	0.18	0.03	0.26
2	0.23	0.01	< 0.01	0.08	0.32
3	0.17	0.02	0.01	0.05	0.25
4	0.11	< 0.01	0.03	0.01	0.15
5	0.09	-	-	< 0.01	0.09
6	0.04	-	-	< 0.01	0.04
7	0.02	-	-	< 0.01	0.02
8	0.01	-	-	< 0.01	0.01
Total	0.72	0.03	0.69	0.17	1.61

of one or more parameters in the bioenergetics model of smallmouth bass, because growth efficiency typically declines with size/age (Brett 1979). The annual food intake was 24% crayfish, < 1% hellgrammites, 69% aquatic insects, and 7% prey fish.

About $8.35 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ of prey were consumed by the rock bass population (ages 0 - 5) in Brooks Pool (Table 20). Gross growth efficiency increased from 20% in age-0 rock bass to 22% in age-1 bass, and then progressively declined to 4% in age-5 bass. Crayfish, hellgrammites, aquatic insects, and prey fish represented 26%, 5%, 69%, and < 1%, respectively, of the annual food intake of the population.

The flathead catfish population (ages 0 - 8) in Brooks Pool consumed about $1.61 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ of prey (Table 21). Gross growth efficiency progressively declined from 33% in age-0 fish to 9% in age-8 fish. The annual food intake of the population was 45% crayfish, 2% hellgrammites, 43% aquatic insects, and 10% prey fish.

Consumption varied seasonally as expected (Figure 11; shown for age-0 and age-2 smallmouth bass only). Trends in production (Figure 10) mimicked trends in consumption.

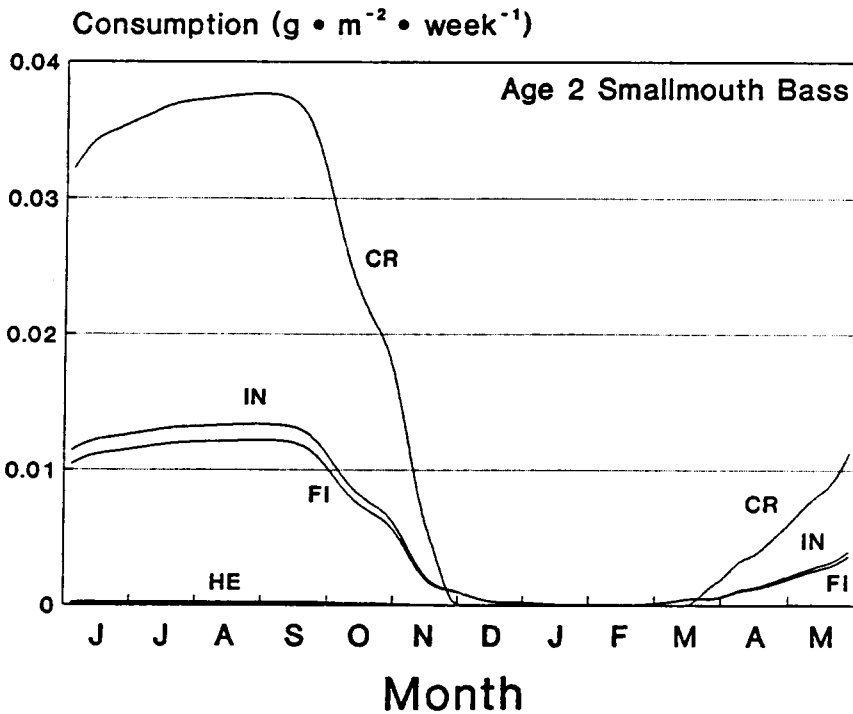
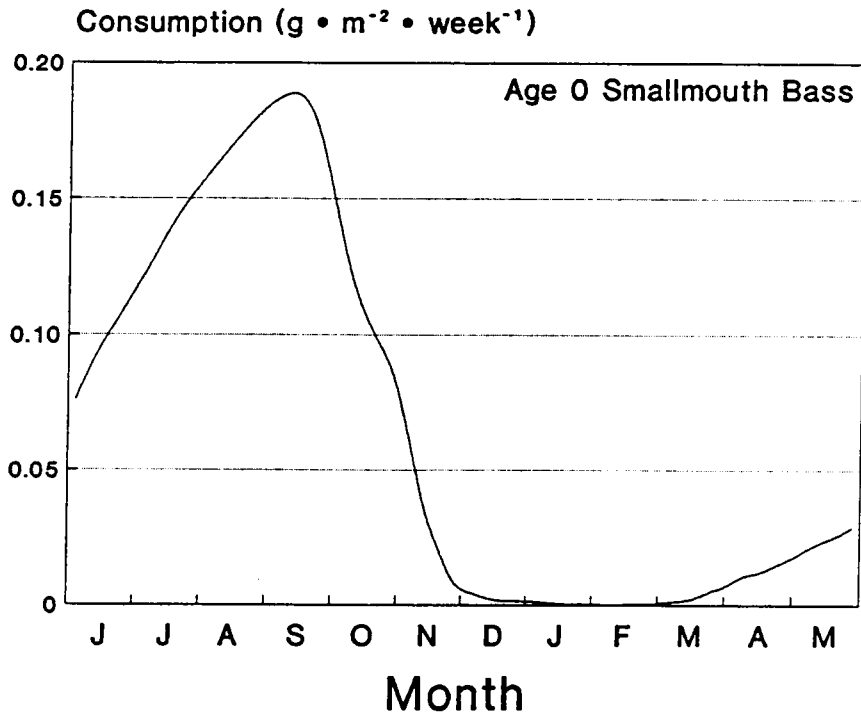


Figure 11. Weekly consumption ($\text{g} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$) by age-0 and age-2 smallmouth bass predicted with bioenergetics simulations.

Discussion

Knowledge of the production, consumption, and harvest of smallmouth bass, rock bass, and flathead catfish, and information about the production and harvest of crayfish and hellgrammites (Chapter 1) provided the opportunity to address two important questions relevant to prey-predator-people interactions in the New River, West Virginia. The first question was: what proportion of the annual production of each population of predatory fish is harvested by people? The second question was: do these fishes and people compete for limited crayfish and hellgrammite stocks? These two questions are addressed here.

Production and Harvest of Predatory Fishes

Central to the evaluation of fish population dynamics is establishment of the validity of estimates of population attributes. The estimates of production of smallmouth bass, rock bass, and flathead catfish were dependent on estimates of abundance, mortality, and growth. The abundance estimates were probably the least accurately measured attribute as a result of few recaptures (Table 11), and thus contributed most to inaccuracies in production estimates. The growth estimates were probably reliable, because each population was comprised mostly of young fish,

which are more accurately assigned ages from examination of scales or spines. Growth in length of New River smallmouth bass and rock bass was greater than the average of growth estimates from several stream-dwelling populations (Figures 5 - 6). Estimates of mortality were also considered reliable, because estimates from catch curve analysis were computed from catch-at-age data collected during two field seasons (Ricker 1975). Mortality estimates for smallmouth bass were also similar to those reported by Austen and Orth (1988) for the same reach of the New River.

A valid comparison of attributes from different populations requires recognition of the variance of attribute estimates. Large variances of attribute estimates generally preclude statements of true population differences. Such was the case in comparisons of fish production in the New River compared to that in other streams. Regardless, production estimates of New River predatory fishes were compared to those corresponding to other stream-dwelling populations, although no statistical significance was claimed.

Age-specific estimates of the annual production of smallmouth bass in the New River (Table 15) were equivalent to those reported for the smallmouth bass population in Courtois Creek, Missouri ($1.80 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ by approximately age-1 and older fish; Funk 1975), and were greater than those reported for populations of smallmouth bass in the Speed River, Ontario ($0.05 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ by age-0 and age-1 fish; Mahon et al. 1979), and in the Red Cedar River, Michigan ($1.36 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ by age-0 and older fish; Vannote and Ball 1972). Similarly, estimates of the annual production of rock bass in the New River (Table 16) were greater than those reported for populations of rock bass in Little Walker Creek and Back Creek in Virginia (1.03 and $1.04 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, respectively, by age-0 and older fish; Pajak and Neves 1987) and in the Speed River, Ontario ($0.24 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ by age-0 fish; Mahon et al. 1979). No accounts of flathead catfish production were found.

Smallmouth bass in the New River are extensively exploited by people. About 91% of the estimated annual production of age-2 and older smallmouth bass (that is, those fully recruited to angling gear) was harvested, and the total annual mortality of age-2 and older smallmouth bass was substantial (about 80%). Although the total annual mortality rate of age-2 and older rock bass was also great (76 - 78%), only about 12% of their annual production was apparently harvested. Conversely, the estimated harvest of age-4 and older flathead catfish was equivalent to 357% of their annual production; the estimated total annual mortality rate was only 56%. The estimates of production equivalents harvested are potentially influenced by several factors. The estimation of production and harvest is inherently difficult, especially in a large river. Estimate bias may explain most or all of the discrepancy between mortality and harvest, but the direction of bias is difficult to ascertain. The estimates for smallmouth bass appear reasonable. For rock bass, the level of estimated harvest is much less than that indicated by their annual mortality rate. Assuming that the estimates of rock bass production and harvest are reasonable, one or more factors may explain the disparity: extensive natural mortality, catch-and-release by anglers, and/or hooking mortality. Flathead catfish entering the study reach from Bluestone Lake may account for the discrepancy between harvest and production of flathead catfish. In 1980, about 307 flathead catfish per kilometer of river were captured in the 4-km river reach immediately below Bluestone Dam, while only about 87 flathead catfish per kilometer were captured in the 13.7-km river reach below the first reach (Pierce et al. 1981). A substantial population of flathead catfish resides in Bluestone Lake, but rock bass and smallmouth bass do poorly there (Edmundson 1974).

High rates of harvest and annual mortality of smallmouth bass and a population comprised primarily of young fish suggested that angling regulations designed to lower the mortality rate of older smallmouth bass were warranted (Austen and Orth

1988). Assuming that the estimates of annual harvest of rock bass are reliable, regulations controlling angler harvest appear unnecessary. Harvest of flathead catfish in the New River does not appear to be excessive as evidenced from annual mortality rate estimates; thus, harvest regulations for flathead catfish are not warranted. However, if flathead catfish from Bluestone Lake augment the riverine population below Bluestone Dam, future changes in management of the lake population should address the potential effects on the tailwater fishery.

Prey Resource Use by Predatory Fishes

Critical evaluation of the trophic basis of production of the smallmouth bass, rock bass, and flathead catfish populations in the New River required knowledge about the production of prey populations and the consumption of prey by each predator population. The principal prey of New River predatory fishes were aquatic insects and crayfish. Aquatic insects were heavily utilized by young fish and were gradually replaced in importance by crayfish as the fish became older (Tables 12 - 14). Because crayfish in the New River are harvested by people for bait (Nielsen and Orth 1988) and are a critical prey of older predatory fishes, the crayfish-fish-people interactions were emphasized here. Aquatic insects in the study reach are very prolific (Voshell 1985; Voshell et al. 1987); thus, young predator fishes are not as likely to be food limited as are older fishes.

The effectiveness of smallmouth bass, rock bass, and flathead catfish as predators on crayfish is shown here and is apparent from previous studies (Minckley and Deacon 1959; Turner and Summerfelt 1970; Vannote and Ball 1972; Scott and Crossman 1973; Edmundson 1974; Coble 1975; Miner 1978; Layher and Boles 1980; Probst

et al. 1984; Austen and Orth 1985). Smallmouth bass and rock bass in the New River appeared to forage similarly for crayfish, which agrees with the findings of Probst et al. (1984). Crayfish species compositions in the diets of the two basses were not statistically significantly different, however significant differences occurred between crayfish species composition in the diet of flathead catfish and that of each bass species. The species composition of crayfish in the diet of smallmouth bass (37% *O. virilis*, 51% *C. sciotensis*, and 12% *O. s. sanbornii*), rock bass (41% *O. virilis*, 48% *C. sciotensis*, and 11% *O. s. sanbornii*), and flathead catfish (64% *O. virilis*, 29% *C. sciotensis*, and 7% *O. s. sanbornii*) in Brooks Pool differed substantially from that in quantitative (13% *O. virilis* and 87% *C. sciotensis*; Chapter 1) and qualitative (7% *O. virilis*, 86% *C. sciotensis*, and 7% *O. s. sanbornii*; Chapter 1) crayfish collections from deeper (1- to 3-m depths), mid-stream locations there. Qualitative crayfish collections from shallower (< 1-m depth) locations in Brooks Pool had species compositions (23% *O. virilis*, 55% *C. sciotensis*, and 22% *O. s. sanbornii*) more closely resembling those of crayfish in the diets of the three fishes than did collections from deeper areas. Probst et al. (1984) found that smallmouth bass and rock bass in two Missouri streams fed on members of two crayfish species in approximate proportion to their abundances. Because flathead catfish have a larger mouth gape and attain a larger size than the two basses, flathead catfish probably also feed indiscriminately on crayfish. Assuming that New River predatory fishes are indiscriminate feeders on crayfish, these predators probably forage for food in shallow locations associated with the stream margins. Smallmouth bass probably forage there during crepuscular periods, when peak foraging activity occurs (Reynolds and Casterlin 1976), and flathead catfish are characteristically nocturnal.

Energy resource overlap was relatively high among the three predatory fishes in the New River. Substantial overlap (0.93) occurred between smallmouth bass and

rock bass. Probst et al. (1984) estimated diet composition overlap of smallmouth bass and rock bass in two Missouri streams using the index of Schoener (1970). Diet overlaps were 0.73 (March-July) and 0.72 (August-November). Diet overlap between fishes can be highest during high food abundance, and is therefore not a reliable indicator of competition (Gee and Northcote 1963; Nilsson 1967; Zaret and Rand 1971; Probst et al. 1984). Smallmouth bass and rock bass in the Missouri streams did not segregate ecologically through food resource partitioning, but rather on the basis of habitat use (Probst et al. 1984).

The sizes of crayfish eaten by the three fishes were similar (Figure 8). Crayfish sizes eaten also indicated a minimum threshold size of vulnerability to predation of about 15 mm carapace length (CL), which is similar to that shown by Probst et al. (1984) for smallmouth bass and rock bass. A maximum threshold size of 35 mm CL was also evident for crayfish eaten by rock bass. Predation on crayfish near the minimum threshold size may be limited by the number and size of available crayfish. In the New River, older fishes were capable of detecting and ingesting aquatic insects, presumably from drifting insects of benthic origin. This suggested that crayfish smaller than the minimum threshold size can be detected by predatory fishes, but are unavailable as prey due to habitat selection differences between fish and crayfish. Predation on the largest crayfish may be limited by abundance (of relatively few older crayfish), mouth gape of the predator (especially that of rock bass), and behavioral responses by the crayfish (Stein and Magnuson 1976). Although probably less important than those factors, the energy gain from crayfish (energy per gram of body weight) declines as crayfish size increases due to corresponding increases in the proportion of indigestible materials (Stein and Murphy 1976).

Smallmouth bass, rock bass, and flathead catfish may compete for limited crayfish resources, given the similarity in crayfish sizes eaten (Figure 8) and in

crayfish species composition in the diet of these three predators. But, competition depends on prey supply and predator demand. Consumption of each prey type by each fish population (predator demand) was estimated via bioenergetics simulations to evaluate total use of crayfish and hellgrammite production (prey supply). Simulation of fish energetics to estimate consumption was considered appropriate in light of other methods. Direct measurement of consumption in the field yields few highly-variable point estimates that are labor intensive to achieve (Kerr 1982; Rice and Cochran 1984; Hewett and Johnson 1987). The energetics approach to estimating consumption was validated by Rice and Cochran (1984) for largemouth bass. The consumption estimates reported here are considered first approximations, and no further attempt will be made to address their reliability.

Smallmouth bass, rock bass, and flathead catfish in the New River relied on insects and crayfish as major sources of energy; hellgrammites and fish were inconsequential in this regard. Ages-1 and -2 crayfish were heavily cropped by all three predator populations. The equivalent of 35, 31, and 10% of the estimated annual production of ages-1 and -2 crayfish (Chapter 1) was consumed by smallmouth bass, rock bass, and flathead catfish, respectively, and 5% was harvested by people for bait (Chapter 1). Smallmouth bass in a Michigan stream consumed an estimated 15% of the annual crayfish production (18% of the annual production of ages-1 and -2 crayfish; Vannote and Ball 1972). Predation by rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) on crayfish in two Michigan lakes did not exceed the equivalent of 15% of the annual crayfish production there (Momot and Gowing 1977b). Given that about 81% of crayfish production in the New River can be attributed to predation and harvest, and considering the unknown use of crayfish by other predators (birds, reptiles, mammals, and other fish), crayfish predators that are strongly dependent on crayfish are probably involved in some degree of compe-

tition for the crayfish resource. Such competition may be expressed in lower growth rates, lower fecundity, or higher mortality of crayfish predators. Sanderson (1958) reported an inverse relationship between growth and condition of smallmouth bass and the abundance of rock bass and redbreast sunfish (*Lepomis auritus*) in the Potomac River and several of its tributaries, but did not speculate on the mechanism for this relation. In the New River, a paucity of fish in the diet of predatory fishes suggested that prey fishes were not abundant or available. The density of prey fish (about 0.2 fish • m⁻²; estimated from Lobb 1986) was much less than the density of crayfish (about 1.6 crayfish • m⁻²; Chapter 1). Low availability or absence of alternative prey may exacerbate the effects of competition for crayfish between predator fishes in the New River by obviating the opportunity for prey switching.

Ages-1 and -2 hellgrammites were consumed less extensively than crayfish by the three fish populations, and were not an important food resource. Rock bass consumed an estimated 13% of the annual production of hellgrammites, followed in importance by flathead catfish (1%) and smallmouth bass (< 1%). Harvest by people was approximately 8%. In addition, hellgrammites likely have few other predators besides fish due to their secretive behavior. Hellgrammites are not a limiting prey resource to predatory fishes in the New River.

Adult predatory fishes in the New River are very dependent on crayfish as an energy source. The sizes of crayfish eaten by fish, the crayfish species composition in the fish diets, the total use of crayfish production, and the high degree of overlap in energy resource use strongly suggested that competition among smallmouth bass, rock bass, and flathead catfish for crayfish resources was occurring. However, processes such as predation, competition, and fishery exploitation operate at different rates in a dynamic system. The dynamics of the trophic interactions among the key populations in the New River were evaluated with a trophic dynamic model to

help understand the roles that predation, competition, and exploitation have in the New River food web. The development, analysis, and application of the model are summarized in the next chapter.

Chapter 3

The Roles of Predation, Competition, and Exploitation in New River Trophic Dynamics: a Modeling Approach

Introduction

Theoretical studies of prey-predator assemblages have suggested that communities are structured by productivity at “lower” trophic levels (Lindeman 1942) and by predation and competition at “higher” levels (Yodzis 1978; Glasser 1979; Huston 1979; Tilman 1982). The underlying theme of the literature that addresses the structuring of natural communities is that productivity at lower levels and habitat quality at all levels provide the template or foundation for community structure, and that population interactions at higher levels, principally predation and competition, mold the biotic assemblage supported by the template (see especially Northcote 1988); a dynamic equilibrium is often stated or implied. However, the extent to which pro-

ductivity, predation, competition, and other processes influence assemblage structure is not well understood.

A generalized conceptual model describing those characteristics and processes that maintain and shape natural assemblages in stream ecosystems has not been proposed. Schlosser (1987) presented an initial framework for small, warmwater streams. For lake communities, the concept of cascading trophic interactions (Carpenter et al. 1985; Kerfoot 1987; Kitchell and Carpenter 1987; Mills et al. 1987) has been used to describe the effects of predation on transition from one community structure to another. This "top-down" regulation of trophic structure by predation is also recognized in stream communities (Peckarsky and Dodson 1980; Obendorfer et al. 1984; Walde and Davies 1984; Bowby and Roff 1986). Among the biological processes that have the potential to structure aquatic communities, predation is best understood, but the indirect effects of predation on community structure have only recently been addressed (Kerfoot and Sih 1987). The effects of other processes such as competition (intra- and interspecific) have not been addressed simultaneously with the effects of predation, because the effects of competition alone are difficult to recognize and measure, and because processes operating concurrently are at least as difficult to distinguish quantitatively. Fishery exploitation may play a role similar to predation in shaping the structure of aquatic communities. May (1973) theorized that exploitation, particularly at high rates, may destabilize community structure. The first phase of the research presented here addressed the roles that predation, interspecific competition, intraspecific regulation, and fishery exploitation have in maintaining and changing the biomass of key populations, and hence community structure, in the New River, a sixth-order warmwater stream in West Virginia.

The perspective of aquatic resources management has evolved rapidly in the last two decades. Two management paradigms, the single-species approach and the

concept of maximum sustainable yield, are being replaced by the more holistic, multispecies approach to managing aquatic food webs (Mercer 1982a). Single-species assessments have not addressed species interactions, particularly predation and competition (Mercer 1982a), and were inadequate predictors of sustainable yields (Andersen and Ursin 1977; May et al. 1979). The traditional concept of maximum sustainable yield also ignored species interactions, and had other practical and conceptual problems (Larkin 1977; Holt and Talbot 1978; Sissenwine 1978; May et al. 1979). The necessity of addressing the management of interacting organisms in a food web context was a logical next step, but this step involved a host of new challenges to researchers.

Early theoretical investigations of fishery exploitation in aquatic prey-predator assemblages, although important to the integration of available knowledge and the development of new theory, considered systems consisting of only one prey and one predator (Larkin 1966; Dickie 1976). Subsequent theoretical investigations (Brauer and Soudack 1979a, 1979b; May et al. 1979; Beddington and May 1980; Beddington and Cooke 1982) have considered the implications of exploitation for two or three interacting populations/trophic levels and also demonstrated the inadequacy of applying maximum sustainable yield concepts to populations individually. However, most real-world problems involve exploitation in more complex food webs. Knowledge of the effects of exploitation in complex food webs is crucial to the resource agencies that regulate harvest in these communities, especially when the ever-increasing global demand in fishery products is considered.

The difficulty of understanding and managing multispecies fisheries has been aptly demonstrated (Larkin 1966; Riffenburgh 1969; Walters 1971; Dickie 1976; Hobson and Lenarz 1977; Brauer and Soudack 1979a, 1979b; May et al. 1979; Beddington and May 1980; Beddington and Cooke 1982; Mercer 1982b; Pauly and Murphy 1982).

Aquatic food web complexity has precluded the development of definitive methods that accurately estimate biomasses and sustainable yields of populations in multi-species fisheries. Complex models of multispecies fisheries in the North Sea (Andersen and Ursin 1977), northeastern Pacific Ocean (Laevastu and Larkins 1981; Laevastu et al. 1982), and the Gulf of Thailand (Larkin and Gazey 1982) have been poor predictors of biomasses of constituent populations (or groups thereof) due to the large scope and extent of these fisheries and quantitative specification of such models with insufficient data. Also, these models were developed as management tools, and were not designed to evaluate the effects of exploitation on the prey-predator assemblage.

The New River system, although simplified conceptually here, is complex due to prey-predator interactions, exploitation of some prey as well as predators, and often-conflicting management and resource use strategies. However, relative to the scope and areal extent of the fisheries previously recounted, the scope and size of the New River system and its recreational and commercial fisheries are limited and thereby afforded the opportunity to address, through modeling, the simultaneous exploitation of key populations within a food web context. In this system, people exploit from two trophic levels by harvesting fish and their macroinvertebrate prey. Crayfish (Decapoda: Cambaridae) and hellgrammites (*Corydalis cornutus* larvae) are harvested by commercially-licensed bait catchers for sale and by anglers for personal use. Smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and flathead catfish (*Pylodictis olivaris*) are the basis of a popular sport fishery. These species prey extensively on crayfish in other aquatic systems (Minckley and Deacon 1959; Turner and Summerfelt 1970; Vannote and Ball 1972; Scott and Crossman 1973; Edmundson 1974; Coble 1975; Miner 1978; Layher and Boles 1980; Probst et al. 1984; Austen and Orth 1988), but extensive predation on hellgrammites by fish has not been

documented. The retail value of crayfish and hellgrammites caught in a 16-km reach of the New River in 1983 was approximately US\$134,000 (Nielsen and Orth 1988). Annual expenditures by anglers fishing there in 1985 were about \$618,000 (estimated from angler trip information in Pierce et al. 1981 and economic data in USFWS 1988). Angling pressure can be expected to increase, following a nationwide trend (USFWS 1988); therefore, bait harvest should also intensify to satisfy the angler demand for live crayfish and hellgrammites. Also, overharvest of sport fish may result if liberal harvest regulations continue. Research on food web interactions and the potential impacts of exploitation was clearly warranted. The second phase of this research was to evaluate the effects of concurrent exploitation of crayfish, hellgrammites, adult smallmouth bass, adult rock bass, and adult flathead catfish. The exploitation of crayfish and adult smallmouth bass was emphasized, because the harvest of these two groups will likely be regulated first (Chapter 2).

Other human activities may alter the aquatic community below Bluestone Dam. Temperature, flow, and habitat alterations may occur due to proposed changes in Bluestone Dam operations. Most notable though is an ongoing program that was begun in 1986 by the State of West Virginia to control nuisance adult black flies (Simuliidae) in the local area by poisoning their larvae downstream from the dam. Voshell (1985) studied the trophic basis of production of the six dominant aquatic insect taxa in the New River immediately below Bluestone Dam in 1983 and 1984. The study was designed to determine direct and indirect impacts of black fly control on the benthic macroinvertebrate assemblage there. He concluded that consistent elimination of black fly larvae there could reduce total benthic community production by about 11%. Several invertebrate predators feed on black fly larvae, and other invertebrates may rely on the role these larvae play in detritus dynamics, so greater production losses were possible (Voshell 1985). Voshell et al. (1988) conducted a

nearly identical investigation in 1986, a year in which black fly larvae in the New River were poisoned. Total production of the dominant aquatic insect taxa was 53% of that in the non-treatment year. Although the difference could not be attributed solely to elimination of black fly larvae, the results of the two studies strongly suggested that black fly larvae have an important role in the trophic dynamics of the New River ecosystem. The third phase of my research was to examine the potential impacts of black fly control on the New River food web.

The influences of community processes, the effects of exploitation, and the impacts of black fly control on the New River ecosystem were not addressable prior to this research due to a limited knowledge base. Information and analysis of the trophic interactions among key prey and predator populations were required. The only quantitative studies of the trophic links in this ecosystem were those of Voshell (1985) and Voshell et al. (1987), who investigated the trophic interactions among benthic macroinvertebrates.

Knowledge of invertebrate bait harvest (from Nielsen and Orth 1988), fish harvest (Pierce et al. 1981), prey and predator population dynamics (Chapters 1 and 2; Voshell 1985; Lobb 1986; Voshell et al. 1987), and trophic linkage between prey and predators (Chapter 2) provided the basis for development of a preliminary concept of how exploited and unexploited populations in the New River interact. Specific objectives addressed here were to:

- (1) integrate the information on bait and fish harvest and the age-specific dynamics of the principal predatory fishes and their prey into a mathematical model of energy flow in the New River,
- (2) identify model parameters that contributed most to the error of model predictions,

- (3) infer which states and/or processes are most influential in structuring the prey-predator assemblage in the New River,
- (4) evaluate through simulation the effects of multispecies exploitation on the New River prey-predator assemblage, and
- (5) assess through simulation the impacts to the system of reductions in aquatic insect production associated with the systematic control of black fly larvae in the New River.

Methods

An energy flow model was developed to represent the interactions among key populations (or groups of functionally-similar populations) of prey and predators in the New River between Bluestone Dam and Sandstone Falls, an area of 408 ha. The development, analysis, and implementation of the New River energy flow model involved four successive steps: (1) conceptual model formulation, (2) quantitative specification, (3) model analysis, and (4) prediction of the effects of exploitation and losses of aquatic insect production.

Conceptual Model Formulation

The system model was defined as the principal predatory fishes, which are smallmouth bass, rock bass, and flathead catfish, and their prey, which are aquatic insects, crayfish, hellgrammites, and forage fish. Energy inputs (sources) to this system were assumed to be that entering as seston (suspended organic and inorganic particles) from Bluestone Lake and solar energy assimilated by primary producers in the study reach. Energy outputs (sinks) from the system were waste losses, respiratory losses, non-predatory natural mortality (from intraspecific regulation), and bait and fish harvest. For modeling purposes, the detrital pool in the

study reach was assumed to be relatively constant, given the considerable input of detritus-like matter in the form of seston (see "Quantitative Specification" below). Also, in regard to the objectives here, detritus dynamics were inconsequential.

Each component of interest in the New River system was represented by a compartment in the system model. Thirteen compartments, representing four prey components and nine predator components, comprised the prey-predator system. The four prey components were aquatic insects (other than hellgrammites), ages-1 and -2 crayfish, ages-1 and -2 hellgrammites, and prey fishes. The sizes of crayfish and hellgrammites caught for bait (Chapter 1) and found in the diet of sport fishes (Chapter 2) corresponded primarily to age-1 and age-2 animals, so only those age groups were represented in the system model. The prey fish component represented only those fishes of a size considered vulnerable to predatory fishes. The nine components representing predatory fishes were age-0, age-1, and age-2 to age-6 smallmouth bass; age-0, age-1, and age-2 to age-5 rock bass; and age-0, age-1 to age-3, and age-4 to age-8 flathead catfish. Age-0 fishes of the three populations were each considered a separate component due to differences in diet from older fish (Chapter 2). Age-2 to age-6 smallmouth bass, age-2 to age-5 rock bass, and age-4 to age-8 flathead catfish were assumed to be fully recruited to the recreational fishery, and were therefore each treated as separate model components. For each species, age groups older than age-0 fish and younger than fully-recruited age groups were arbitrarily considered as one component. Juvenile and/or adult fish of other fish species (white crappie, *Pomoxis annularis*; spotted bass, *Micropterus punctulatus*; sunfishes, *Lepomis* spp.; bigmouth chub, *Nocomis platyrhynchus*; common carp, *Cyprinus carpio*; and muskellunge, *Esox masquinongy*) were not represented in the model, because they were relatively few in number (Lobb 1986).

The state of each component in the system model was represented by the energy equivalent of annual mean biomass, which was in terms of kilojoules per meter squared ($\text{kJ} \cdot \text{m}^{-2}$). Annual energy flows (consumption, waste losses, respiratory losses, natural mortality, and harvest) and annual production were expressed in terms of kilojoules per meter squared per year ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$). States and flows were derived and employed as values that were representative of the study reach.

Quantitative Specification

Four prey components and nine predator components were the state variables ($X_1 - X_{13}$) in the energy flow model of the prey-predator system. The annual mean biomass of aquatic insects (X_1) was estimated from estimates of total biomass (kg dry weight) reported by Voshell et al. (1987) for benthic macroinvertebrates in riffle areas of the study reach. Aquatic insect biomass was considered negligible in pools, based on my qualitative observations and those of J. Reese Voshell (Associate Professor, Department of Entomology, Virginia Polytechnic Institute and State University; personal communication), and was ignored. Total biomass in riffles (117,707 kg dry weight $\cdot \text{ha}^{-1}$) was converted to an energy equivalent (representative of the study reach) with a weight conversion factor of 6 g wet weight $\cdot \text{g}^{-1}$ dry weight (Waters 1977), an energy density of 5.648 $\text{kJ} \cdot \text{g}^{-1}$ wet weight (Chapter 2), and estimates of the areas of riffles (197 ha) and pools (211 ha) in the study reach (Chapter 1).

The annual mean biomasses of ages-1 and -2 crayfish ($4.63 \text{ g} \cdot \text{m}^{-2} = X_2$; Chapter 1) and ages-1 and -2 hellgrammites ($1.83 \text{ g} \cdot \text{m}^{-2} = X_3$; Chapter 1) were converted to energy equivalents with energy densities of 3.766 and 6.565 $\text{kJ} \cdot \text{g}^{-1}$ wet weight (Chapter 2), respectively.

The annual mean biomass of prey fish (X_4) was estimated from abundances reported by Lobb (1986) for several species-life stage groups counted along underwater transects in the study reach. He recognized eight habitat types, which were sampled in approximate proportion to their areal extent. Because a relatively large range in sizes of fish occurred, two size groups of prey fish were distinguished to facilitate calculation of a more accurate biomass estimate. The first group (9.5 fish \cdot 100 m⁻²) was comprised of smaller fishes (bluntnose minnow, *Pimephales notatus*; logperch, *Percina caprodes*; shiners, *Notropis* spp.; greenside darter, *Etheostoma blennioides*; rainbow darter, *Etheostoma caeruleum*; sharpnose darter, *Percina oxyrhyncha*; unidentified darters; and young-of-the-year bigmouth chub). Prey fish were represented as invertivores in the model, so central stonerollers (*Campostoma anomalum*), which are algivorous, were excluded from this group. Central stonerollers represented only 3% of the total biomass of prey fish. A mean live weight of 1 g was assumed for this group, based on length-weight data provided by Paul L. Angermeier (Assistant Leader, Virginia Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute & State University, Blacksburg, Virginia) for the same or similar fish species caught in the New River, Virginia. The second group (11.5 fish \cdot 100 m⁻²) included larger fishes (young-of-the-year and juvenile northern hogsucker, *Hypentelium nigricans*; young-of-the-year spotted bass; and young-of-the-year and juvenile sunfishes) for which a mean live weight of 3 g was chosen based on my data. The biomass estimates of both groups were summed, and the result was considered representative of the study reach. An energy density of 4.184 kJ \cdot g⁻¹ wet weight was assumed for all prey fishes (Chapter 2).

Age-0 smallmouth bass, rock bass, and flathead catfish were not included with prey fish, because they were represented as separate components in the model. The annual mean biomass of each of the nine components (X_5 - X_{13}) representing

predatory fishes (computed from Table 18 in Chapter 2) was considered representative of the study reach. Each estimate was converted to an energy equivalent with an energy density of $4.184 \text{ kJ} \cdot \text{g}^{-1}$ wet weight (Chapter 2).

Seston from Bluestone Lake and periphyton (here considered epilithic algae) and aquatic macrophytes within the study reach were considered the principal energy sources of the prey-predator system. The annual energy input ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) to the study reach as organic seston from Bluestone Lake was calculated from a conservative estimate of total seston input of $1.64 \times 10^9 \text{ kg}$ ash-free dry weight (AFDW) $\cdot \text{year}^{-1}$ (Voshell et al. 1987), an energy density of $20.083 \text{ kJ} \cdot \text{g}^{-1}$ AFDW (VPISU 1985), and the total area of the study reach (408 ha).

The annual contribution of energy by periphyton in the study reach was estimated from a value of annual input reported by Hill and Webster (1982). They estimated annual inputs of periphyton in a softwater reach and a hardwater reach of the New River, Virginia. The estimate for the hardwater reach, $1,423.4 \times 10^9 \text{ kg}$ AFDW, was more appropriate for estimating periphyton input in the study reach of the New River, West Virginia, because the New River there is typically of a hardwater nature. In Virginia, the hardwater reach was about 30% of the area of the total reach, which was 135 km in length and averaged 167 m wide (Hill and Webster 1982). The estimate of periphyton input was converted to the appropriate units using the area of the hardwater reach ($6,763,500 \text{ m}^2$) and an energy density of periphyton of $18.912 \text{ kJ} \cdot \text{g}^{-1}$ AFDW (Cummins and Wuycheck 1971).

The annual energy input by aquatic macrophytes in the study reach was estimated from standing crops reported by Voshell (1985), Voshell et al. (1989), and Rodgers et al. (1983). The standing crops of *Podostemum ceratophyllum* on rock outcrops immediately below Bluestone Dam in August 1983 and immediately above Sandstone Falls in June 1987 were 326 g dry weight (DW) $\cdot \text{m}^{-2}$ (Voshell 1985) and 240

g DW • m⁻² (Voshell et al. 1989), respectively, or an average of 283 g DW • m⁻². *P. ceratophyllum* occupied about 99 ha in the study reach (Voshell et al. 1987), so the standing crop representative of the study reach was about 69 g DW • m⁻². Assuming that this value represents the maximum standing crop (and thus the annual input), and further assuming an energy density of 13.000 kJ • g⁻¹ DW (based on energy densities reported for several submergent aquatic macrophytes by Cummins and Wuycheck 1971), the annual energy input by *P. ceratophyllum* to the study reach was about 897 kJ • m⁻² • year⁻¹. Rodgers et al. (1983) estimated the annual inputs of the predominant aquatic macrophytes in the New River near Glen Lyn, Virginia, which is immediately upstream from Bluestone Lake. Forty-two percent of the river bed there was colonized by aquatic macrophytes. For each of six macrophyte species, Rodgers et al. (1983) estimated the maximum standing crop (and thus the annual input) and the percentage of the total colonized area that was occupied by each species. I used this information to estimate the maximum standing crop of each species per average unit area. *Typha latifolia* was ignored, because this species is scarce between Bluestone Dam and Sandstone Falls. *P. ceratophyllum* was ignored, because more appropriate estimates were obtained from other sources (see above). Respective estimates of maximum standing crop of *Justicia americana*, *Elodea nuttallii*, *Heteranthera dubia*, and *Potamogeton crispus* were 24.1, 9.5, 13.0, and 0.1 g AFDW • m⁻² • year⁻¹. Energy densities of 18.343, 17.677, and 18.489 kJ • g⁻¹ AFDW were estimated for *E. nuttallii*, *H. dubia*, and *P. crispus*, respectively, from energy density estimates reported by Cummins and Wuycheck (1971) for the same species or species in the same genus. An energy density of 18.000 kJ • g⁻¹ AFDW was arbitrarily assumed for *J. americana*. The annual energy input by each species was calculated from the appropriate estimates of maximum standing crop and energy density and then summed with that of *P. ceratophyllum* to gain a first approximation of the total annual energy input (1,736.7

$\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) by the aquatic macrophyte assemblage in the study reach below Bluestone Dam.

Seston was assumed to be the exclusive energy source of aquatic insects, because seston was 99.9% of total energy inputs to the reach, and because the aquatic insect assemblage below the dam was dominated by collector-filterers and collector-gatherers (Voshell et al. 1987). Voshell (1985) and Voshell et al. (1989) estimated the consumption of the six dominant taxa of aquatic insects in riffles immediately below Bluestone Dam and immediately above Sandstone Falls, respectively. The estimate of consumption at Bluestone Dam ($13,961,189 \text{ mg dry weight (DW)} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) corresponded to the period from June 1983 to May 1984. The estimate of consumption at Sandstone Falls ($607,908 \text{ mg DW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) corresponded to the period from June 1987 to November 1987. The black fly larvicide was not applied during these periods. The estimate from the area of the dam was assumed applicable to the first five riffle areas below the dam (Figure 2 in Chapter 1; area of 127 ha computed from Table 1 in Chapter 1), and the estimate from the falls area was assumed applicable to the remaining riffle areas in the study reach (70 ha). Consumption by aquatic insects in pools was assumed to be negligible as was done for the estimation of aquatic insect biomass. The estimate of consumption by aquatic insects in the study reach ($4,450,060 \text{ mg DW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was converted to its energy equivalent ($77,698.048 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) with an energy density of $17.460 \text{ kJ} \cdot \text{g}^{-1} \text{ DW}$. The calculation of energy density of seston was based on the diet composition of aquatic insects reported by (Voshell 1985). The diet composition (percent of dry weight) of the five dominant insect taxa there was 2.0% animal, 25.7% diatoms, 19.1% other algae, and 53.2% fine detritus. Respective estimates of energy density of these food types were derived from energy densities reported by Cummins and Wuycheck (1971) for cladoceran zooplankton ($21.928 \text{ kJ} \cdot \text{g}^{-1} \text{ DW}$), Chrysophyta

(Bacillariophyceae; $15.958 \text{ kJ} \cdot \text{g}^{-1} \text{ DW}$), Chlorophyta ($16.108 \text{ kJ} \cdot \text{g}^{-1} \text{ DW}$), and detritus ($18.502 \text{ kJ} \cdot \text{g}^{-1} \text{ DW}$). The energy density of each food type was multiplied by the corresponding percent composition in the diet, and the four resulting values were summed. Thus, the energy density of seston consumed by aquatic insects in the study reach was $17.460 \text{ kJ} \cdot \text{g}^{-1} \text{ DW}$.

The annual energy intake by ages-1 and -2 crayfish in the study reach was assumed to be comprised of 80% seston, 10% aquatic insects, 5% aquatic macrophyte detritus, and 5% periphyton, which is in general agreement with other studies (Tack 1941; Bovbjerg 1952; Vannote and Ball 1972). Budd et al. (1978) demonstrated that crayfish, particularly young crayfish, are efficient filter-feeders. Crayfish downstream from Bluestone Dam probably capitalize on the fine particles of energy-rich seston released from Bluestone Lake. The annual energy intake by crayfish, calculated from annual production ($6.98 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 1), the energy density of crayfish, and a gross growth efficiency (the ratio of annual production to annual consumption) of 0.1, was $262.839 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. The growth efficiency was a compromise between gross growth efficiencies of 7.3% reported by Kossakowski and Orzechowski (1975) for *O. limosus* and 15.1% reported by Mason (1975) for *Pacifastacus leniusculus*. Total intake was then apportioned among the four food sources using the corresponding percentages. Seston, aquatic insects, aquatic macrophytes, and periphyton therefore provided 210.271, 26.284, 13.142, and $13.142 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, respectively, to the crayfish component.

Aquatic insects were assumed to be the only source of energy to ages-1 and -2 hellgrammites (Davis 1903; Stewart et al. 1973; Kondratieff and Voshell 1983; Merritt and Cummins 1984). The annual consumption of aquatic insects by hellgrammites ($61.467 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was calculated as the ratio of annual production and gross growth efficiency. The annual production of hellgrammites in the study reach (3.09

$\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 1) was converted to an energy equivalent with the aforementioned energy density of hellgrammites. Gross growth efficiency (0.33) was calculated from annual production and annual consumption estimates reported by Brown and Fitzpatrick (1978) for hellgrammites in a Texas river.

Prey fish were assumed to derive all their energy from aquatic insects, because virtually all of the species of prey fish residing below Bluestone Dam were invertivores (Lobb 1986). The annual energy intake by prey fish ($30.246 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was calculated as for hellgrammites. The annual production of prey fish ($4.234 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was calculated as the product of annual mean biomass ($1.841 \text{ kJ} \cdot \text{m}^{-2}$) and a production/mean biomass (P/B) ratio of 2.3. The P/B ratio was based on the average of P/B ratios reported by Neves (1981) for several small non-game fishes in streams. Gross growth efficiency (0.14) was computed from annual production and annual consumption estimates reported by Small (1975) for two darter species in a Kentucky stream.

The annual consumption ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of each prey type by each age group of smallmouth bass, rock bass, and flathead catfish (Tables 19 - 21 in Chapter 2) was converted to an energy equivalent with the energy density of each prey. The values of total consumption by each age group were then summed according to the representation of age groups in the model. Consumption of age-0 smallmouth bass, rock bass, and flathead catfish by age-1 and older smallmouth bass and flathead catfish was distinguished from the energy provided by prey fish using the species composition of fish (percentages of total wet weight) in the diet of smallmouth bass and flathead catfish in 1984 and 1985 combined. Fish in the rock bass diet were unidentifiable. Unidentifiable fishes in the diet were assumed to be other than young predators, resulting in a more conservative estimate of predation on young predators.

Aquatic insects and crayfish were the only system components that fed on energy sources (seston, periphyton, and aquatic macrophytes) that were external to the defined model system. For each component, consumption of external energy sources was represented as one energy flow, and was modeled as a linear, recipient-controlled function of component biomass as follows:

$$C_{0i} = Z_i \cdot X_i , \quad [1]$$

where

C_{0i} = the consumption by component i of energy from external sources ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$),

Z_i = the coefficient of annual energy transfer (year^{-1}), and

X_i = the annual mean biomass of component i ($\text{kJ} \cdot \text{m}^{-2}$).

This formulation allows the component to acquire energy from external sources as needed; therefore, the external energy source was assumed to be available in excess. This assumption was considered valid for at least seston, because seston represented virtually all of the external source of energy and was supplied in great quantity.

The trophic interaction expression of DeAngelis et al. (1975), as modified by O'Neill et al. (1980), was used in the model to represent predation (consumption) by one component upon another component. The expression provides for predator feeding saturation at high prey abundance, intraspecific feeding interference of the predator, and availability of prey. Other trophic interaction terms (Lotka 1925; Volterra 1928; Holling 1959; Watt 1959; Ivlev 1961) were insufficient in some respects (DeAngelis et al. 1975; Hall 1988). DeAngelis et al. (1975) provided extensive analysis and justification for their expression. The expression has the form:

$$C_{ij} = \frac{f_{ij} \cdot w_{ij} \cdot X_i \cdot X_j}{b_{ij} + w_{ij} \cdot X_i + X_j} , \quad [2]$$

where

C_{ij} = the annual flow of energy from component i to component j
($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$),

X_i = the annual mean biomass of component i as prey ($\text{kJ} \cdot \text{m}^{-2}$),

X_j = the annual mean biomass of component j as predators ($\text{kJ} \cdot \text{m}^{-2}$),

f_{ij} = the coefficient of annual energy transfer (year^{-1}),

b_{ij} = a variable that relates the densities of the prey i and the predator j to the environment in which they interact ($\text{kJ} \cdot \text{m}^{-2}$; DeAngelis et al. 1975),

w_{ij} = the fraction of prey biomass (X_i) available to predator j , and reflects the foraging efficiency of the predator (unitless; O'Neill et al. 1980).

The f_{ij} parameter defines the maximum per capita feeding rate of the predator when prey are superabundant (DeAngelis et al. 1975). The b_{ij} parameter determines the rate at which the per capita feeding rate of the predator approaches its maximum as prey biomass increases. For example, the predator realizes a given per capita feeding rate at a lower prey biomass when the value of b_{ij} is large relative to when it is small. Given the estimates of C_{ij} and X_j , the f_{ij} parameters were estimated as follows:

$$f_{ij} = PR_{ij} \cdot \frac{1}{P_j} \cdot \frac{\sum_{i=1}^{13} C_{ij}}{X_j} , \quad [3]$$

where

PR_{ij} = the proportion of the total annual energy flow to component j that is from component i , and

P_j = the proportion of the maximum per capita feeding rate realized in nature.

The estimates of P_j for the nine components representing predatory fishes were calculated from the largest values of P estimated in the bioenergetics procedure (Appendix Tables 6 - 8 from Chapter 2). This approach resulted in conservative estimates of $f_{i,j}$. For crayfish, hellgrammites, and prey fish feeding on aquatic insects, an estimate of P_j of 0.3, similar to values of P_j for age-0 predator fishes feeding on aquatic insects, was used. Assuming an arbitrary value of 0.5 for all $w_{i,j}$ (half of the prey are available to the predator), estimates of $b_{i,j}$ were derived by solving Equation 2.

The sum of the annual energy losses from each component due to the processes of egestion, excretion, and apparent specific dynamic action (SDA) was modeled as a proportion ($E_{i,j}$) of the annual consumption of each prey type. The sum of annual energy losses from each component due to the processes of standard and activity metabolism (heat of respiration) was modeled as a multiple (M_i) of annual mean biomass. The total metabolic energy loss of each component was used to specify these physiological parameters. Total metabolic loss was calculated as the difference between annual consumption and annual production, and was then apportioned among the fates represented by $E_{i,j}$ and M_i . For each component, the energy lost to egestion, excretion, and SDA was estimated, and then that value was subtracted from total metabolic losses to estimate the energy lost to standard and activity metabolism. The annual consumption of each component and the annual production of crayfish, hellgrammites, and prey fish have been described.

Voshell (1985) and Voshell et al. (1989) estimated the production of the six dominant taxa of aquatic insects in riffles immediately below Bluestone Dam (612,291 mg DW • m⁻² • year⁻¹; June 1983 - May 1984) and immediately above Sandstone Falls

(30,759 mg DW • m⁻² • year⁻¹; June 1987 - November 1987). These estimates coincided directly with previously-described estimates of consumption by aquatic insects. Estimation of annual production representative of the study reach (6,638.046 kJ • m⁻² • year⁻¹) was done in a manner similar to that of consumption except that a weight conversion factor of 6 g wet weight • g⁻¹ dry weight (Waters 1977) and an energy density of 5.648 kJ • g⁻¹ wet weight (Chapter 2) were used. The assimilation efficiency of aquatic insects feeding on seston was assumed to be 20% as reported by Webster (1983) for benthic macroinvertebrates feeding on detritus. I was unable to find published accounts of bioenergetics studies that distinguished SDA energy losses from other metabolic losses in aquatic insects. Given that aquatic insect production and egestion accounted for 88.5% of annual consumption, the proportion of energy lost to excretion and SDA was assumed to be 5% of annual consumption (22.5% of assimilated energy). Thus, energy lost to standard and activity metabolism was, by difference, about 6.5% of annual consumption. Thus, E_{0,1} was 0.85, and M₁ was 26.05 • year⁻¹.

Digestibility differences among energy sources of the other components required that values of E_{i,j} be computed for each energy source of each component. Assimilation efficiency of *Orconectes virilis* feeding on algae is about 70% (Jones and Momot 1983), which was used as the assimilation efficiency of New River crayfish feeding on energy sources external to the system. An assimilation efficiency of 85%, used for predatory fishes feeding on aquatic insects (Chapter 2), was used for crayfish feeding on aquatic insects. Jones and Momot (1983) estimated SDA of *O. virilis* in three size groups. Estimates of SDA of the two larger groups, comparable to ages-1 and -2 crayfish in the New River, were 10% and 20%. A value of 15% was used for SDA of New River crayfish. The proportion of assimilated energy excreted was as-

sumed to be 0.10, which was comparable to that used for the predatory fishes (0.088; Chapter 2). Thus, $E_{0,2}$ was 0.48, and $E_{1,2}$ was 0.37; M_2 was $6.57 \cdot \text{year}^{-1}$.

Hellgrammites use about 28% of consumed energy for standard and activity metabolism (Brown and Fitzpatrick 1978). Total metabolic losses minus this respiratory heat loss was the total energy lost to egestion, excretion, and SDA. $E_{1,3}$ was 0.39, and M_3 was $1.43 \cdot \text{year}^{-1}$.

The annual production of prey fishes was previously described. The estimates of annual production of the predatory fishes (Tables 15 - 17 in Chapter 2) were converted to energy equivalents with an energy density of $4.184 \text{ kJ} \cdot \text{g}^{-1}$ wet weight. The assimilation efficiency of prey fishes feeding on aquatic insects was assumed to be the same as that of predatory fishes eating aquatic insects. Assimilation efficiencies of predatory fishes feeding on crayfish, hellgrammites, aquatic insects, and fish were 82%, 85%, 85%, and 90% (Chapter 2), and the proportions of assimilated energy excreted and used in SDA were 0.088 and 0.17 (Chapter 2), respectively. Thus, the values of $E_{i,j}$ of any of these components feeding on crayfish, hellgrammites, aquatic insects, and fish were 0.39, 0.37, 0.37, and 0.34, respectively. Each value of M_i was dependent on the value of the difference between total metabolic loss and the total of energy lost to egestion, excretion, and SDA.

Harvests from the crayfish, hellgrammite, and adult sport fish components were each modeled as a multiple (H_i) of annual mean biomass. The estimates of annual harvest of ages-1 and -2 crayfish ($0.36 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 1), ages-1 and -2 hellgrammites ($0.24 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 1), age-2 to age-6 smallmouth bass ($0.78 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 2), age-2 to age-5 rock bass ($0.07 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 2), and age-4 to age-8 flathead catfish ($0.25 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$; Chapter 2) were each converted to an energy equivalent with the appropriate energy density. The estimate of

flathead catfish harvest was in excess of annual production, so harvest was considered to be 90% of annual production as estimated for adult smallmouth bass.

Energy losses due to intraspecific regulation (non-predatory natural mortality) within each component were modeled as a multiple (R_i) of the squared value of each component's biomass (Kostitzin 1939; Larkin 1966). The energy lost due to intraspecific regulation was assumed equivalent to that portion of annual production remaining after accounting for predation and harvest losses (similarly calculated by O'Neill et al. 1980). Therefore, an equilibrium state was implied for all state variables to facilitate initial model specification.

Competition among system components was not modeled explicitly. During simulations with the model, competition was manifested through predators feeding on one or more of the same prey. When prey biomass was great, the effects of competition on predator biomass were slight. Low prey biomass resulted in mutually-deleterious effects on the biomass of predators utilizing that prey.

A differential equation was used for each system component to represent inputs, outputs, and accumulation of energy. Net energy change of a component during an interval of time ($dX_i \cdot dt^{-1}$) was a function of energy inputs from consumption and energy losses due to egestion, excretion, SDA, standard and activity metabolism, predation, harvest, and intraspecific regulation. Other potential energy losses or gains such as predation from outside the system, emigration from the system, and immigration to the system were considered negligible and ignored in the model. Specifically, energy inputs and outputs were modeled for each component as follows:

$$\frac{dX_i}{dt} = C_i - F_i - (M_i \cdot X_i) - P_i - (H_i \cdot X_i) - (R_i \cdot X_i^2) , \quad [4]$$

where

$\frac{dX_i}{dt}$ = the change in energy of component i over a given time interval
($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$),

$C_i = Z_i \cdot X_i + \sum_{j=1}^{13} \left(\frac{f_{ji} \cdot w_{ji} \cdot X_j \cdot X_i}{b_{ji} + w_{ji} \cdot X_j + X_i} \right)$, the annual consumption of energy by component i ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$),

$F_i = Z_i \cdot X_i \cdot E_{0i} + \sum_{j=1}^{13} \left(\frac{f_{ji} \cdot w_{ji} \cdot X_j \cdot X_i}{b_{ji} + w_{ji} \cdot X_j + X_i} \cdot E_{ji} \right)$, the annual loss of consumed energy through the processes of egestion, excretion, and SDA ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$),

E_{ji} = the proportion of the energy consumed from component j that is lost from component i through the processes of egestion, excretion, and SDA,

M_i = the multiple of annual mean biomass that represents standard and activity metabolism (year^{-1}),

$P_i = \sum_{j=1}^{13} \left(\frac{f_{ij} \cdot w_{ij} \cdot X_i \cdot X_j}{b_{ij} + w_{ij} \cdot X_i + X_j} \right)$, predation on component i by other components ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$),

H_i = the multiple of annual mean biomass that is harvested by humans (year^{-1}),
and

R_i = the coefficient for intraspecific regulation within component i
($\text{kJ}^{-1} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$).

For simulation purposes, numerical integration was used to solve each differential equation for X_i . Simultaneous integration of the equations was accomplished with a four step Runge-Kutta numerical integration procedure using a time step of 0.001 year. In addition, the annual production ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) and annual harvest ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of selected components were also calculated by numerical integration. Annual production in the model was calculated as the difference between the annual energy inputs from consumption and annual energy outputs of egestion,

excretion, SDA, and standard and activity metabolism. Annual harvest was computed as a multiple of annual mean biomass. The model represents the summation of states and processes occurring over a year and does not predict seasonal trends. The model as specified above represented the initial conditions (a benchmark) to which the results of model simulations were compared.

Model Analysis

Error analysis (*sensu* O'Neill et al. 1980; Gardner et al. 1980a; Gardner et al. 1980b) was applied to the New River energy flow model for two purposes: (1) to identify those model parameters that most influenced the variability of biomass representing each component; and (2) to make inferences regarding those states and/or processes that were most influential in structuring the prey-predator assemblage in the New River. The procedure involved two steps. First, a Monte Carlo procedure was used to propagate error through the model via standardized variability in selected input parameters. Second, multiple regression analysis was used to identify input parameters that explained substantial variation in biomass of each component. Thus, error analysis as applied to the New River model addressed concerns about the prediction capabilities of this deterministic model, and was not an attempt to represent stochastic phenomena known to occur in real systems (Gardner et al. 1980a).

One hundred thirty-nine input parameters were chosen for the analysis. These parameters corresponded to states and processes representing interactions among organisms in the system, and included all X_i , f_{ij} , b_{ij} , w_{ij} , R_i , and H_i parameters. Parameters representing physiological processes (E_i and M_i) and energy inputs to the

system (Z) were excluded from the analysis, because initial attempts to perform error analysis including these parameters resulted in predictions of extreme values of component biomasses in the majority of the simulations. This suggested that these parameters are estimable with higher precision than that used in the error analysis procedure (20% coefficient of variation; see below). Exclusion of these parameters from the analysis did not detract from attempts to identify key mechanisms involved in the structuring of the model prey-predator assemblage.

Two hundred, one-year simulations of energy flow were conducted with the model in the Monte Carlo procedure. Each simulation used a different set of values for the input parameters, and the value of the end-of-the-year biomass of each component was recorded. Independent values for input parameters were randomly chosen for each simulation from normal distributions using a stratified random sampling procedure (Iman and Conover 1980), which ensured adequate sampling from the entire distribution; sampling was restricted to within three standard deviations of the mean. The distribution of each input parameter was defined by a mean (the estimate used in the deterministic model) and a variance corresponding to a 20% coefficient of variation (Bartell et al. 1988), which represents a reasonable level of variation for ecological parameters (O'Neill et al. 1980).

Multiple regression was used to relate end-of-the-year biomass of each component (dependent variable) to the input parameters (independent variables). For each component, the two hundred estimates of end-of-the-year biomass were regressed (via the method of least squares) with the two hundred corresponding values randomly chosen for each of the 139 input parameters; a first-order model (each independent variable included but no cross-product terms or terms in powers of the independent variables are included; Ott 1984) was assumed. The partial sum of squares (PSS) was calculated for each input parameter. The PSS is a measure of the

amount of residual variation in biomass explained by the independent variable after adjusting for the effects of all other independent variables. Thus, the proportion of the total PSS of all independent variables accounted for by a single independent variable (or group of independent variables) is a relative measure of the expected improvement in model precision uniquely associated with improved estimation of that parameter (Bartell et al. 1988).

The error analysis results were also used to infer the states or population processes that were most influential to the structure of the model system. From the perspective of an individual component, model parameters could be grouped to collectively represent states or processes such as the biomasses of all prey, predation on all prey, predation from all predators, and so on. The PSS of the parameters in each group could then be pooled to provide a measure of the effect of that state or process on the biomass of each model component, and hence the structure of the model system.

The PSS were pooled for the following groups of parameters: the f_{ij} , b_{ij} , and w_{ij} parameters representing predation by the component, predation on the component, support of the component's prey by aquatic insects, predation on alternative prey by the component's predators, predation by competitors on the component's prey, or predation by competitors on non-mutual prey; the X_i parameters representing the initial biomasses of all prey, all predators, and all competitors; the H_i parameters representing the harvest rates of all exploited prey, all exploited predators, and all exploited competitors; and the R_i parameters representing the coefficients of intraspecific regulation of all prey, all predators, and all competitors. Only the PSS corresponding to the initial biomass, the harvest rate, and the coefficient of intraspecific regulation of the component under consideration were considered individually (that is, not pooled with the PSS of other input parameters). In this manner, the contrib-

utions to prediction error by the parameters associated with predation, exploitation, interspecific competition for food, and intraspecific regulation could be identified for each model component. Further, the effects of bottom-up versus top-down regulation on each component's biomass could be addressed. Bottom-up regulation of a component included effects from states or processes involved with prey components or trophically "lower" components, and top-down regulation was regarded as effects from states or processes associated with predator components or trophically "higher" components. This approach allowed development of hypotheses concerning the most and least influential processes affecting general trophic structure in the New River.

Effects of Exploitation

The energy flow model was used to predict the effects of annual harvest rate of crayfish and adult smallmouth bass on the annual mean biomass, annual production, and annual harvest of the same. Only the exploitation of these two groups was considered, owing to their strong trophic interaction and the interest in regulations to control their harvest. Three scenarios were evaluated: (1) the effects of changes in the instantaneous annual harvest rate of crayfish (H_2), while the instantaneous annual harvest rate of adult smallmouth bass (H_7) was held constant; (2) the effects of changes in the instantaneous annual harvest rate of adult smallmouth bass, while the instantaneous annual harvest rate of crayfish was held constant; and (3) the effects of simultaneous changes in the instantaneous annual harvest rates of both groups. For each of the first two scenarios, individual simulations were conducted for each of several instantaneous harvest rates ($0 - 1.6 \cdot \text{year}^{-1}$ in $0.05 \cdot \text{year}^{-1}$ increments

for crayfish harvest; $0 - 2.6 \cdot \text{year}^{-1}$ in $0.05 \cdot \text{year}^{-1}$ for smallmouth bass harvest). In evaluating the third scenario, forty-one randomly-paired rates of crayfish harvest and smallmouth bass harvest were simulated to develop the three-variable "response surface" of crayfish harvest rate versus smallmouth bass harvest rate versus a response variable. Harvest rates for each group ranged between 0 and $2 \cdot \text{year}^{-1}$ in $0.05 \cdot \text{year}^{-1}$ increments; an additional simulation with both rates equal to $0 \cdot \text{year}^{-1}$ was included. In all three procedures, each simulation was performed until a new steady state was attained. Response variables were annual mean biomass, annual production, and annual harvest of crayfish and adult smallmouth bass. In addition, response surfaces were similarly developed for annual mean biomass of adult rock bass and adult flathead catfish to evaluate the indirect effects of crayfish and smallmouth bass harvest.

Impacts from Reductions in Aquatic Insect Production

An effort was made by the State of West Virginia in 1986 and since 1988 to control black fly larvae below Bluestone Dam with the potential benefit of reducing the number of nuisance adult black flies in the local area. The energy flow model was used to predict the effects of reductions in aquatic insect production on each model system component, providing a first approximation of real system behavior associated with these conditions. Human-induced mortality of aquatic insects was simulated in a manner similar to that described for fish harvest in the previous section. Instantaneous mortality rates between 0 and $40 \cdot \text{year}^{-1}$ in $2 \cdot \text{year}^{-1}$ increments were used.

Results

Energy Flow Model

The state of each component in the energy flow model was represented by annual mean biomass, which ranged from $0.368 \text{ kJ} \cdot \text{m}^{-2}$ for age-0 flathead catfish (X_{11}) to $192.615 \text{ kJ} \cdot \text{m}^{-2}$ for aquatic insects (X_4 ; Table 22). The coefficients for feeding on external energy sources by aquatic insects (on seston) and crayfish (on seston, aquatic macrophytes, and periphyton) were $403.4 \cdot \text{year}^{-1}$ ($= Z_1$) and $13.6 \cdot \text{year}^{-1}$ ($= Z_2$), respectively; no other component fed on energy sources that were external to the model system. Annual energy flows between system components (Figure 12) ranged from $0.004 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (prey fish fed on by age-2 to age-5 rock bass) to $61.467 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (aquatic insects fed on by hellgrammites). Each inter-component flow of energy was represented in the model by the DeAngelis et al. (1975) trophic interaction algorithm, which required estimates of three parameters for each interaction; the w_{ij} parameters were assigned values of 0.5 for all interactions, and the values of the f_{ij} and b_{ij} parameters (Tables 23 and 24, respectively) were derived for each interaction (see “Quantitative Specification” in Methods). The proportion of annual consumption lost by each component to the processes of egestion, excretion, and SDA (E_{ij} parameters; Table 25) was prey-specific. The coefficients representing standard and activity respiration (M_i parameters) and intraspecific regulation (R_i pa-

Table 22. Annual mean biomass (X_i ; $\text{kJ} \cdot \text{m}^{-2}$) and the coefficients for external feeding (Z_i ; year^{-1}), standard and activity metabolism (M_i ; year^{-1}), intraspecific regulation (R_i ; $\text{kJ}^{-1} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), and annual harvest (H_i ; year^{-1}) for each component in the New River energy flow model. (All values, except those of X_i , have been rounded to the fourth decimal position.)

Component	Annual Mean Biomass (X_i)	External Feeding Coefficient (Z_i)	Respiration Coefficient (M_i)	Regulation Coefficient (R_i)	Annual Harvest Rate (H_i)
1 - Aquatic Insects	192.615	403.3821	26.0451	0.7280	0
2 - Ages 1 - 2 Crayfish	17.435	13.5680	6.5665	0.0680	0.0778
3 - Ages 1 - 2 Hellgrammites	12.012	0	1.4328	0.4615	0.1313
4 - Prey Fish	1.841	0	8.0621	2.1488	0
5 - Age 0 Smallmouth Bass	2.372	0	2.5258	3.9410	0
6 - Age 1 Smallmouth Bass	2.498	0	1.1458	2.6038	0
7 - Ages 2 - 6 Smallmouth Bass	4.418	0	0.7219	0.0771	0.7358
8 - Age 0 Rock Bass	1.753	0	4.6374	4.8986	0
9 - Age 1 Rock Bass	1.381	0	2.9925	4.8209	0
10 - Ages 2 - 5 Rock Bass	2.628	0	2.4720	1.3109	0.1115
11 - Age 0 Flathead Catfish	0.368	0	2.1420	17.1746	0
12 - Ages 1 - 3 Flathead Catfish	1.142	0	1.0060	3.6764	0
13 - Ages 4 - 8 Flathead Catfish	0.757	0	0.5741	0.2442	0.3757

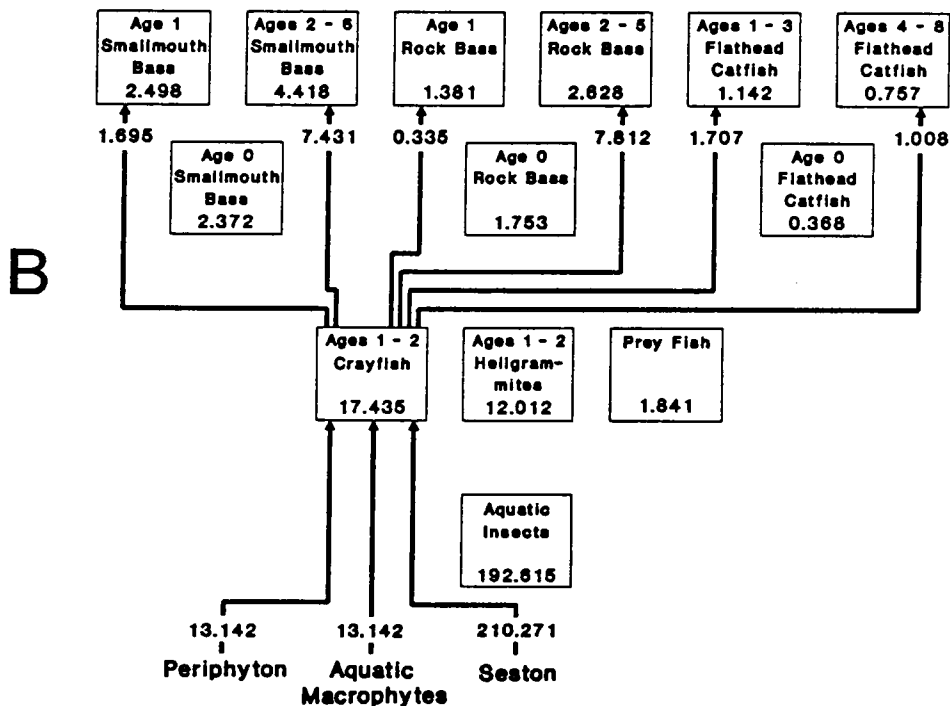
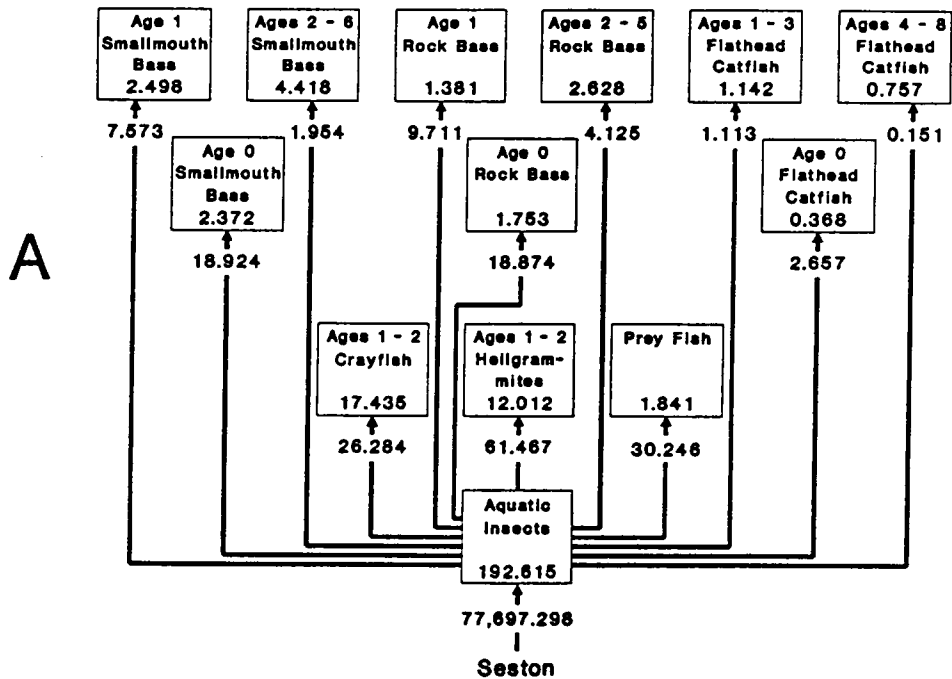
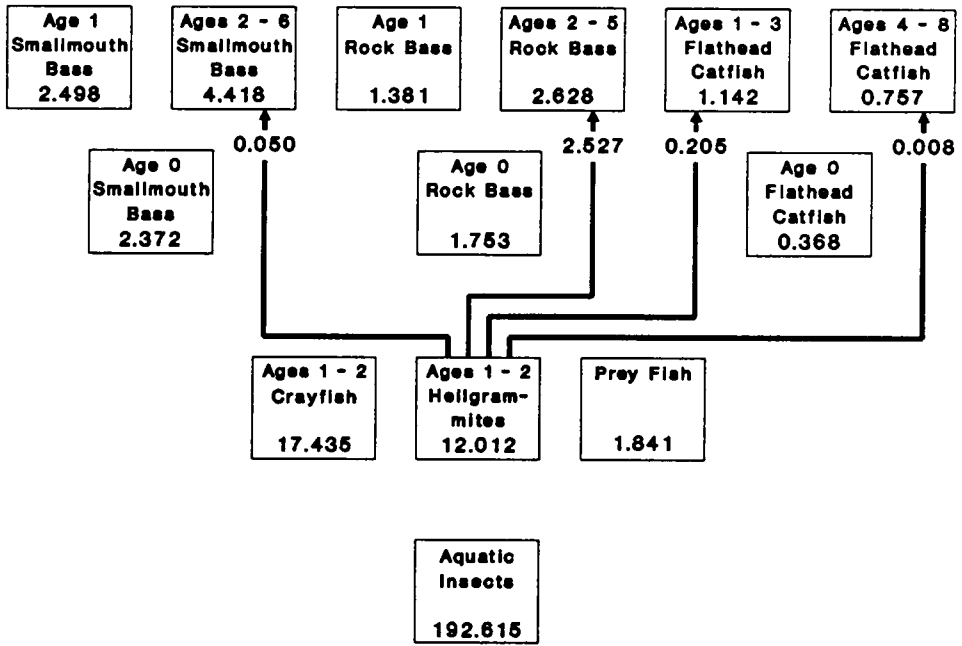


Figure 12. Estimated annual energy flows ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) for trophic interactions among key components in the prey-predator assemblage of the New River, West Virginia. The value in each component box is annual mean biomass ($\text{kJ} \cdot \text{m}^{-2}$).

C



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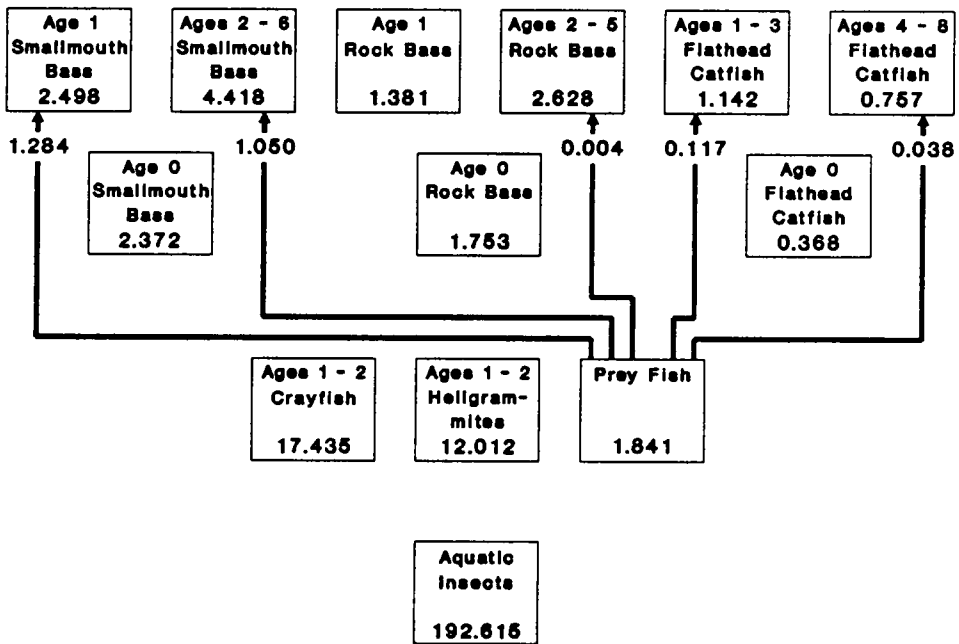


Figure 12. Continued.

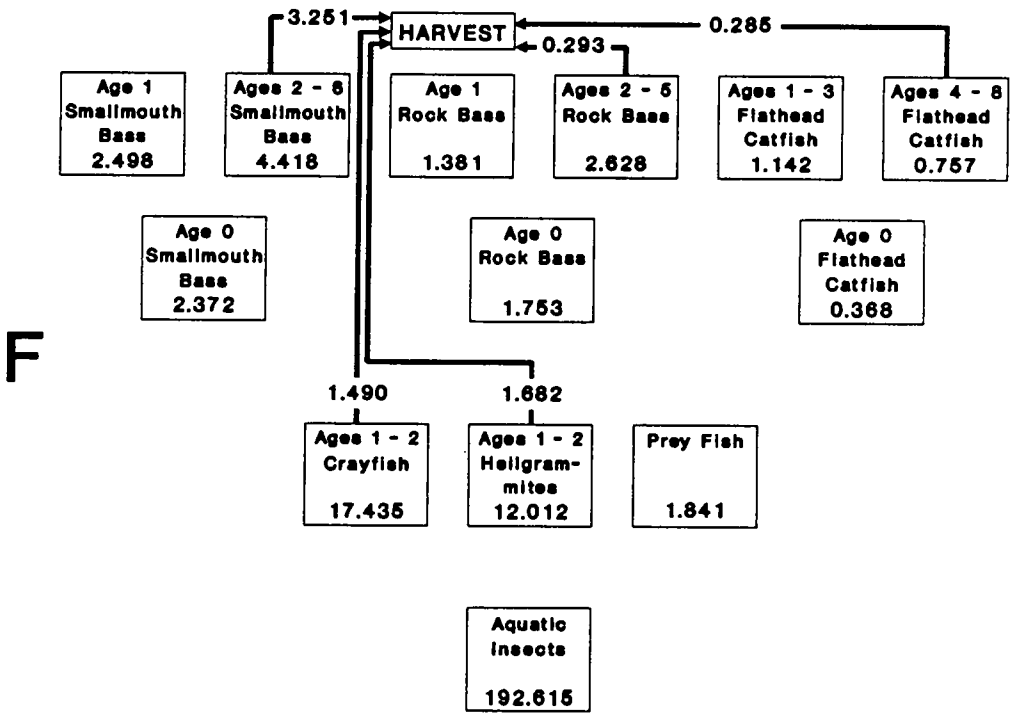
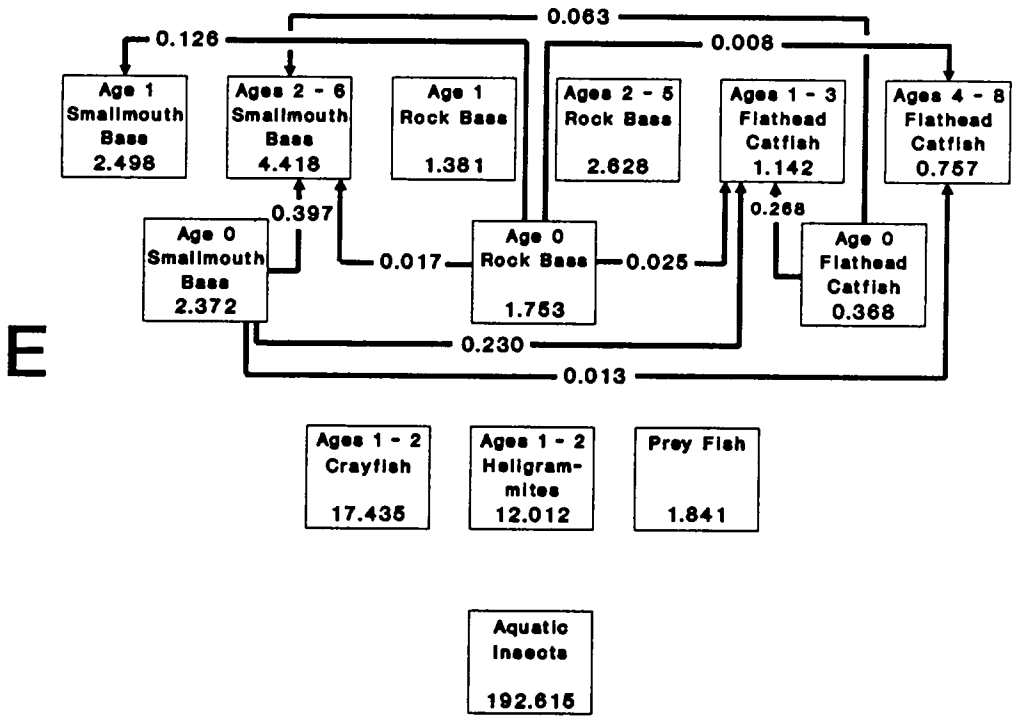


Figure 12. Concluded.

Table 23. Estimated values of f_{ij} (year⁻¹) for all trophic interactions represented in the New River energy flow model. (All values have been rounded to at least the third decimal position.)

Donor Component	Recipient Component												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1 - Aquatic Insects	0	5.03	17.06	54.77	36.26	12.13	1.58	38.45	21.98	3.34	23.28	4.43	1.53
2 - Ages 1 - 2 Crayfish	0	0	0	0	0	2.71	6.01	0	0.76	6.33	0	6.79	10.24
3 - Ages 1 - 2 Hellgrammites	0	0	0	0	0	0	0.041	0	0	2.05	0	0.82	0.085
4 - Prey Fish	0	0	0	0	0	2.06	1.38	0	0	0.006	0	0.47	0.38
5 - Age 0 Smallmouth Bass	0	0	0	0	0	0	0.43	0	0	0	0	0.92	0.13
6 - Age 1 Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
7 - Ages 2 - 6 Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
8 - Age 0 Rock Bass	0	0	0	0	0	0.20	0.023	0	0	0	0	0.10	0.085
9 - Age 1 Rock Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
10 - Ages 2 - 5 Rock Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
11 - Age 0 Flathead Catfish	0	0	0	0	0	0	0.355	0	0	0	0	1.69	0
12 - Ages 1 - 3 Flathead Catfish	0	0	0	0	0	0	0	0	0	0	0	0	0
13 - Ages 4 - 8 Flathead Catfish	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 24. Estimated values of b_{ij} ($\text{kJ} \cdot \text{m}^{-2}$) for all trophic interactions represented in the New River energy flow model. (All values have been rounded to at least the third decimal position.)

Donor Component	Recipient Component												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1 - Aquatic Insects	0	207.3	212.7	222.9	339.1	286.4	243.2	245.9	203.3	106.0	214.0	340.3	643.8
2 - Ages 1 - 2 Crayfish	0	0	0	0	0	23.7	18.0	0	17.1	7.2	0	29.8	57.6
3 - Ages 1 - 2 Hellgrammites	0	0	0	0	0	0	11.0	0	0	4.1	0	20.2	39.5
4 - Prey Fish	0	0	0	0	0	0.26	0.004	0	0	0.004	0	2.1	5.4
5 - Age 0 Smallmouth Bass	0	0	0	0	0	0	0.004	0	0	0	0	3.1	7.2
6 - Age 1 Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
7 - Ages 2 - 6 Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
8 - Age 0 Rock Bass	0	0	0	0	0	0.13	0.004	0	0	0	0	2.0	5.1
9 - Age 1 Rock Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
10 - Ages 2 - 5 Rock Bass	0	0	0	0	0	0	0	0	0	0	0	0	0
11 - Age 0 Flathead Catfish	0	0	0	0	0	0	0.004	0	0	0	0	0.004	0
12 - Ages 1 - 3 Flathead Catfish	0	0	0	0	0	0	0	0	0	0	0	0	0
13 - Ages 4 - 8 Flathead Catfish	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 25. Estimated values of E_{ij} (year^{-1}), which represent in the New River energy flow model the proportion of consumption of each prey type (donor component) by each predator (recipient component) that was lost to the processes of egestion, excretion, and specific dynamic action. (All values have been rounded to the fourth decimal position.)

Donor Component	Recipient Component													
	1	2	3	4	5	6	7	8	9	10	11	12	13	
0 - External Energy Source	0.8500	0.4750	0	0	0	0	0	0	0	0	0	0	0	0
1 - Aquatic Insects	0	0.3693	0.3900	0.3693	0.3693	0.3693	0.3693	0.3693	0.3693	0.3693	0.3693	0.3693	0.3693	0.3693
2 - Ages 1 - 2 Crayfish	0	0	0	0	0	0.3916	0.3916	0	0.3916	0.3916	0	0.3916	0.3916	0.3916
3 - Ages 1 - 2 Hellgrammites	0	0	0	0	0	0	0.3693	0	0	0.3693	0	0.3693	0.3693	0.3693
4 - Prey Fish	0	0	0	0	0	0.3352	0.3352	0	0	0.3352	0	0.3352	0.3352	0.3352
5 - Age 0 Smallmouth Bass	0	0	0	0	0	0	0.3352	0	0	0.3352	0	0	0.3352	0.3352
6 - Age 1 Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 - Ages 2 - 6 Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 - Age 0 Rock Bass	0	0	0	0	0	0.3352	0.3352	0	0	0.3352	0.3352	0	0.3352	0.3352
9 - Age 1 Rock Bass	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 - Ages 2 - 5 Rock Bass	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 - Age 0 Flathead Catfish	0	0	0	0	0	0	0.3352	0	0	0.3352	0	0.3352	0.3352	0
12 - Ages 1 - 3 Flathead Catfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13 - Ages 4 - 8 Flathead Catfish	0	0	0	0	0	0	0	0	0	0	0	0	0	0

rameters) are listed in Table 22. The instantaneous annual harvest rates for crayfish (H_2), hellgrammites (H_3), adult smallmouth bass (H_7), adult rock bass (H_{10}), and adult flathead catfish (H_{13}) were 0.08, 0.13, 0.74, 0.11, and 0.38 $\cdot \text{year}^{-1}$, respectively.

The estimated annual energy input to the river reach between Bluestone Dam and Sandstone Falls was more than 8 million $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. Organic seston inputs to the reach from Bluestone Lake ($8.073 \times 10^6 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) represented virtually all (99.9%) of the estimated annual input. Periphyton and aquatic macrophytes contributed about 3,980 and 1,737 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, respectively.

Energy flow into the model system via aquatic insects and crayfish was 77,934 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Figure 12); seston contributed 77,908 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ and periphyton and aquatic macrophytes each contributed 13 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. Inter-component flows (predation) in the system totaled 222 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Figure 12). Predation on aquatic insects accounted for 88% (196 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of total predation, while predation on crayfish (20.0 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), hellgrammites (2.8 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), prey fish (2.5 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), and age-0 fishes (1.1 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was much less in magnitude. Crayfish were preyed upon most by adult smallmouth bass and adult rock bass. Predation by adult rock bass represented the greatest flow from hellgrammites. The greatest flows from prey fish were to age-1 and adult smallmouth bass. Cannibalism by adult smallmouth bass on age-0 smallmouth bass represented the greatest flow from age-0 predatory fishes to their predators.

Harvest from the system was 6.8 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Figure 12). Anglers annually harvested about 3.8 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ of the three predatory fishes, and anglers and commercial bait catchers harvested 2.9 $\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ in crayfish and hellgrammites combined. Adult smallmouth bass represented 48% of the total harvest from the system, and the harvest of crayfish and hellgrammites represented 20% and 23%, respectively, of the total harvest.

Model Analysis

Error analysis was performed on the New River energy flow model to: (1) identify individual model parameters that contributed substantially to the error of prediction of each component's biomass; and (2) indicate which states and/or processes might be most influential in structuring the New River prey-predator assemblage. The second exercise assumed that the model reasonably represented actual system structure (disposition of biomass among real system components) and function (energy flow).

The model parameters that accounted for the greatest proportion of the total partial sums of squares (TPSS) of each component were, in general, the f_{ij} , b_{ij} , and w_{ij} parameters defining the trophic interaction between each component and its single most important source of energy (Table 26). Of the 12 components functioning as predators in the model system, the f_{ij} parameter associated with the strongest trophic interaction between a component and one prey component was the single most important parameter to nine components (15 - 31% of the TPSS), and was the second, third, or fourth most important parameter to the other three components (7 - 16% of the TPSS). The f_{ij} parameter defines the maximum per capita feeding rate that a predator can realize. Only crayfish were notably influenced by the trophic interaction parameters representing predation on a component (specifically $f_{2,10}$, $f_{2,7}$). The coefficient of intraspecific regulation of aquatic insects (R_1) was the most important parameter to aquatic insects (81% of the TPSS), age-1 smallmouth bass (21%), and age-1 to age-3 flathead catfish (18%); that parameter also accounted for 11 - 18% of the TPSS in seven other components. The coefficient of intraspecific regulation (other than that of aquatic insects) accounted for 6 - 14% of the TPSS in eight components; it was not influential to adult smallmouth bass and adult flathead catfish,

Table 26. Rank order of the fewest model parameters that accounted for at least 75% of the total partial sums of squares (TPSS) of each model component as identified by error analysis. The percentage of the TPSS of each component is in parentheses.

Rank	Aquatic Insects		Crayfish		Hellgrammites		Prey Fish		Smallmouth Bass					
									Age 0		Age 1		Ages 2-6	
1	R ₁	(81)	f _{1,2}	(23)	f _{1,3}	(22)	f _{1,4}	(19)	f _{1,5}	(21)	R ₁	(21)	f _{2,7}	(16)
2			X ₂	(13)	R ₁	(18)	w _{1,4}	(15)	w _{1,5}	(17)	f _{1,8}	(16)	R ₁	(12)
3			w _{1,2}	(8)	w _{1,3}	(13)	b _{1,4}	(7)	R ₁	(14)	w _{1,8}	(12)	H ₇	(9)
4			f _{2,10}	(7)	R ₃	(10)	R ₁	(6)	b _{1,5}	(13)	R ₆	(11)	w _{2,7}	(9)
5			f _{2,7}	(7)	b _{1,3}	(10)	w _{3,10}	(4)	R ₅	(8)	b _{1,8}	(9)	X ₂	(8)
6			b _{1,2}	(7)	b _{5,7}	(2)	X ₁₁	(3)	b _{2,7}	(2)	w _{1,4}	(2)	X ₇	(7)
7			R ₁	(3)			b _{11,12}	(3)			b _{1,11}	(1)	f _{1,2}	(3)
8			w _{2,7}	(3)			w _{5,12}	(2)			f _{2,8}	(1)	b _{2,7}	(3)
9			X ₇	(2)			X ₄	(2)			X ₁₀	(1)	f _{1,4}	(3)
10			X ₁₀	(1)			f _{1,9}	(2)			w _{8,8}	(1)	w _{1,4}	(2)
11			f _{1,13}	(1)			w _{4,10}	(2)					f _{1,7}	(2)
12							R ₄	(2)					w _{4,7}	(2)
13							w _{1,11}	(2)						
14							b _{1,5}	(1)						
15							w _{1,8}	(1)						
16							X ₈	(1)						
17							b _{5,12}	(1)						
18							f _{1,8}	(1)						
19							f _{2,12}	(1)						

Table 26. Concluded.

Rank	Rock Bass			Flathead Catfish		
	Age 0	Age 1	Ages 2-5	Age 0	Ages 1-3	Ages 4-8
1	$b_{1,8}$ (21)	$f_{1,9}$ (31)	$f_{2,10}$ (20)	$f_{1,11}$ (20)	R_1 (18)	$f_{2,13}$ (15)
2	$w_{1,8}$ (14)	$b_{1,9}$ (19)	R_1 (15)	R_1 (18)	R_{12} (14)	$b_{2,13}$ (13)
3	$f_{1,8}$ (13)	$w_{1,9}$ (14)	X_2 (9)	$b_{1,11}$ (13)	$w_{1,12}$ (7)	X_{13} (13)
4	R_1 (11)	R_1 (12)	R_{10} (6)	$w_{1,11}$ (10)	$f_{2,12}$ (7)	$w_{2,13}$ (7)
5	R_8 (6)		$f_{1,10}$ (6)	R_{11} (6)	$b_{2,12}$ (6)	X_2 (7)
6	$b_{1,2}$ (1)		$w_{2,10}$ (5)	$f_{4,8}$ (1)	$w_{2,12}$ (5)	$f_{1,2}$ (5)
7	$b_{1,6}$ (1)		$b_{2,10}$ (4)	R_2 (1)	$b_{1,12}$ (4)	$f_{2,10}$ (3)
8	$b_{1,9}$ (1)		$f_{3,10}$ (3)	X_6 (1)	X_{12} (4)	R_1 (3)
9	$f_{3,12}$ (1)		$w_{1,10}$ (3)	X_{10} (1)	$f_{1,12}$ (4)	$w_{1,2}$ (1)
10	$w_{3,10}$ (1)		$f_{1,2}$ (2)	$w_{1,8}$ (1)	X_2 (3)	H_{10} (1)
11	$f_{2,8}$ (1)		$b_{1,2}$ (2)	R_8 (1)	$f_{1,2}$ (2)	$f_{5,12}$ (1)
12	$b_{1,4}$ (1)			$w_{1,7}$ (1)	$f_{4,8}$ (2)	X_{10} (1)
13	$f_{1,5}$ (1)			R_5 (1)		$f_{2,7}$ (1)
14	$w_{11,12}$ (1)					H_3 (1)
15	R_{10} (1)					$b_{1,7}$ (1)
16						$b_{2,7}$ (1)
17						X_1 (1)
18						
19						

which were intensively harvested, or to crayfish and prey fish, which experienced extensive predation pressure. Other parameters were important to their respective components, such as the initial biomass of crayfish (X_2 ; 13% of the TPSS), the initial biomass (X_7 ; 7%) and harvest rate (H_7 ; 9%) of adult smallmouth bass, and the initial biomass of adult flathead catfish (X_{13} ; 13%). The initial biomass of crayfish (X_2) was influential to adult smallmouth bass (8% of the TPSS), adult rock bass (9%), and adult flathead catfish (7%).

Error analysis was also used to infer those population states and processes that most affect the biomass of each system component and thus the structure of the model system. In this regard, predation by components, intraspecific regulation of prey, and predation by potential competitors on the prey of components were the most influential processes. Those parameters describing predation (f_{ij} , b_{ij} , and w_{ij}) by each component on its prey accounted for the greatest percentages (34 - 64%) of the TPSS of every component except aquatic insects (Table 27), which were not predatory in the model system. Intraspecific regulation of a component's prey was influential to nine components (11 - 22%). Predation by potential competitors on the prey of a component was important to seven components (10 - 20%).

Other states and/or processes were secondary in importance. Initial biomass influenced crayfish (13% of the TPSS), adult smallmouth bass (7%), and adult flathead catfish (13%). Predation on a component was most influential to crayfish (24%). The initial biomass of prey and the trophic support of prey by aquatic insects were most influential to adult smallmouth bass (9% and 12%, respectively), adult rock bass (10% and 8%, respectively), and adult flathead catfish (9% for both factors). Predation on alternative prey by the predators of a component most affected aquatic insects (9%), hellgrammites (10%), prey fish (20%), age-0 smallmouth bass (10%), and age-0 rock bass (14%); with respect to each component's predators, prey other than

Table 27. Percentages of the total partial sums of squares of each model component attributed to states and processes affecting the biomass of each component.

State/Process	Aquatic Insects	Crayfish	Hellgrammites	Prey Fish
Initial Biomass of Component :	<1	13	<1	2
Predation				
Predation by Component :	na	38	44	42
Predation on Component :	5	24	3	6
Initial Biomass of Prey :	na	<1	<1	<1
Initial Biomass of Predators :	1	5	1	1
Support of Prey by Aquatic Insects :	na	na	na	na
Predation on Alternative Prey by Component's Predators :	9	6	10	20
Exploitation				
Harvest Rate of Component :	na	<1	<1	na
Harvest Rate of Prey :	na	na	na	na
Harvest Rate of Predators :	1	1	1	1
Harvest Rate of Competitors :	na	<1	<1	<1
Intraspecific Regulation				
Intraspecific Regulation of Component :	81	1	10	1
Intraspecific Regulation of Prey :	na	3	18	6
Intraspecific Regulation of Predators :	2	<1	<1	1
Intraspecific Regulation of Competitors :	na	1	1	1
Competition for Food				
Initial Biomass of Competitors :	na	<1	2	4
Predation by Potential Competitors on Component's Prey :	na	7	5	13
Predation by Potential Competitors on Non-mutual Prey :	na	na	4	1

Table 27. Continued.

State/Process	Age 0 Smallmouth Bass	Age 1 Smallmouth Bass	Ages 2 - 6 Smallmouth Bass
Initial Biomass of Component :	<1	<1	7
Predation			
Predation by Component :	50	42	34
Predation on Component :	1	na	na
Initial Biomass of Prey :	<1	2	9
Initial Biomass of Predators :	1	na	na
Support of Prey by Aquatic Insects :	na	4	12
Predation on Alternative Prey by Component's Predators :	10	na	na
Exploitation			
Harvest Rate of Component :	na	na	9
Harvest Rate of Prey :	na	<1	<1
Harvest Rate of Predators :	<1	na	na
Harvest Rate of Competitors :	1	<1	<1
Intraspecific Regulation			
Intraspecific Regulation of Component :	8	11	<1
Intraspecific Regulation of Prey :	14	22	14
Intraspecific Regulation of Predators :	<1	na	na
Intraspecific Regulation of Competitors :	2	1	1
Competition for Food			
Initial Biomass of Competitors :	1	1	1
Predation by Potential Competitors on Component's Prey :	7	13	12
Predation by Potential Competitors on Non-mutual Prey :	4	3	na

Table 27. Continued.

State/Process	Age 0 Rock Bass	Age 1 Rock Bass	Ages 2 - 5 Rock Bass
Initial Biomass of Component :	<1	<1	1
Predation			
Predation by Component :	48	64	43
Predation on Component :	2	na	na
Initial Biomass of Prey :	<1	<1	10
Initial Biomass of Predators :	<1	na	na
Support of Prey by Aquatic Insects :	na	1	8
Predation on Alternative Prey by Component's Predators :	14	na	na
Exploitation			
Harvest Rate of Component :	na	na	<1
Harvest Rate of Prey :	na	<1	<1
Harvest Rate of Predators :	<1	na	na
Harvest Rate of Competitors :	<1	1	<1
Intraspecific Regulation			
Intraspecific Regulation of Component :	6	4	6
Intraspecific Regulation of Prey :	11	12	15
Intraspecific Regulation of Predators :	1	na	na
Intraspecific Regulation of Competitors :	1	1	2
Competition for Food			
Initial Biomass of Competitors :	1	2	1
Predation by Potential Competitors on Component's Prey :	13	7	10
Predation by Potential Competitors on Non-mutual Prey :	2	7	3

Table 27. Concluded.

State/Process	Age 0 Flathead Catfish	Ages 1 - 3 Flathead Catfish	Ages 4 - 8 Flathead Catfish
Initial Biomass of Component :	1	4	13
Predation			
Predation by Component :	42	35	38
Predation on Component :	1	na	na
Initial Biomass of Prey :	<1	4	9
Initial Biomass of Predators :	1	na	na
Support of Prey by Aquatic Insects :	na	7	9
Predation on Alternative Prey by Component's Predators :	1	na	na
Exploitation			
Harvest Rate of Component :	na	na	<1
Harvest Rate of Prey :	na	<1	2
Harvest Rate of Predators :	<1	na	na
Harvest Rate of Competitors :	1	<1	1
Intraspecific Regulation			
Intraspecific Regulation of Component :	6	14	<1
Intraspecific Regulation of Prey :	17	19	4
Intraspecific Regulation of Predators :	<1	na	na
Intraspecific Regulation of Competitors :	5	<1	1
Competition for Food			
Initial Biomass of Competitors :	3	<1	1
Predation by Potential Competitors on Component's Prey :	7	14	20
Predation by Potential Competitors on Non-mutual Prey :	14	na	1

the component of interest were considered alternative prey. Harvest rate accounted for 9% of the TPSS of adult smallmouth bass. Intraspecific regulation was the most important process affecting aquatic insects (81%) and was secondary in importance to hellgrammites (10%), age-0 smallmouth bass (8%), age-1 smallmouth bass (11%), and ages-1 to -3 flathead catfish (14%). Predation by potential competitors on non-mutual prey was important to age-0 flathead catfish (14%); prey used by a component's potential competitors but not by the component were considered non-mutual prey.

Exploitation of a component or of its prey, predators, or potential competitors was unimportant to every model component except adult smallmouth bass, which were affected directly by exploitation. The initial biomass and intraspecific regulation of each component's predators and potential competitors were also unimportant.

Exploitation of Macroinvertebrates and Predatory Fishes

The effects of harvest of both crayfish and adult smallmouth bass were evaluated with the energy flow model in three procedures. In the first procedure, 33 annual rates of crayfish harvest ($0 - 1.60 \cdot \text{year}^{-1}$ in $0.05 \cdot \text{year}^{-1}$ increments) were assessed, while the annual rate of harvest of adult smallmouth bass ($0.74 \cdot \text{year}^{-1}$) remained constant. The annual mean biomass and annual production of crayfish declined steadily with increasing harvest rate of crayfish, achieving near-zero values at a harvest rate of $1.50 \cdot \text{year}^{-1}$ (Figure 13). The annual harvest of crayfish increased to a maximum of $5.7 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ at a harvest rate of $0.65 \cdot \text{year}^{-1}$, and then declined to a near-zero value at a harvest rate of $1.50 \cdot \text{year}^{-1}$. Under a regime of no

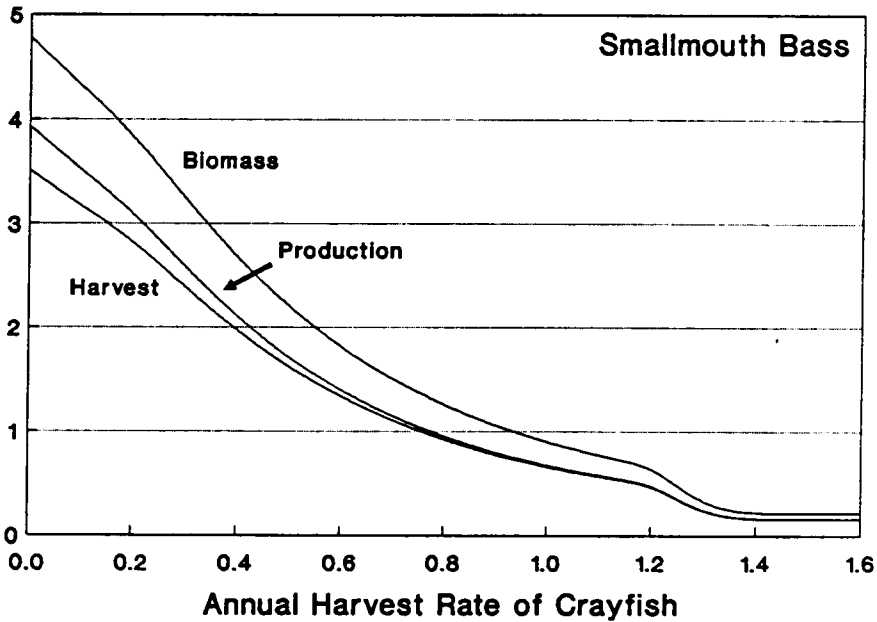
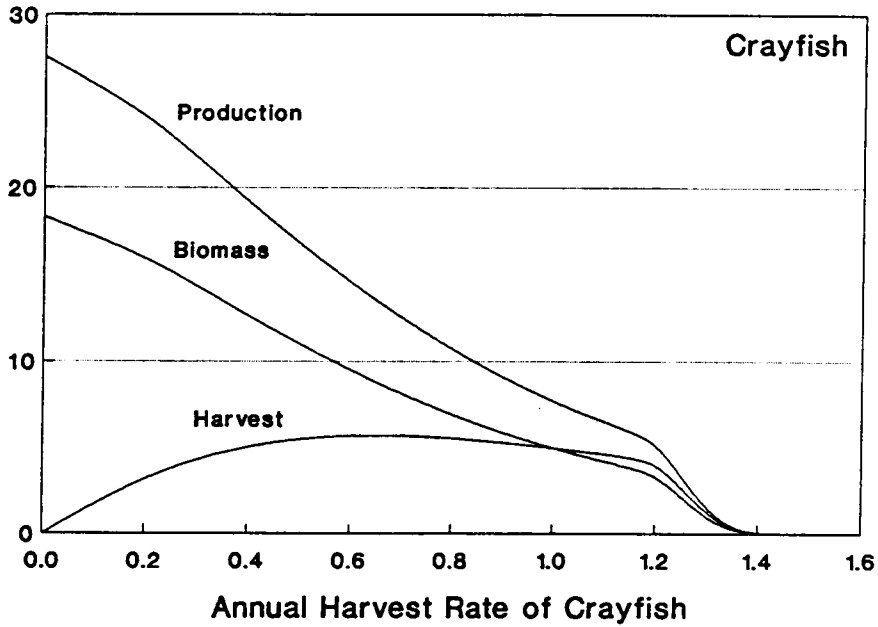


Figure 13. Model predictions of the effects of the annual harvest rate of crayfish (year⁻¹) on the annual mean biomass (kJ · m⁻²), annual production (kJ · m⁻² · year⁻¹), and annual harvest (kJ · m⁻² · year⁻¹) of crayfish (top) and adult smallmouth bass (bottom) in the New River, West Virginia. The empirical estimate of the annual rate of crayfish harvest was 0.08 · year⁻¹.

crayfish harvest, crayfish biomass and production increased only 5% from initial conditions (a crayfish harvest rate of $0.08 \cdot \text{year}^{-1}$).

Annual mean biomass, annual production, and annual harvest of adult smallmouth bass declined gradually with increasing harvest rate of crayfish, achieving much lower, stable values at crayfish harvest rates of $1.40 \cdot \text{year}^{-1}$ and greater (Figure 13). From initial conditions, smallmouth bass biomass, production, and harvest increased 8%, 9%, and 8%, respectively, under a regime of no crayfish harvest.

Increases in the annual rate of crayfish harvest had virtually no effect on the biomass of some system components, but very pronounced effects on other components (Figure 14). Components least affected were aquatic insects (< 1% increase; not shown in Figure 14), hellgrammites (16% increase), age-0 smallmouth bass (9% increase), age-1 smallmouth bass (14% decrease), age-0 rock bass (1% increase), age-1 rock bass (9% decrease), and age-0 flathead catfish (16% increase). Prey fish (74% increase), adult rock bass (100% decrease), age-1 to age-3 flathead catfish (61% decrease), and adult flathead catfish (100% decrease) were most influenced by increases in crayfish harvest rate.

The second procedure involved evaluation of 53 annual harvest rates ($0 - 2.60 \cdot \text{year}^{-1}$ in $0.05 \cdot \text{year}^{-1}$ increments) of adult smallmouth bass, while the annual harvest rate of crayfish ($0.08 \cdot \text{year}^{-1}$) remained constant. As the harvest rate of smallmouth bass increased, biomass, production, and harvest of crayfish increased 43%, 41%, and 43%, respectively, from their values for initial conditions (a smallmouth bass harvest rate of $0.74 \cdot \text{year}^{-1}$) to their maximum predicted values (Figure 15). Under a regime of no harvest of adult smallmouth bass, crayfish biomass, production, and harvest decreased 56%, 55%, and 56%, respectively, from their values estimated for initial conditions.

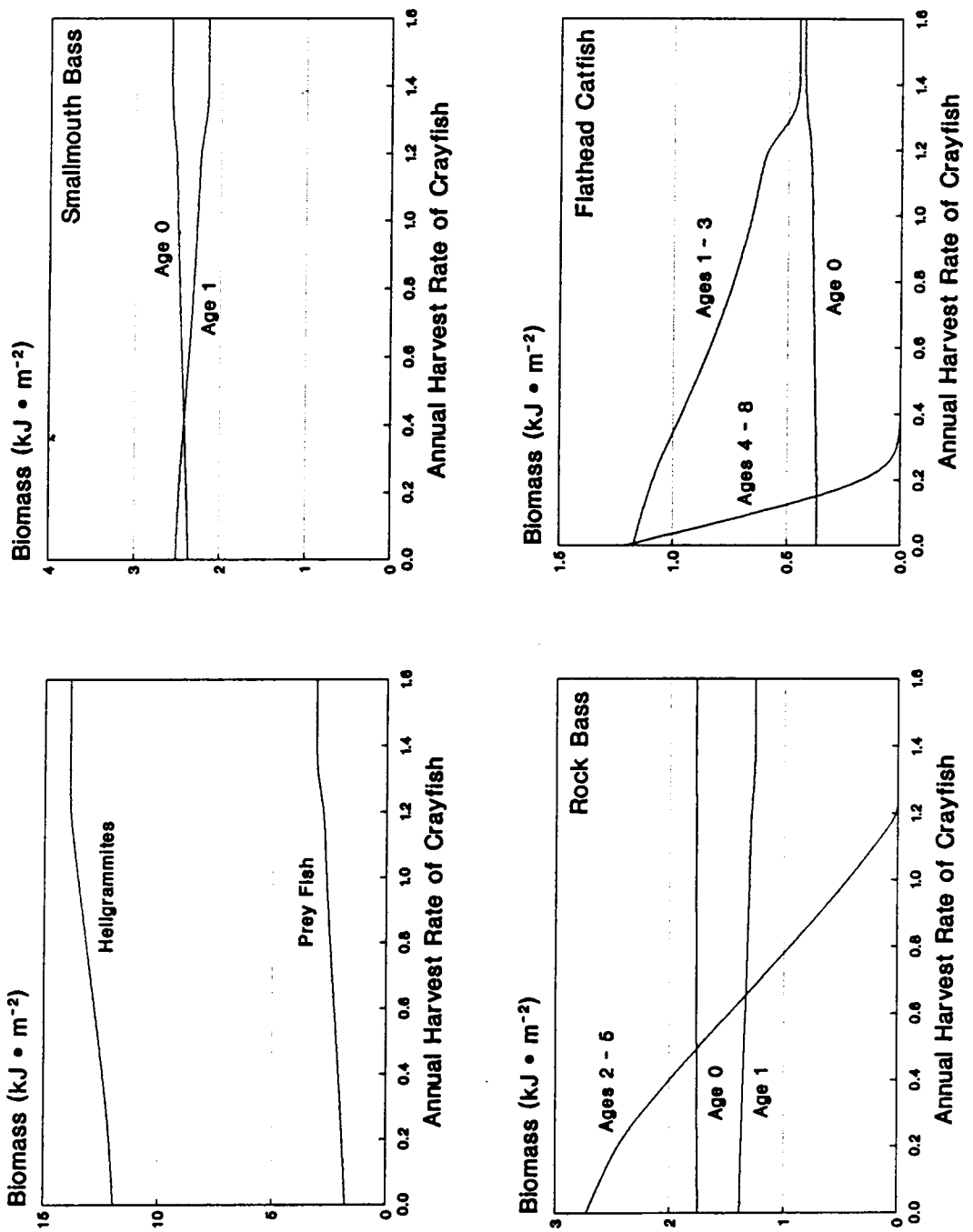


Figure 14. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) on the annual mean biomass ($\text{kJ} \cdot \text{m}^{-2}$) of prey fish; helgrammites; age-0 and age-1 smallmouth bass; age-0, age-1, and age-2 to age-5 rock bass; and age-0, age-1 to age-3, and age-4 to age-8 flathead catfish in the New River, West Virginia. The empirical estimate of the annual rate of crayfish harvest was $0.08 \cdot \text{year}^{-1}$.

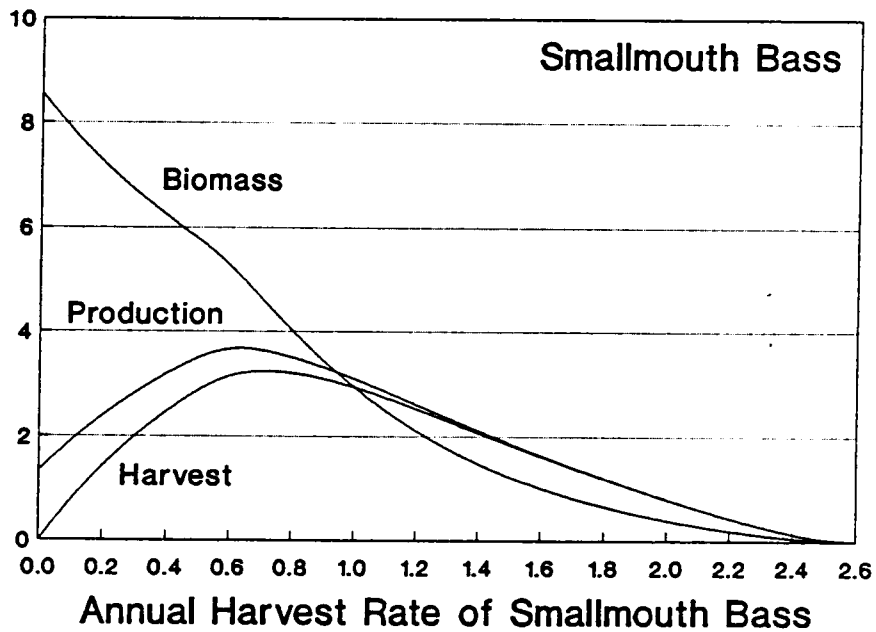
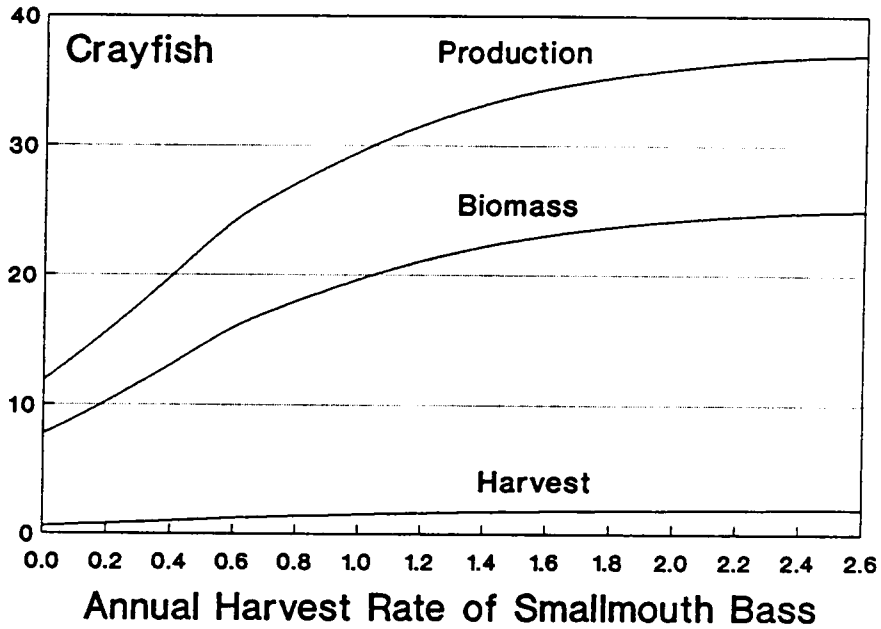


Figure 15. Model predictions of the effects of the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual mean biomass ($\text{kJ} \cdot \text{m}^{-2}$), annual production ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), and annual harvest ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) of crayfish (top) and adult smallmouth bass (bottom) in the New River, West Virginia. The empirical estimate of the annual rate of smallmouth bass harvest was $0.74 \cdot \text{year}^{-1}$.

Annual mean biomass of adult smallmouth bass declined gradually with increasing harvest rate of smallmouth bass (Figure 15). Smallmouth bass were predicted to be at near-zero biomass at harvest rates of $2.60 \cdot \text{year}^{-1}$ and greater. Biomass was 94% greater under a regime of no harvest of smallmouth bass than that estimated for initial conditions. Annual production of smallmouth bass increased from $1.3 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (no harvest of smallmouth bass) to a maximum of $3.7 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (harvest rate of $0.65 \cdot \text{year}^{-1}$), but then declined to zero at a harvest rate of $2.60 \cdot \text{year}^{-1}$. Maximum production was 2% greater than production estimated for initial conditions. Annual harvest predictions mimicked that of production, achieving a maximum value of $3.3 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ when the harvest rate was $0.70 \cdot \text{year}^{-1}$, and becoming zero at a harvest rate of $2.60 \cdot \text{year}^{-1}$. Maximum harvest was the same as that estimated for initial conditions.

The biomass of each of the other 11 components responded differently to progressively greater rates of smallmouth bass harvest (Figure 16). The components least affected were aquatic insects (< 1% decrease; not shown in Figure 16), hellgrammites (12% decrease), age-0 smallmouth bass (4% increase), age-0 rock bass (2% decrease), age-1 rock bass (6% increase), and age-0 flathead catfish (6% increase). Those components moderately affected were prey fish (49% increase) and age-1 smallmouth bass (25% increase). The most dynamic responses occurred for adult rock bass (199% increase), age-1 to age-3 flathead catfish (91% increase), and adult flathead catfish (increase from 0 to $4.6 \text{ kJ} \cdot \text{m}^{-2}$), suggesting that competition was occurring between each of these groups and adult smallmouth bass.

The third procedure involved evaluation of the effects of simultaneous changes in both the annual harvest rate of crayfish and the annual harvest rate of adult smallmouth bass on eight response variables. The response variables were the annual mean biomass, annual production, and annual harvest of crayfish and adult

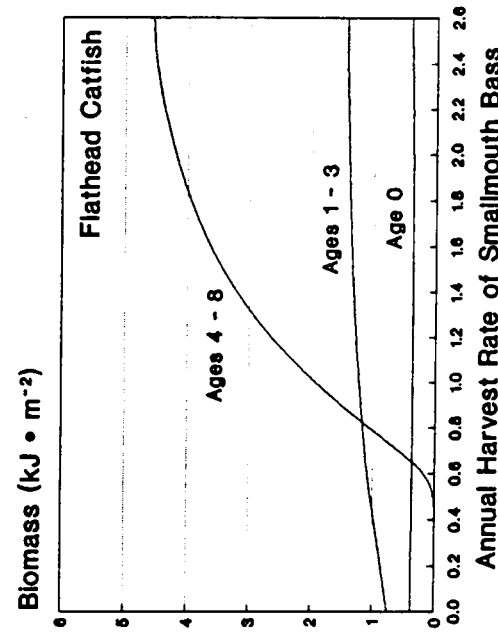
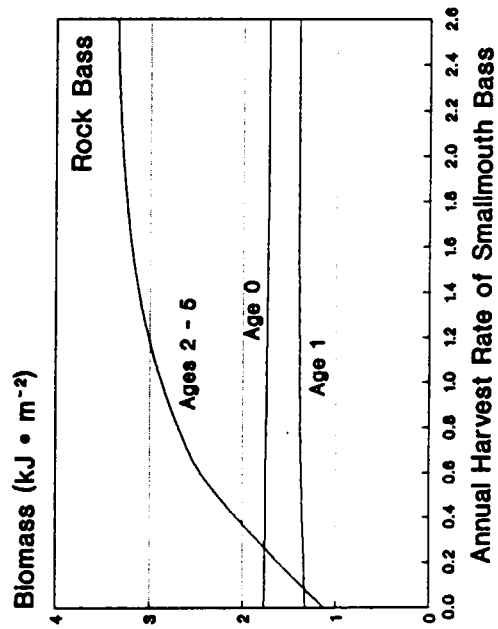
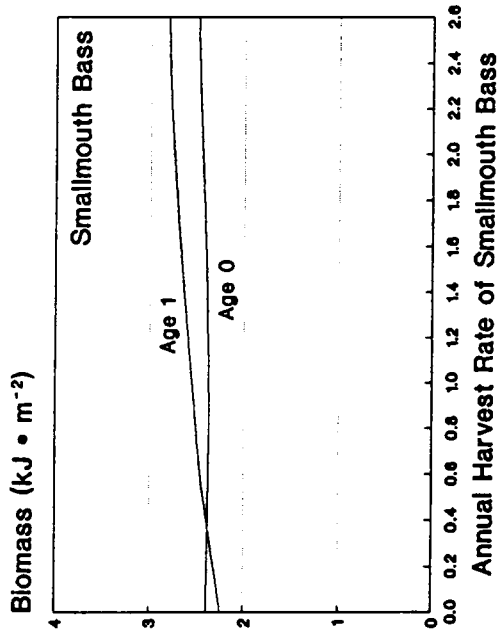
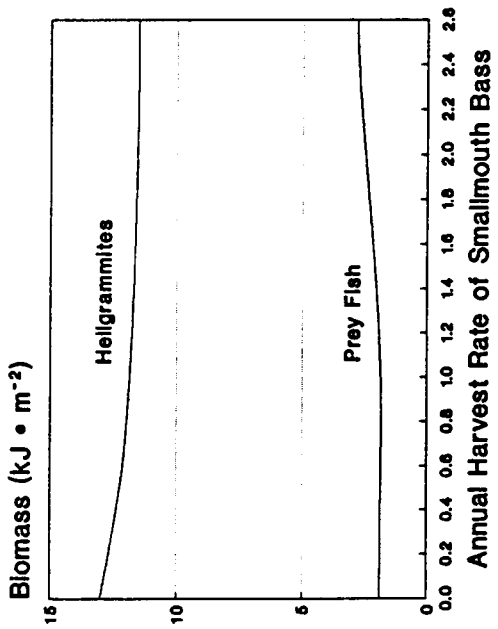


Figure 16. Model predictions of the effects of the annual harvest rate of adult smallmouth bass (year⁻¹) on the annual mean biomass (kJ • m⁻²) of prey fish; hellgrammites; age-0 and age-1 smallmouth bass; age-0, age-1, and age-2 to age-5 rock bass; and age-0, age-1 to age-3, and age-4 to age-8 flathead catfish in the New River, West Virginia. The empirical estimate of the annual rate of smallmouth bass harvest was 0.74 • year⁻¹.

smallmouth bass, and the annual mean biomass of adult rock bass and adult flathead catfish.

All eight response variables exhibited relatively dynamic relationships with crayfish harvest rate and smallmouth bass harvest rate, particularly at harvest rates of both groups between $0 \cdot \text{year}^{-1}$ and about $1.6 \cdot \text{year}^{-1}$. Crayfish production (Figure 17) and biomass responded virtually identically. The response of crayfish harvest exhibited a ridge-like configuration (Figure 18). Smallmouth bass biomass was most dynamic at low harvest rates of both crayfish and smallmouth bass (Figure 19). The responses of smallmouth bass production and harvest were similar (Figures 20 and 21, respectively), achieving their greatest values at low crayfish harvest rates and low to intermediate rates of smallmouth bass harvest. The biomass of adult rock bass (Figure 22) responded in a manner similar to that of crayfish, the primary prey of adult rock bass. The response of adult flathead catfish biomass was similar to that of adult rock bass, but was restricted to low crayfish harvest rates and intermediate to high smallmouth bass harvest rates (Figure 23).

Impacts from Reductions in Aquatic Insect Production

The biomass of each model component responded to simulated reductions in aquatic insect production in one of two patterns (Figure 24). The biomass of crayfish and adult flathead catfish responded in a dome-shaped manner. Crayfish biomass gradually increased as a direct effect of progressively lower predator biomass, which was an indirect effect of progressively lower aquatic insect biomass. The biomass of adult flathead catfish initially increased in response to increases in crayfish biomass, and then decreased as a result of prey losses associated with further re-

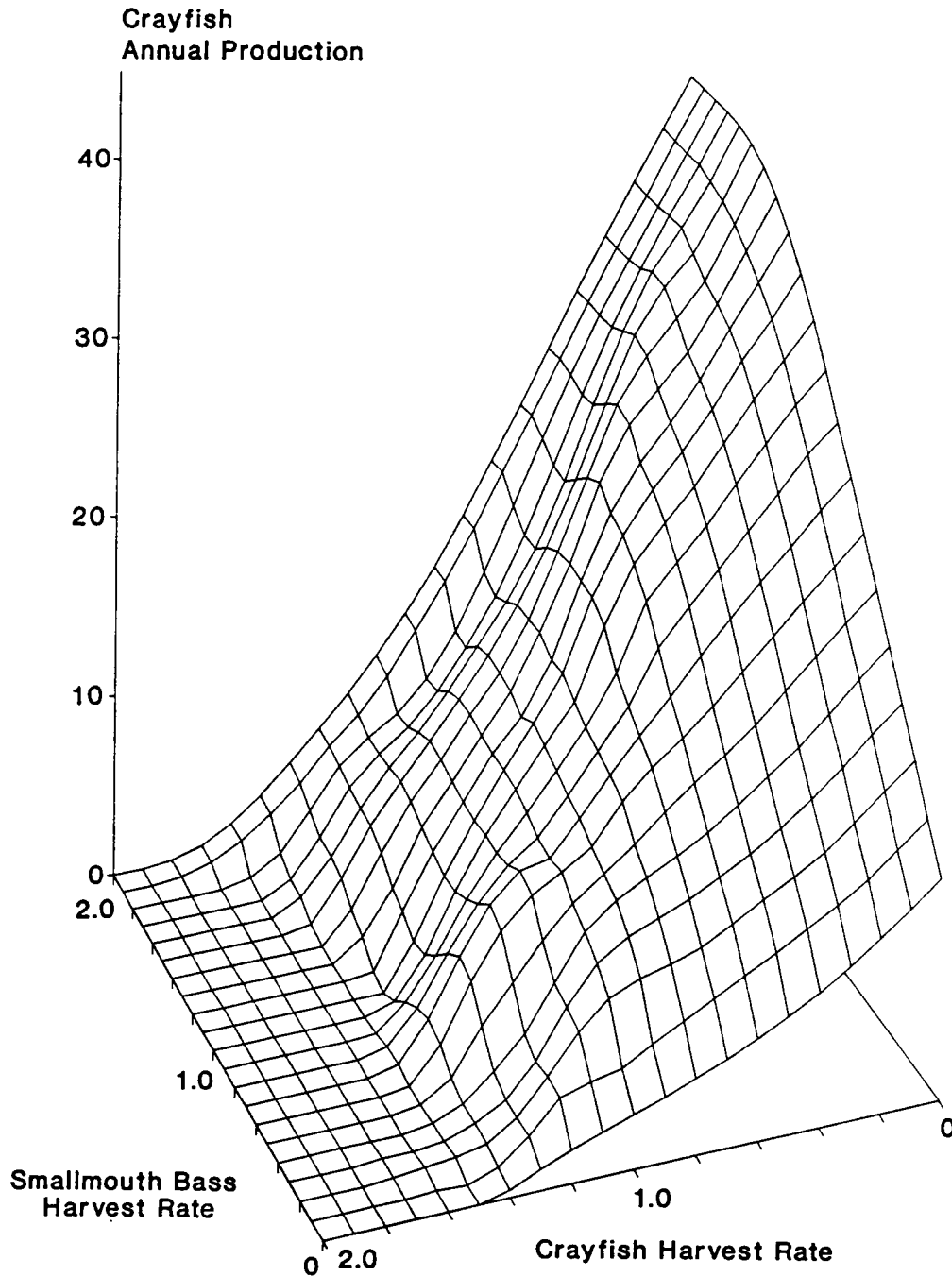


Figure 17. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) and the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual production of crayfish ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot \text{year}^{-1}$, respectively.

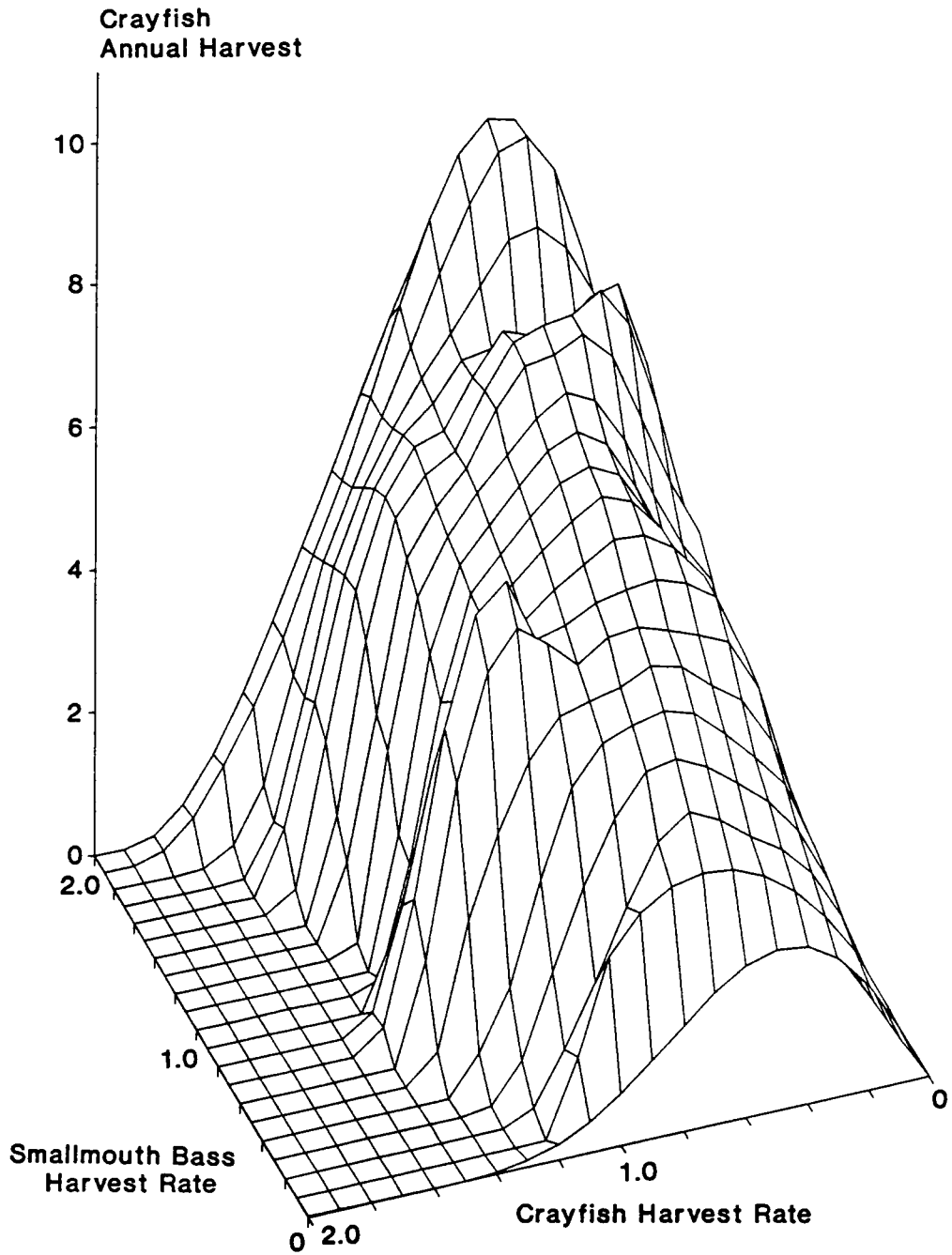


Figure 18. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) and the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual harvest of crayfish ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot \text{year}^{-1}$, respectively.

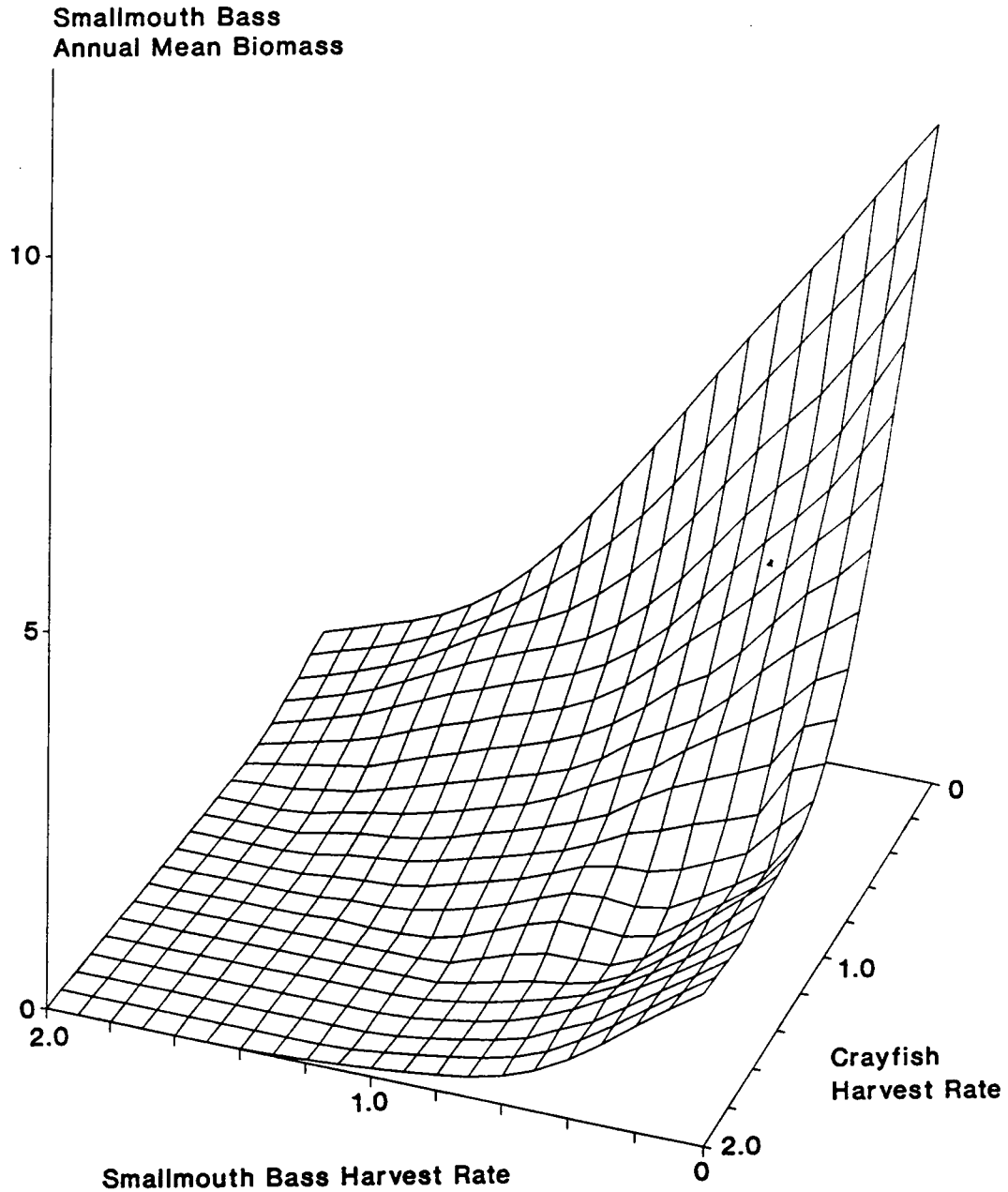


Figure 19. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) and the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual mean biomass of adult smallmouth bass ($\text{kJ} \cdot \text{m}^{-2}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot \text{year}^{-1}$, respectively.

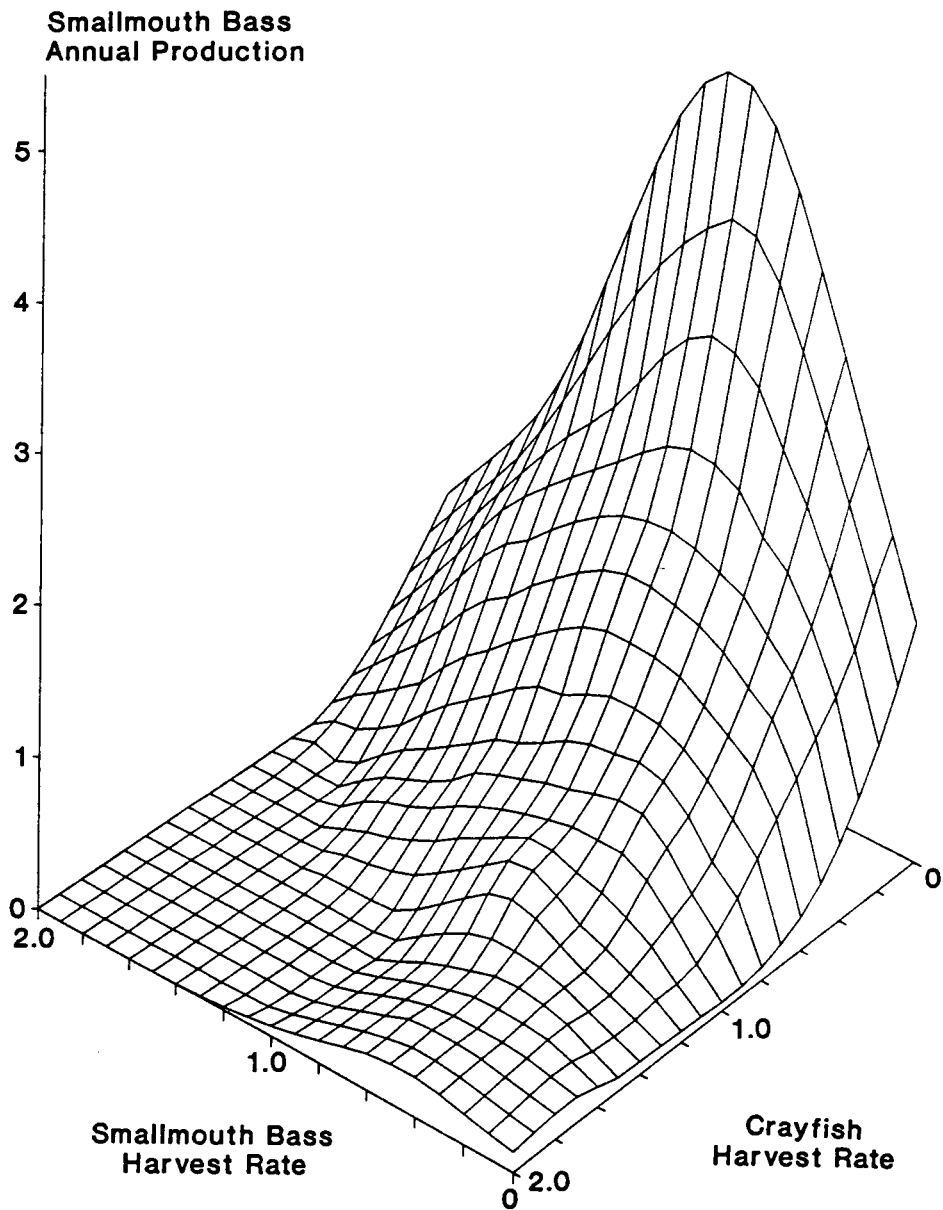


Figure 20. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) and the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual production of adult smallmouth bass ($\text{kJ} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot \text{year}^{-1}$, respectively.

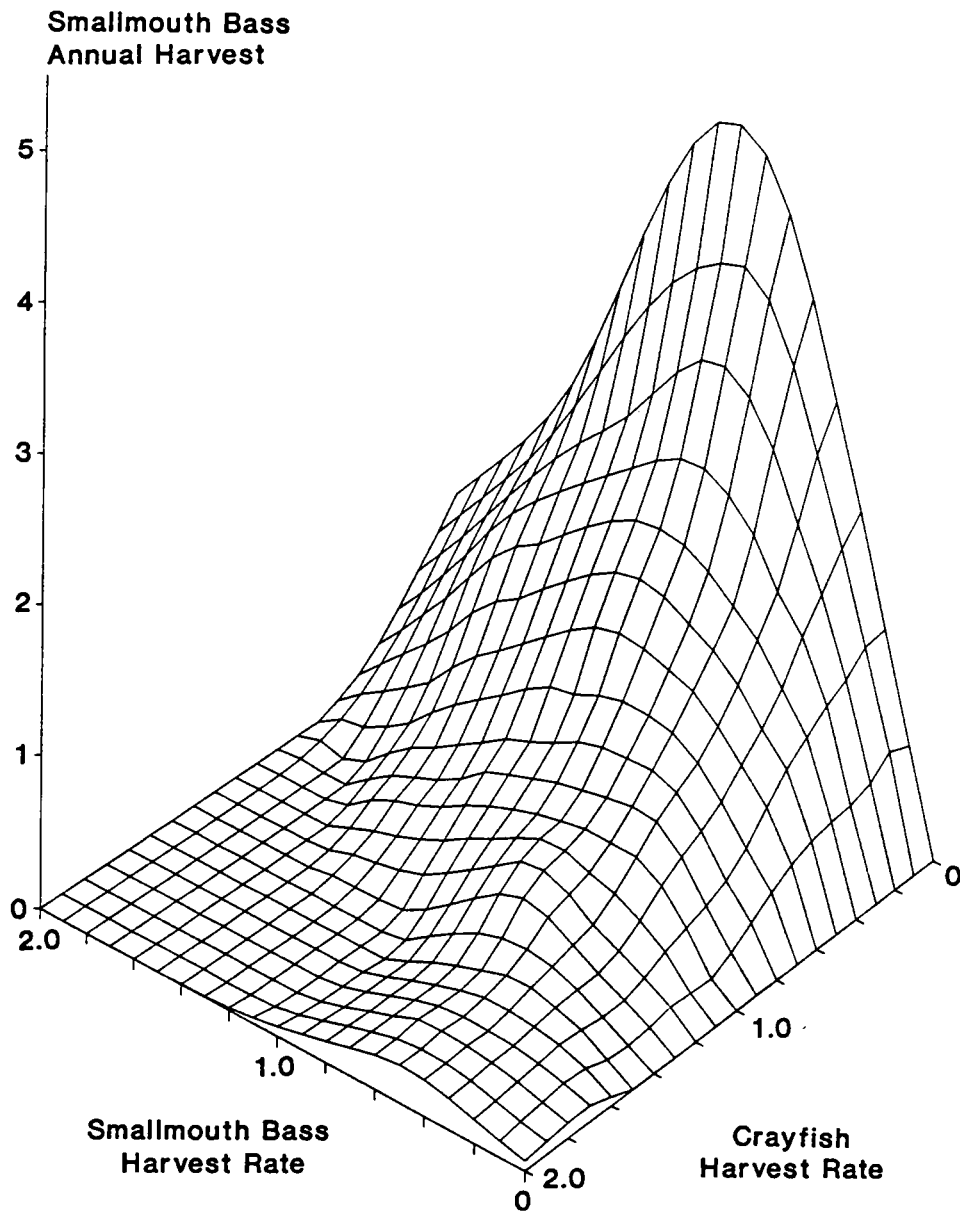


Figure 21. Model predictions of the effects of the annual harvest rate of crayfish ($year^{-1}$) and the annual harvest rate of adult smallmouth bass ($year^{-1}$) on the annual harvest of adult smallmouth bass ($kJ \cdot m^{-2} \cdot year^{-1}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot year^{-1}$, respectively.

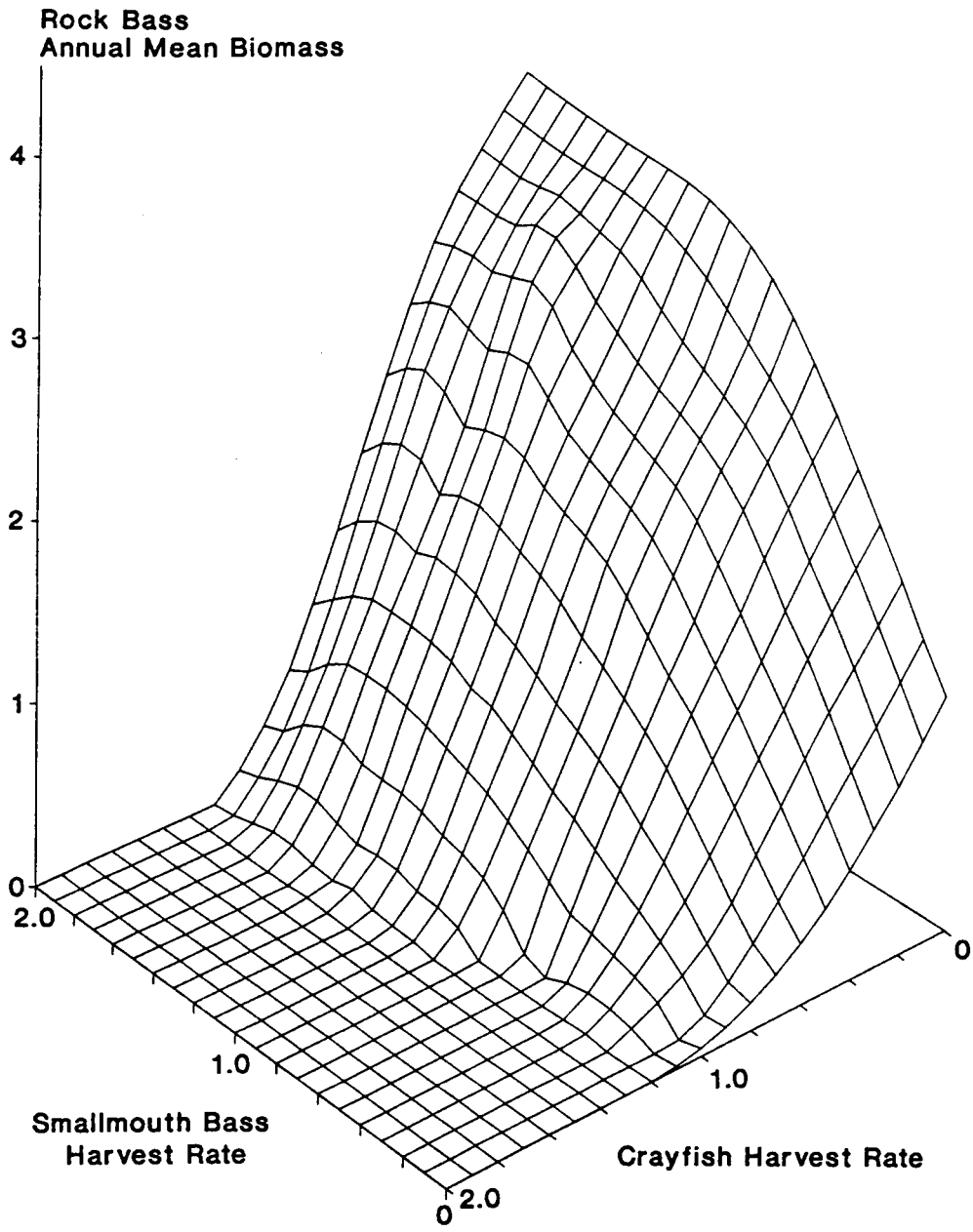


Figure 22. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) and the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual mean biomass of adult rock bass ($\text{kJ} \cdot \text{m}^{-2}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot \text{year}^{-1}$, respectively.

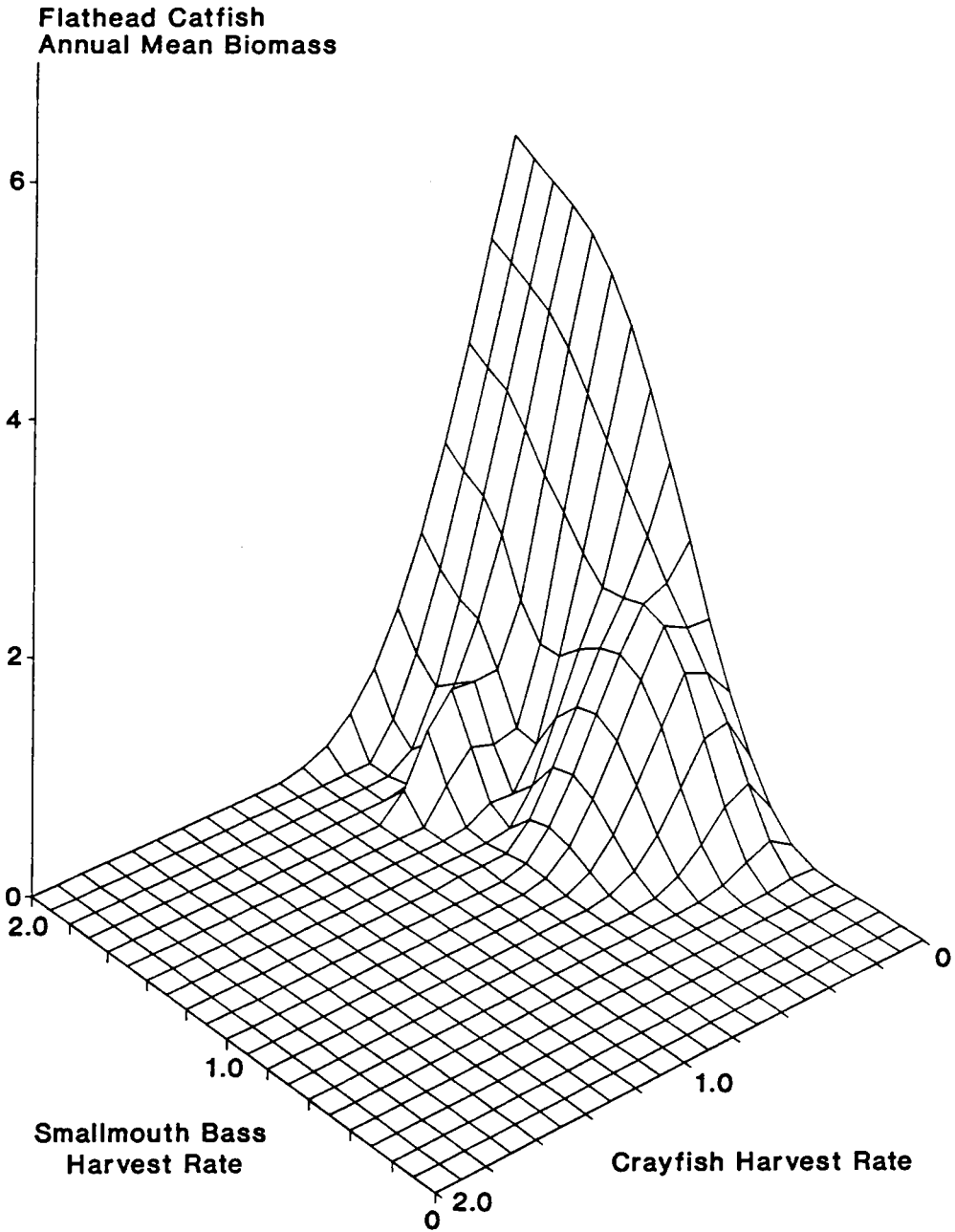


Figure 23. Model predictions of the effects of the annual harvest rate of crayfish (year^{-1}) and the annual harvest rate of adult smallmouth bass (year^{-1}) on the annual mean biomass of adult flathead catfish ($\text{kJ} \cdot \text{m}^{-2}$) in the New River, West Virginia. The empirical estimates of the annual rates of crayfish harvest and adult smallmouth bass harvest were 0.08 and $0.74 \cdot \text{year}^{-1}$, respectively.

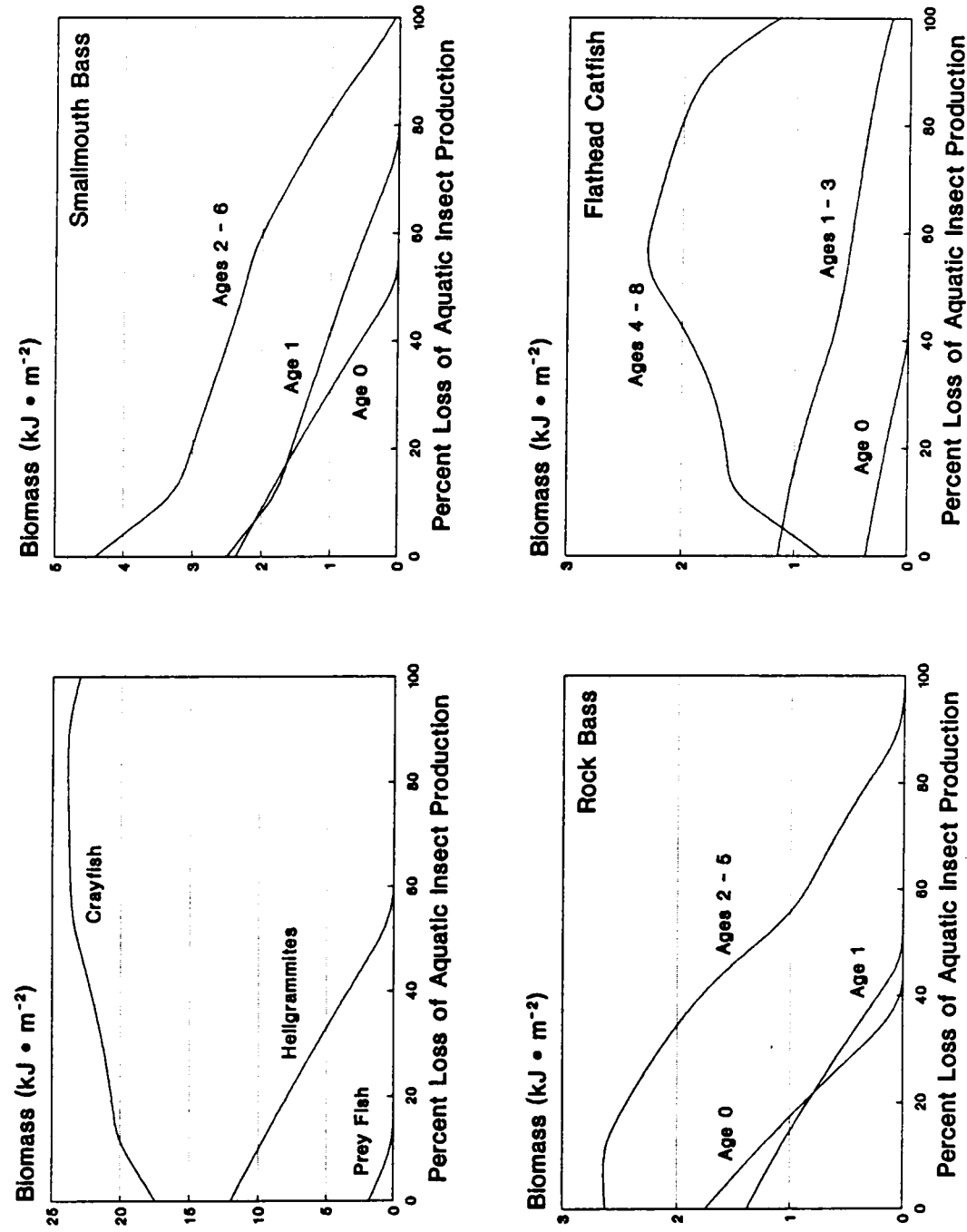


Figure 24. Model predictions of the effects of reductions in aquatic insect production (percent) on the annual mean biomass ($\text{kJ} \cdot \text{m}^{-2}$) of all other system components in the New River, West Virginia.

ductions in aquatic insects. The other ten components exhibited nearly linear decreases as an effect of diminished aquatic insect production and subsequent biomass reductions of other prey.

Discussion

An energy flow model representing key populations in the prey-predator assemblage of the New River was developed to: (1) identify the population processes that were most influential in maintaining the structure of the assemblage; (2) evaluate the direct and indirect effects of fishery exploitation; and (3) predict the impacts of black fly control on the assemblage. Model validation and analysis, system structure and function, exploitation of macroinvertebrates and predatory fishes, and the impacts of black fly control are addressed.

Model Validation

Abstraction of reality into a mathematical model necessarily involves oversimplification of states and processes to a point where model specification is achievable while maintaining reasonable system "behavior". Therefore, continual re-evaluation of the validity of a particular model from inception to completion is necessary. Model validation addresses at least four questions (Grant 1986):

1. Is the model capable of addressing the problem(s) of interest?
2. Is model structure plausible and capable of representing mechanisms (processes) of interest?

3. Does the modeled system “behave” in a reasonable manner?
4. Does the behavior of the model correspond reasonably well with real system behavior?

In meeting these criteria, even approximately, and recognizing the limitations of a model, one can be confident about the results and hypotheses generated during model use.

The first two questions about model appropriateness and model structure can be addressed simultaneously with regard to structure of the New River energy flow model. A constraint in the development of any model should be that the model is developed only to the point where it is capable (or assumed capable) of addressing explicitly-stated objectives or hypotheses. Under-specification (too simple) and over-specification (too complex) of a model is counter-productive; a compromise between holism and practicality is necessary (Sharp et al. 1983; Grant 1986). An under-specified model results in misrepresentation of observed processes and can produce potentially spurious results, but it requires less information and development time. An over-specified model may result in masking of the phenomena of interest, and it requires more information, development time, and computer resources.

In development of the New River model, strict attention was paid to recognizing only those components that directly affect prey-predator interactions among the principal predatory fishes, the exploited invertebrate prey, and other important prey. In addition, each age group of a species was not recognized as an individual component in the model, but rather particular age groups were lumped into a single component, while others were recognized as a component in their own right based on similarity and dissimilarity of diet and susceptibility to predation or exploitation. For example, the smallmouth bass population (recognized as age groups 0 through 6) was represented by three components in the model. One component represented

age-2 to age-6 smallmouth bass because age-2 and older smallmouth bass are exploited by humans and have marked differences in diet from younger smallmouth bass. Two components represented age-0 and age-1 smallmouth bass because of diet differences with not only each other but also with older bass.

All major fates of energy entering each component were accounted for: egestion, excretion, SDA, standard and activity metabolism, intraspecific regulation, predation, and harvest. Most important was the representation of the flow of energy between any two components; predation was considered to be well-represented by the DeAngelis et al. (1975) trophic interaction function. This algorithm provides for predator feeding saturation, intraspecific interference of the predator, and availability of prey. This function accords with the experimental data of Salt (1974), who quantified the trophic relationship between two protozoans. Other trophic interaction terms (Lotka 1925; Volterra 1928; Holling 1959; Watt 1959; Ivlev 1961), while similar in some respects, had important shortcomings (DeAngelis et al. 1975; Hall 1988).

At least six factors were not considered in the model: (1) allochthonous energy inputs to the system from riparian vegetation; (2) allochthonous energy inputs via terrestrial insects; (3) inputs or outputs due to immigration or emigration; (4) recruitment; (5) seasonal considerations such as temperature and discharge; and (6) system stochasticity. Allochthonous input of leaf litter from riparian vegetation is apparently not a significant source of energy to the New River biota. Although input of leaf litter was considered by (Hill 1981) to be significant in the New River, Virginia, and the Greenbrier River may supply large quantities of leaf litter to the New River in West Virginia, Voshell et al. (1987) considered leaf litter inputs to be inconsequential between Bluestone Dam and Sandstone Falls for three reasons. First, the dam limits transport of leaf litter from upstream reaches. The second reason is that the high ratio of river surface area to shoreline length results in relatively low leaf litter input.

Lastly, aquatic insects that feed on leaves (the shredder functional feeding guild) were few in number.

Allochthonous inputs as terrestrial insects were ignored. Terrestrial insects represented a small proportion of the diet of predatory fishes in the New River system (Chapter 2); there was no information about the relative importance of aquatic and terrestrial insects to non-game fishes. Given the extremely high abundance and production of aquatic insects in this system (Voshell 1985; Voshell et al. 1987, 1989), it was reasonable to assume that most insectivory involved aquatic insects. Immigration was limited to inputs from Bluestone Lake (through the dam) and from the Greenbrier River, and emigration was limited to outputs to below Sandstone Falls and upstream into the Greenbrier River. Although there is no information about inputs to and outputs from this system, other information suggests that flathead catfish may immigrate to the study reach from Bluestone Lake (Chapter 2). In the model, inputs and outputs were assumed to balance and therefore have no net effect on the annual dynamics in the system. Data insufficiencies regarding recruitment, effects of seasonality, and stochasticity of community processes precluded explicit representation of these factors in the model. Because recruitment was not modeled, simulation of the temporal trophic dynamics of successive cohorts of each species was not possible. Regardless of the above limitations and uncertainties, the model was considered useful for predicting the outcome of system trophic dynamics that occurred over a period of one year.

Analysis of the model involved hundreds of simulations with different sets of parameter values and initial conditions. The results suggested that model behavior was reasonable, because the biomass of each component usually changed in accord with intuitive expectations. Thus, when the biomass of a predator was reduced, the

biomass of prey and other predators increased. When prey biomass was reduced, all predators that were dependent on that prey exhibited biomass declines.

The most important constraint was that the model mimicked the biomass dynamics of the real system. Biomass data that was independent of that used to specify the energy flow model were not available to test model realism; model validation would require further research. Nevertheless, the model represented an integration of existing knowledge of the trophic dynamics among key components in the New River system, and remained a well-developed hypothesis. Errors from population dynamics estimation and process representation were fully recognized and certainly present in the model. Error analysis provided an assessment of the importance of errors.

Model Analysis and Future Model Refinement

Error analysis was performed on the energy flow model, and served to quantify the influence of errors in model parameters on the predictions of biomass of model components. The analysis identified the parameters that represented predation and intraspecific regulation as the most influential parameters in the model (Table 26). These parameters represented processes that were nonlinear functions of component biomass. Model parameters involved with nonlinear processes have been shown to be strongly influential to model predictions (O'Neill et al. 1980; Bartell et al. 1986). Predation-related parameters representing consumption of prey by a component were found to be most important in the model, which agrees with the findings of Gardner et al. (1980b), who conducted error analyses on six trophic interaction models (see "Predation" in the following section).

The results of error analysis are dependent on the values of parameters chosen for the model. For example, application of error analysis to a model of the pristine New River system (that is, no effects from human activities) would produce results different from those produced from the present model. Support for this argument is suggested in the current analysis. For example, parameters associated with predation on any one component were relatively unimportant to all components except crayfish (Tables 26 and 27), which exhibited strong trophic interactions with several predator components. If the trophic link between hellgrammites and predators had been stronger, parameters representing this interaction would probably have been indicated by error analysis as significant contributors to the variability of hellgrammite biomass. Thus, conclusions based on the error analysis are dependent on model specification.

Future research directed at improving model realism should focus on the parameters that represent predation and intraspecific regulation. Improved estimation of these parameters will prove difficult due to the technical problems of quantifying trophic interactions at various abundances of prey (specifically prey availability) and predator, and the difficulty of distinguishing concurrent effects from intraspecific regulation. However, simultaneous measurement of parameters that co-vary can further constrain prediction error in a model (O'Neill et al. 1980). Salt (1974) quantified the trophic interactions of two protozoans at different densities of prey and predator. Similar research on trophic interactions between vertebrate prey and predators has apparently not been done, suggesting that such endeavors with "higher" organisms are problematic.

Recruitment is an important process that was not included in the model due to the lack of knowledge concerning each population's adult-recruit relationship. Recruitment was implicitly assumed in the model to be annually constant, but

recruitment in wild fish stocks typically fluctuates from year to year as a function of several abiotic and biotic factors. Knowledge of factors that are most influential to year-class strength of populations in the New River, especially crayfish and predatory fishes, would probably improve model utility.

The stochastic nature of population parameters should be recognized when decisions are made based on the predictions of a deterministic model of biological phenomena (May et al. 1979). Knowledge of parameter variability would allow explicit evaluation of uncertainty through a risk analysis approach (Brown and Patil 1986).

System Structure and Function

Error analysis was also used to identify the most important processes involved in *maintaining* the community structure represented by the deterministic model of the New River food web. Some processes are probably more influential in particular specifications of the model than in others. For example, if the model was specified to represent the previously unexploited New River system, different processes governing maintenance of community structure might be implicated that would otherwise be less important in the exploited system (such as interspecific competition and intraspecific regulation). Transitions to another community structure can occur as a result of, for example, changes in exploitation, human-induced increases or decreases of populations, and successful introduction or elimination of species. Predation, interspecific competition, intraspecific regulation, and exploitation were the processes considered here.

Predation

Predation entails the killing of one animal by another for food (Taylor 1984), and will therefore have some definite impact, significant or not, on the maintenance or transition of community structure. Analysis of the New River food web model suggested that the predation interactions between each component (except aquatic insects) and its prey accounted for the most variability of component biomass (Table 27). Predation parameters associated with bottom-up regulation were therefore most influential in maintaining the structure of the model prey-predator assemblage. The predation interactions between each component and its predators (top-down regulation) were less influential to each component except crayfish (Table 27). Crayfish exhibited strong trophic linkage with adult predatory fishes relative to other prey (Figure 12). Gardner et al. (1980b), who evaluated each of six predation interaction models in a one prey - one predator model, reported similar results. The predator population was very sensitive to the predation interaction term (relative to other model terms), because the term defines the only energy input to the predator component. The prey population was less sensitive to the predation interaction term, because predation represented one of two possible outputs from the prey component. In the New River model, the trophic interaction term represented one of four or five possible outputs from each component, thus predation on a component was not a strong structuring agent, except to crayfish.

Simulations of progressively greater rates of crayfish harvest (Figures 13 and 14), progressively greater rates of adult smallmouth bass harvest (Figure 16), or reductions in aquatic insect production (Figure 24) demonstrated transitions in community structure that were consistent with bottom-up regulation, although only components strongly linked to either aquatic insects or crayfish showed bottom-up effects. Transitions in community structure characteristic of top-down regulation

were apparent for crayfish in simulations of progressively greater rates of adult smallmouth bass harvest (Figure 15). The role of predation in community structure transition through bottom-up and top-down effects has been demonstrated in streams. Productivity at lower trophic levels has been shown to be an influential structuring agent of higher trophic levels (bottom-up regulation: Warren et al. 1964; Hawkins and Sedell 1981; Murphy et al. 1981; Hawkins et al. 1982; Taylor and Roff 1982). Top-down regulation has also been reported (Peckarsky and Dodson 1980; Obendorfer et al. 1984; Walde and Davies 1984; Angermeier 1985; Bowlby and Roff 1986), but its effects were less pervasive. Streambed substrata (specifically gravel-cobble) presumably acted as a buffer to many fish that prey on benthic macroinvertebrates (Allan 1982; Reice 1983; Angermeier 1985; Bowlby and Roff 1986). In the pelagic communities of lakes, top-down regulation has been a major determinant of community structure transition, presumably because most trophic level components are readily accessible to consumers (Kerfoot 1987). Such cascading trophic interactions in lakes (Carpenter et al. 1985; Kerfoot 1987; Kitchell and Carpenter 1987; Mills et al. 1987) may influence up to four trophic levels (piscivores - zooplanktivores - zooplankton - phytoplankton). In the New River and perhaps many streams, cascading effects may not occur throughout the food chain (piscivores - crayfish/insectivorous fish - benthic macroinvertebrates - epilithic algae/detritus) due to high turnover rates of benthic invertebrates and/or benthic refugia for same.

Several processes (including those presented below) probably contribute to structuring of the New River prey-predator assemblage. The studies recounted above focused on or intended to implicate only one process (two in the case of Bowlby and Roff 1986). Error analysis of the New River model suggested that bottom-up regulation was the strongest process, but that top-down regulation played a lesser, al-

though notable, structuring role. Top-down effects were significant for strong interactors, namely crayfish and adult predatory fishes.

Interspecific Competition

Interspecific competition occurs when the members of two or more populations (or subgroups thereof) contend for resources with the result that the abundance of each population and/or the growth rates of members in each population are adversely affected. This mechanism probably operates on a continuum from weak or no competition (competitors coexist) to intense competition (potential elimination of one or more competitors). Assessment of interspecific competition in the New River was restricted to exploitative competition for food, because interference competition (the other realm of interspecific competition) required knowledge of the behavior of potential competitors; behavior was not observed in this research.

Error analysis of the food web model suggested that competition between a component and potential competitors for prey (other components feeding on the same prey) had a secondary role (compared to predation) in maintaining community structure. Those components feeding exclusively on aquatic insects were moderately affected by competition with each other despite the high production rate of aquatic insects. In addition, simulations of progressively greater rates of adult smallmouth bass harvest, each representative of transitions to new community structures, resulted in substantial increases in biomass of adult rock bass, age-1 to age-3 flathead catfish, and adult flathead catfish, this is consistent with the hypothesis that these predators compete with adult smallmouth bass for crayfish. Increases in biomass of these potential competitors can also be attributed to indirect effects on

other prey. However, most of these responses are probably due to increases in crayfish biomass, which was extensively preyed upon by adult smallmouth bass and other predatory fishes (Chapter 2).

Predation and exploitation can potentially affect the outcome of interspecific competition. Paine (1966), in his studies of species inhabiting rocky intertidal zones, proposed that predators maintain prey population abundances at reduced levels, and thereby diminish interspecific competition among prey populations. Competition intensity among prey species could be expected to increase if one or more predator populations were reduced in abundance (for example, through exploitation) or extirpated. Similar conclusions have been made by others (Glasser 1979; Huston 1979; Case 1982). Bowlby and Roff (1986) suggested that competition may prevail among trophically-similar organisms that are relatively free of predation.

The adult predatory fishes in the New River are in general heavily exploited, and crayfish, their principal prey, appear to be lightly exploited, thus diminishing the effect of interspecific competition among these predators. The three crayfish populations, represented as one component in the model, may exhibit intensive interspecific competition, because their principal predators are heavily exploited. The success of new crayfish species introduced to a system may depend on the predation pressure on crayfish.

Interspecific competition therefore appears to play a structuring role in the New River, depending on trophic interactions within the system and the level of exploitation of particular components. Changes in harvest regulations can be expected to alter the influence of interspecific competition.

Intraspecific Regulation

Intraspecific regulation is a density-dependent mechanism that regulates abundance within a given population. Such regulation is due to exploitative and/or interference competition among population members for limited resources, and is typically depicted as a function of the square of population abundance or biomass (Lotka 1925; Volterra 1928). Thus, regulation is weak at low abundance and strong at high abundance. Intraspecific regulation in aquatic communities may operate by predisposing population members to mortality factors such as predation, disease, or starvation, although emigration may also play an important regulatory role in some populations.

Error analysis of the New River food web model suggested that intraspecific regulation was the process that explained the most variability of aquatic insect biomass, but was secondary in importance for nine other components (Table 27). The turnover rate of aquatic insects in the New River (about $34 \cdot \text{year}^{-1}$) is substantially greater than the rate of predation on aquatic insects, so predation is probably not a strong regulatory mechanism of aquatic insect biomass. Therefore, regulatory mechanisms within the aquatic insect assemblage (interspecific competition and intraspecific regulation) may control their biomass and abundance.

Predation and exploitation can probably diminish the regulatory effect of intraspecific regulation occurring at high population abundance. This was suggested by the error analysis, especially for adult smallmouth bass and adult flathead catfish, which sustained relatively high exploitation rates, and crayfish, which experienced extensive predation from predatory fishes. Density-dependent control of mortality and fecundity in crayfish (*O. virilis*) has been documented (Momot and Gowing 1977a). Freeman et al. (1988) suggested that intraspecific competition was partly responsible for regulating population abundance of two benthic-dwelling fish species that were

relatively free of predation. Intraspecific regulation most affects populations that experience low predation and exploitation.

Exploitation

Exploitation was less important than predation, interspecific competition, and intraspecific regulation in maintaining the structure of the model food web (Table 27). This finding was expected from error analysis, because annual harvest was modeled as a linear function of biomass; parameters associated with nonlinear terms are typically more influential in a model (O'Neill et al. 1980; Bartell et al. 1986). Exploitation was of secondary importance to only adult smallmouth bass, because they sustained a high rate of harvest ($0.74 \cdot \text{year}^{-1}$).

Transition to a new community structure can occur with changes in the harvest regime of exploited populations. Changes in exploitation restructured the model New River food web in two important ways. First, harvest rate changes directly affected those components that were exploited, and, second, prey biomass ("availability") and predator biomass (predation pressure) were altered, resulting in changes to components that were directly and indirectly linked to exploited components. Crayfish, the primary prey of adult smallmouth bass, exhibited a 213% increase in biomass from a regime of no smallmouth bass harvest to one of extreme harvest (Figure 15). Potential competitors of adult smallmouth bass for food (adult rock bass, age-1 to age-3 flathead catfish, and adult flathead catfish) exhibited considerable increases in biomass as the harvest rate of smallmouth bass increased. As expected, due to the high turnover rate of aquatic insects, aquatic insects and those components highly dependent on aquatic insects as a food source were relatively unaffected by changes

in the harvest rate of smallmouth bass. An indirect effect of increases in smallmouth bass harvest rate was the decrease in hellgrammite biomass due to biomass increases of their principal predator, adult rock bass.

Changes in the annual harvest rate of crayfish had dramatic effects (Figures 13 and 14) on those predators greatly dependent on crayfish as an energy source. Adult smallmouth bass, adult rock bass, and adult flathead catfish were reduced to near-zero levels of biomass under regimes of moderate to extreme crayfish harvest. This had the indirect effect of increasing the biomass of hellgrammites, age-0 smallmouth bass, and age-0 flathead catfish, because predation pressure was eliminated. Aquatic insects and prey fish were basically unaffected owing to turnover rates that were high relative to predation pressure.

Exploitation of Macroinvertebrates and Predatory Fishes

Simulations of adult smallmouth bass harvest suggested that adult smallmouth bass were being harvested at maximum sustainable yield at the rate of $0.74 \cdot \text{year}^{-1}$ (Figure 15). May et al. (1979) suggested that maximum sustainable yield may be a useful concept for top predators that experience little natural predation. When the exploitation rate of top predators increases, their prey will increase initially (Larkin 1966; Dickie 1976), and then remain at some greater biomass that is limited by a lower predation pressure and higher intraspecific regulation (Figures 15 and 16); the reverse can presumably occur when exploitation rate of top predators is reduced.

Simulations of crayfish harvest demonstrated that management of the New River crayfish stocks for maximum sustainable yield would substantially reduce biomass, production, and harvest of adult smallmouth bass (Figure 13) and other

predators dependent on crayfish as prey (Figure 14). Several researchers (Andersen and Ursin 1977; May et al. 1979; Beddington and May 1980) have emphasized the inadequacy of applying the concept of maximum sustainable yield to populations individually (that is, in isolation of other populations within the same food web), especially if other populations were also exploited. However, even in a food web context, maximum sustainable yield is inappropriate for populations other than top predators. Organisms comprising lower trophic levels typically have higher turnover rates than those in higher trophic levels, and can therefore sustain greater rates of harvest (see "Crayfish" in Figure 13 and "Smallmouth Bass" in Figure 15). Such process rates must be considered in the development of management programs that govern multispecies fisheries (May et al. 1979).

Estimation of near-optimal harvest rates for two or more target populations in a food web is not credible without addressing the effects of changes in harvest rates for all target populations simultaneously. Further, the development of regulations governing harvest in multispecies fisheries must consider biological, social, economic, and political attributes associated with the system. The model of the New River food web predicted complex responses of biomass, production, and/or harvest of crayfish and predatory fishes to simultaneous changes in harvest rates of crayfish and smallmouth bass (Figures 17 - 23). As expected, simulations showed that the harvest rates of crayfish and adult smallmouth bass associated with maximum crayfish harvest (Figure 18) did not correspond with those associated with maximum harvest of smallmouth bass (Figure 21).

A reduction in the rate of smallmouth bass harvest would not increase total annual bass harvest (Figures 15 and 21), but a reduction in the total annual mortality rate of age-2 and older smallmouth bass could be expected, and should have two important results. First, biomass (and numbers) of smallmouth bass should increase,

providing anglers with the opportunity for higher catch rates. Second, the size distribution of the catch should become less dominated by younger (age-2 to age-3) bass, and older bass should become more prevalent. An increase in the rate of crayfish harvest to about $0.50 \cdot \text{year}^{-1}$ would approximate maximum crayfish harvest at all smallmouth bass harvest rates (Figure 18). Some of this increased harvest would be by commercial retailers, and therefore would represent more revenue for the local economy. However, prey and predator populations cannot be successfully managed concurrently for maximum sustainable yield.

The food web model predicted considerable declines in the biomasses of adult smallmouth bass, rock bass, and flathead catfish with increasing harvest rate of crayfish (Figures 13 and 14). Predicted biomasses were considerably less at the rate corresponding to maximum crayfish harvest. Other species not modeled here, but those strongly linked trophically to crayfish, would probably also exhibit notable declines. Clearly, the management of living resources in the New River must be addressed in a food web context.

Management for maximum sustainable yield typically involves only biological considerations, but social, political, and economic factors are also necessary inputs to the development of credible management programs. In 1980, the estimated number of angler trips on the New River between Bluestone Dam and Sandstone Falls was 26,848 trips (Pierce et al. 1981). The number of angler trips has probably increased since 1980, and will likely continue to increase (USFWS 1988). Assuming that the average daily expenditures per angler trip are \$23 (USFWS 1988), the estimated value of the sport fishery in the New River is at least \$618,000. Benefits from the smallmouth bass fishery should be optimized, because the revenue that enters the local economy from anglers attracted by a well-managed smallmouth bass fishery will exceed the revenue entering from bait sales. However, because commercial bait

harvest is economically important to West Virginia citizens near the New River (annual value of \$132,000; Nielsen and Orth 1988), continued low harvest of crayfish should be permitted. The benefits to the smallmouth bass fishery as a result of curtailed bait harvest would not likely be detectable given the difficulty of assessing the dynamics of riverine fish populations and the variable nature of those populations.

Living aquatic resources must be actively and properly managed to meet the demand by people for high-quality sport fishing and fishery products. In a global perspective, most aquatic food webs are presently heavily exploited, but appropriate assessment and management of these systems is in its infancy. Effective management of whole food webs will require innovative research and a greater reliance on biological aspects of fisheries in addition to political, social, and economic motivations. For the New River, integration of all appropriate resource agencies into the decision-making process should prove beneficial to the management of this unique and productive resource.

Impacts from Reductions in Aquatic Insect Production

Recent human actions concerning the control of "nuisance" organisms in the New River may have important effects on energy source and flow for aquatic biota below Bluestone Dam. In 1986 and 1988, a bacterial insecticide, *Bacillus thuringiensis israelensis* (BTI), was systematically applied to the New River below Bluestone Dam and selected tributaries to consistently eliminate black fly larvae, thereby controlling the abundance of nuisance adult black flies in the local area. Voshell (1985) estimated that the elimination of black fly larvae immediately below Bluestone Dam could reduce the annual production of the six dominant taxa of aquatic insects by about

11%. Other evidence suggested that chironomids are also killed by BTI, although likely at a higher dosage (Ali et al. 1981; Gaugler and Finney 1982; Pistrang and Burger 1984). If chironomids were also eliminated below Bluestone Dam, total production by the benthic fauna could be reduced by 69% (Voshell 1985). In 1986, a Bti treatment year, Voshell et al. (1988) reported a 53% reduction in production of these taxa compared to their production in 1983 (a non-treatment year).

Reductions in aquatic insect production, simulated with the New River food web model, demonstrated the potential for adverse impacts on the aquatic biota downstream of Bluestone Dam. A 50% reduction in aquatic insect production resulted in substantial reductions in biomass of 10 model components (Figure 24), because some groups preyed extensively on aquatic insects and/or because the prey of some groups depended on aquatic insects as a food source. In contrast, crayfish showed a gradual increase in biomass as a consequence of reduced predation pressure and a diversified diet (aquatic insects, seston, aquatic macrophytes, and periphyton). Adult flathead catfish displayed a considerable increase in biomass, because their diet was comprised of a higher proportion of crayfish than was the diet of other crayfish predators, and because competition with other predators in the system was reduced.

Model predictions are most dependent on values of parameters that represent predation in the system. This was demonstrated in the analysis of the model. Results substantially different from those reported could occur with another set of values for the predation parameters. Quantification of trophic interactions within the aquatic insect assemblage and further clarification of feeding relationships between this assemblage and other predators would facilitate evaluation of impacts of losses in aquatic insect production. Therefore, the evaluation here of such impacts should be regarded as a first approximation to real-system impacts.

This exercise demonstrated the pervasive effects that substantial reductions in aquatic insect production can have in the New River food web. The impacts of human actions involving the resources of the New River should be anticipated and addressed well before such actions occur.

Summary and Conclusions

A model representing energy flow among key components in the New River, West Virginia, between Bluestone Dam and Sandstone Falls was developed for three major purposes. The first purpose was to infer the population processes that are most influential to the maintenance and transition of community structure in the New River. Secondly, the model was used to evaluate through simulation the effects of multispecies exploitation on the prey-predator assemblage of the New River. The last purpose was to assess through simulation the impacts to the prey-predator assemblage of reductions in aquatic insect production associated with the systematic control of black fly larvae in the New River. These conclusions were developed:

1. Model parameters corresponding to predation and intraspecific regulation had the most influence on model predictions, because these parameters represented mechanisms that were modeled as nonlinear functions of component biomass. Future research to improve predictive power of the model should focus on improving the accuracy of estimation of these parameters.
2. Further development of the model should focus on improved clarification of predation relationships and intraspecific regulation in the system, and on recruitment, seasonality (especially temperature and discharge), and stochasticity of population parameters and processes.

3. Predation was the most influential agent in *maintaining* community structure; intraspecific regulation and interspecific competition had secondary roles in that regard. From the perspective of a particular population, bottom-up regulation (predation on prey) was more influential than top-down regulation (mortality caused by predators).
4. Changes in exploitation rates of populations in aquatic food webs are probably a major cause of *transitions* in community structure.
5. Moderate to large reductions in aquatic insect production will have adverse impacts on the aquatic biota below Bluestone Dam. Hellgrammites, prey fishes, and age-0 and age-1 predator fishes will be most affected.
6. Adult smallmouth bass are presently harvested at maximum sustainable yield. Harvest regulations designed to lower their fishing mortality rate are necessary if improved quality of the smallmouth bass fishery is a goal.
7. Management of crayfish harvest for maximum sustainable yield is inappropriate. Predators that are dependent on crayfish as an energy source will exhibit pronounced declines in biomass under such a management scenario.
8. Harvest regimes of populations in a community must be evaluated simultaneously in a food web context, because population-level interactions are ignored in traditional assessment procedures.
9. Benefits from the smallmouth bass fishery should be optimized in the presence of low crayfish harvest, which presently represents substantial revenue (about \$132,000). Although the effects of black fly control on the economics of the sport fishery and bait fishery are difficult to quantify, substantial losses in aquatic insect productivity will probably result in long term productivity losses of both fisheries. Such losses will translate to revenue losses in local economies.

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Appendix

Table 1. Morphometric relationships between carapace length (CL; mm), wet weight (WW; g), and chela width (CW; mm) each for *Orconectes virilis*, *Cambarus sciotensis*, and *Orconectes sanbornii sanbornii*; and between head capsule width (HCW; mm) and wet weight (WW; g) for *Corydalis cornutus* larvae from the study reach of the New River, West Virginia. $P < 0.0001$ for all regressions. MSE is mean square error.

Predictive Equation	N	R ²	MSE
<i>Orconectes virilis</i>			
$\log_{10} WW = - 3.808 + 3.156 \bullet \log_{10} CL$	40	0.95	0.014
$CL = 8.11 + 2.61 \bullet CW$	87	0.95	5.740
<i>Cambarus sciotensis</i>			
$\log_{10} WW = - 3.787 + 3.173 \bullet \log_{10} CL$	15	0.99	0.002
$CL = 8.63 + 1.90 \bullet CW$	129	0.95	4.666
<i>Orconectes sanbornii sanbornii</i>			
$\log_{10} WW = - 4.115 + 3.366 \bullet \log_{10} CL$	15	0.99	0.002
$CL = 11.93 + 1.96 \bullet CW$	97	0.79	3.222
<i>Corydalis cornutus</i>			
$\log_{10} WW = - 2.306 + 2.698 \bullet \log_{10} HCW$	45	0.89	0.044

Table 2. Length-frequency distributions of carapace lengths (CL) measured from *Orconectes virilis* that were caught in the study reach of the New River, West Virginia.

CL Midpoint (mm)	Equivalent Date ^a				
	5 May ^b	20 Jun ^c	2 Aug ^d	6 Sep ^e	12 Oct ^f
1			1		
3					
5		1			
7		11	1		
9		18	6		
11		18	21	5	
13		14	19	13	
15		5	16	22	1
17		6	18	17	3
19	3	1	19	14	3
21	1	1	21	13	5
23	3	1	20	16	2
25	2	1	12	20	8
27	2		16	16	11
29	8	2	18	23	9
31	4	2	11	28	6
33	2		10	24	2
35	4	1	11	16	2
37	2	2	8	11	4
39	1	4	3	6	2
41	2	1	7	5	
43	2	2	9	3	1
45	2		7	2	1
47	1		9	3	
49	3		8	1	1
51	3		2	3	
53			1	1	
55					
57	1	2		1	
59	1				
61				1	

^a Equivalent dates correspond to the following pooled samples: 5 May (5 May 1985), 20 Jun (26 June 1983, and 13, 14, 22, and 23 June 1985 pooled), 2 Aug (26 July and 1 August 1983, 7 and 8 August 1984, 30 and 31 July 1985, and 2 August 1985 pooled), 6 Sep (29 August 1983, and 4, 5, 6, 10, and 11 September 1985 pooled), and 12 Oct (9, 13, and 14 October 1984 pooled).

^b Age 1 is CL < 26, age 2 is 26 ≤ CL < 38, and age 3 is CL ≥ 38.

^c Age 0 is CL < 18, age 1 is 18 ≤ CL < 32, age 2 is 34 ≤ CL < 44, and age 3 is ≥ 56.

^d Age 0 is CL < 24, age 1 is 24 ≤ CL < 38, and age 2 is ≥ 38.

^e Age 0 is CL < 20, age 1 is 20 ≤ CL < 44, and age 2 is ≥ 44.

^f Age 0 is CL < 22, age 1 is 22 ≤ CL < 40, and age 2 is ≥ 42.

Table 3. Length-frequency distributions of carapace lengths (CL) measured from *Orconectes sanbornii sanbornii* that were caught in the study reach of the New River, West Virginia.

CL Midpoint (mm)	Equivalent Date ^a				
	<u>5 May</u> ^b	<u>20 Jun</u> ^c	<u>1 Aug</u> ^d	<u>7 Sep</u> ^e	<u>12 Oct</u> ^f
1					
3					
5					
7		8			
9		22	11		
11		20	45		
13		13	53		2
15			51	1	3
17			51	1	17
19		8	29	3	10
21	3	33	7	9	11
23	6	35	8	8	1
25	1	59	22	2	2
27	1	59	16	3	1
29		45	15	8	1
31		22	11	3	
33	1	14	4	2	
35		2	2		
37		1			
39			1		

^a Equivalent dates correspond to the following samples pooled: 5 May (5 May 1985), 20 Jun (26 June 1983, and 13, 14, 22, and 23 June 1985 pooled), 1 Aug (26 July 1983, 7 and 8 August 1984, 30 and 31 July 1985, and 2 August 1985 pooled), 7 Sep (4, 5, 6, 10, and 11 September 1985 pooled), and 12 Oct (9, 13, and 14 October 1984 pooled).

^b Age 1 is CL < 28 and age 2 is CL ≥ 32.

^c Age 0 is CL < 14, age 1 is 18 ≤ CL < 34, and age 2 is CL ≥ 34.

^d Age 0 is CL < 22, age 1 is 22 ≤ CL < 36, and age 2 is CL ≥ 38.

^e Age 0 is CL < 24 and age 1 is CL ≥ 24.

^f Age 0 is CL < 22 and age 1 is CL ≥ 22.

Table 4. Length-frequency distributions of carapace lengths (CL) measured from *Cambarus sciotensis* that were caught in the study reach of the New River, West Virginia.

CL Midpoint (mm)	Equivalent Date ^a			
	20 Jun ^b	3 Aug ^c	7 Sep ^d	12 Oct ^e
1				
3				1
5				42
7				3
9				
11	8			
13	33			
15	92	5	3	
17	57	16	14	
19	15	19	38	2
21	1	3	59	7
23		10	48	12
25		2	23	12
27	3	7	11	2
29	8	8	14	3
31	5	3	10	5
33	14	7	16	9
35	15	6	18	11
37	16	5	20	11
39	12	1	10	8
41	6	4	7	9
43	8	5	2	4
45	3	2		
47	1	1	1	
49	1			1

^aEquivalent dates correspond to the following samples pooled: 20 Jun (26 June 1983, and 13, 14, 22, and 23 June 1985 pooled), 3 Aug (7 and 8 August 1984, 30 and 31 July 1985, and 2 August 1985 pooled), 7 Sep (4, 5, 6, 10, and 11 September 1985 pooled), and 12 Oct (9, 13, and 14 October 1984 pooled).

^bAge 1 is CL < 20, age 2 is 20 ≤ CL < 30, and age 3 is ≥ 30.

^cAge 1 is CL < 24, age 2 is 24 ≤ CL < 38, and age 3 is ≥ 38.

^dAge 1 is CL < 30, age 2 is 30 ≤ CL < 44, and age 3 is ≥ 46.

^eAge 0 is CL < 8, age 1 is 8 ≤ CL < 26, age 2 is 26 ≤ CL < 44, and age 3 ≥ 48.

Table 5. Length-frequency distributions of head capsule widths (HCW) measured from *Corydalis cornutus* larvae that were caught in riffles near Brooks Pool of the New River, West Virginia.

HCW Midpoint (mm)	Equivalent Date ^a				
	19 Jun ^b	30 Jul ^c	8 Aug ^d	1 Sep ^e	14 Oct ^f
1.125				4	1
1.875				8	10
2.625	3		1	10	12
3.375	14		6	1	8
4.125	15		5	5	2
4.875	8	1	20	2	1
5.625	6	1	25	8	6
6.375	7	2	12	13	10
7.125	8	1	18	25	28
7.875	15	8	13	14	17
8.625	22	8	9	10	7
9.375	30	12	3	17	11
10.125	14	9	3	14	7
10.875	10	4	1	17	
11.625		4	2	8	1

^a Equivalent dates correspond to the following pooled samples: 19 Jun (14 and 23 June 1985 pooled), 30 Jul (30 July 1985), 8 Aug (8 August 1985), 1 Sep (29 August 1983 and 4 September 1985 pooled), and 14 Oct (14 October 1985).

^b Age 1 is HCW < 5.625 and age 2 is HCW ≥ 5.625.

^c Age 1 is HCW < 7.125 and age 2 is HCW ≥ 7.125.

^d Age 1 is HCW < 10.875 and age 2 is HCW ≥ 10.875.

^e Age 0 is HCW < 3.375 and age 1 is HCW ≥ 3.375.

^f Age 0 is HCW < 4.875 and age 1 is HCW ≥ 4.875.

Table 6. Site-specific information and iteratively-fit values of P used to estimate the annual consumption by smallmouth bass. Abundance is that in Brooks Pool.

Age/Cohort	Days Represented ¹	Starting Weight (g)	Final Weight (g)	Starting Abundance	Daily Mortality Rate	P
0	1 - 175	1	15	109993	0.0062731	0.21929
	176 - 294	15	13	36568	0.0062731	0.09647
	295 - 365	13	15	17293	0.0062731	0.16244
1	1 - 175	15	85	11062	0.0033351	0.25232
	176 - 294	85	78	6165	0.0033351	0.06527
	295 - 365	78	85	4143	0.0033351	0.14344
2	1 - 175	85	199	3268	0.0033351	0.24661
	176 - 294	199	188	1821	0.0033351	0.11724
	295 - 365	188	199	1224	0.0033351	0.16119
3	1 - 175	199	381	967	0.0033351	0.26886
	176 - 294	381	364	539	0.0033351	0.11364
	295 - 365	364	381	362	0.0033351	0.17755
4	1 - 175	381	719	286	0.0033351	0.29839
	176 - 294	719	693	159	0.0033351	0.10507
	295 - 365	693	719	107	0.0033351	0.17468
5	1 - 175	719	1198	84	0.0033351	0.29038
	176 - 294	1198	1162	47	0.0033351	0.10000
	295 - 365	1162	1198	31	0.0033351	0.17176
6	1 - 175	1198	1781	25	0.0033351	0.27076
	176 - 294	1781	1734	14	0.0033351	0.10000
	295 - 365	1734	1781	9	0.0033351	0.17000

¹ Day 1 is 1 June, the day of annulus formation; Day 176 is 23 November, the day water temperature drops below 10 °C; Day 295 is 22 March, the day water temperature equals or rises above 10 °C.

Table 7. Site-specific information and iteratively-fit values of P used to estimate the annual consumption by rock bass. Abundance is that in Brooks Pool.

Age/Cohort	Days Represented ¹	Starting Weight (g)	Final Weight (g)	Starting Abundance	Daily Mortality Rate	P
0	29 - 175	1	5	242589	0.0082075	0.24861
	176 - 294	5	3.6	72232	0.0082075	0.20716
	295 - 365	3.6	5	27090	0.0082075	0.27965
1	1 - 175	5	34	15090	0.0030546	0.31015
	176 - 294	34	26	8834	0.0030546	0.26131
	295 - 365	26	34	6139	0.0030546	0.32106
2	1 - 175	34	103	4940	0.0030546	0.37189
	176 - 294	103	84	2892	0.0030546	0.33400
	295 - 365	84	103	2010	0.0030546	0.41156
3	1 - 175	103	186	1620	0.0047017	0.37986
	176 - 294	186	156	710	0.0047017	0.37821
	295 - 365	156	186	405	0.0047017	0.47729
4	1 - 175	186	256	290	0.0047017	0.34722
	176 - 294	256	217	127	0.0047017	0.38371
	295 - 365	217	256	73	0.0047017	0.48879
5	1 - 175	256	290	52	0.0047017	0.31369
	176 - 294	290	247	23	0.0047017	0.39165
	295 - 365	247	290	13	0.0047017	0.49254

¹ Day 1 is 1 June, the day of annulus formation; Day 176 is 23 November, the day water temperature drops below 10 °C; Day 295 is 22 March, the day water temperature equals or rises above 10 °C.

Table 8. Site-specific information and iteratively-fit values of P used to estimate the annual consumption by flathead catfish. Abundance is that in Brooks Pool.

Age/Cohort	Days Represented ¹	Starting Weight (g)	Final Weight (g)	Starting Abundance	Daily Mortality Rate	P
0	50 - 161	1	8	29409	0.0082075	0.30656
	162 - 280	8	6.6	11685	0.0082075	0.14363
	281 - 365	6.6	8	4382	0.0082075	0.16125
1	1 - 161	8	42	2175	0.0022400	0.22807
	162 - 280	42	38	1516	0.0022400	0.16916
	281 - 365	38	42	1161	0.0022400	0.12487
2	1 - 161	42	115	959	0.0022400	0.23746
	162 - 280	115	105	668	0.0022400	0.11650
	281 - 365	105	115	512	0.0022400	0.14920
3	1 - 161	115	255	423	0.0022400	0.20855
	162 - 280	255	239	295	0.0022400	0.11000
	281 - 365	239	255	226	0.0022400	0.12403
4	1 - 161	255	420	187	0.0022400	0.16693
	162 - 280	420	400	130	0.0022400	0.10000
	281 - 365	400	420	100	0.0022400	0.11317
5	1 - 161	420	617	82	0.0022400	0.16132
	162 - 280	617	590	57	0.0022400	0.10806
	281 - 365	590	617	44	0.0022400	0.11836
6	1 - 161	617	810	36	0.0022400	0.13639
	162 - 280	810	776	25	0.0022400	0.09352
	281 - 365	776	810	19	0.0022400	0.11508
7	1 - 161	810	962	15	0.0022400	0.11178
	162 - 280	962	924	10	0.0022400	0.09000
	281 - 365	924	962	8	0.0022400	0.11193
8	1 - 161	962	1034	7	0.0022400	0.08591
	162 - 280	1034	994	5	0.0022400	0.09000
	281 - 365	994	1034	4	0.0022400	0.11079

¹ Day 1 is 15 June, the day of annulus formation; Day 162 is 23 November, the day water temperature drops below 10 °C; Day 281 is 22 March, the day water temperature equals or rises above 10 °C.

Table 9. Mean lengths-at-annulus (and associated information) of smallmouth bass from Brooks Pool of the New River, West Virginia. (Data from 1984 and 1985 were pooled.)

<u>Annulus</u>	<u>N</u>	<u>Mean (mm)</u>	<u>Standard Deviation</u>	<u>Minimum Value</u>	<u>Maximum Value</u>
1	661	106	16	65	160
2	396	190	16	115	230
3	176	252	20	182	334
4	52	313	29	247	391
5	15	387	42	311	446
6	5	459	34	400	481
7	2	524	17	511	536
8	1	548	-	548	548

Table 10. Mean lengths-at-annulus (and associated information) of rock bass from Brooks Pool of the New River, West Virginia. (Data from 1984 and 1985 were pooled.)

<u>Annulus</u>	<u>N</u>	<u>Mean (mm)</u>	<u>Standard Deviation</u>	<u>Minimum Value</u>	<u>Maximum Value</u>
1	825	63	9	38	107
2	687	119	14	79	219
3	275	172	16	135	206
4	65	209	14	173	234
5	21	232	10	211	250
6	10	242	11	223	264

Table 11. Mean lengths-at-annulus (and associated information) of flathead catfish from Brooks Pool of the New River, West Virginia. (Data from 1984 and 1985 were pooled.)

<u>Annulus</u>	<u>N</u>	<u>Mean (mm)</u>	<u>Standard Deviation</u>	<u>Minimum Value</u>	<u>Maximum Value</u>
1	374	98	17	55	206
2	357	166	27	77	313
3	277	231	31	152	382
4	169	299	37	216	454
5	75	352	47	253	533
6	41	399	53	331	594
7	25	436	69	355	662
8	12	461	47	407	546
9	5	472	52	438	563
10	4	511	63	470	605
11	1	534	-	534	534

Table 12. Length-weight equations and seasonal von Bertalanffy growth equations for smallmouth bass, rock bass, and flathead catfish caught from Brooks Pool of the New River, West Virginia, in 1984 and 1985.

Predictive Equation	N	R ²	Mean Square Error
Smallmouth Bass			
1984 : $\log_{10} W = - 4.859 + 2.979 \cdot \log_{10} L$	566	0.989	0.00330
1985 : $\log_{10} W = - 4.993 + 3.040 \cdot \log_{10} L$	165	0.994	0.00159
All : $\log_{10} W = - 4.891 + 2.994 \cdot \log_{10} L$	731	0.990	0.00293
Growth : $L_t = 2600 \cdot (1 - e^{-0.0287 \cdot (t+0.7082)+0.0087 \cdot \sin(8.2832 \cdot (t-0.8498))})$	18	-	37.09290
Rock Bass			
1984 : $\log_{10} W = - 4.775 + 3.035 \cdot \log_{10} L$	659	0.992	0.00111
1985 : $\log_{10} W = - 4.722 + 3.016 \cdot \log_{10} L$	263	0.991	0.00150
All : $\log_{10} W = - 4.766 + 3.033 \cdot \log_{10} L$	922	0.992	0.00126
Growth : $L_t = 320 \cdot (1 - e^{-0.2618 \cdot (t)+0.1279 \cdot \sin(8.2832 \cdot (t-0.5448))})$	20	-	24.71080
Flathead Catfish			
1984 : $\log_{10} W = - 5.118 + 3.040 \cdot \log_{10} L$	271	0.994	0.00177
1985 : $\log_{10} W = - 5.340 + 3.128 \cdot \log_{10} L$	145	0.997	0.00090
All : $\log_{10} W = - 5.188 + 3.068 \cdot \log_{10} L$	416	0.995	0.00154

Table 13. The proportion of preserved wet weight of each prey type in the diet of smallmouth bass that were caught in Brooks Pool of the New River, West Virginia.

Age/Cohort ¹	Days Represented ²	Wet Weight Proportion by Prey Type			
		Crayfish	Hellgrammites	Insects	Fish
0	1 - 365	0	0	1.0000	0
1	1 - 175	0.2125	0	0.6291	0.1584
	176 - 294	0	0	0.8000	0.2000
	295 - 365	0.2125	0	0.6291	0.1584
2	1 - 175	0.5934	0.0038	0.2107	0.1921
	176 - 294	0	0	0.5000	0.5000
	295 - 365	0.5934	0.0038	0.2107	0.1921
3	1 - 175	0.8909	0.0016	0.0379	0.0696
	176 - 294	0	0	0.3500	0.6500
	295 - 365	0.8909	0.0016	0.0379	0.0696
4	1 - 175	0.8909	0.0016	0.0379	0.0696
	176 - 294	0	0	0.3500	0.6500
	295 - 365	0.8909	0.0016	0.0379	0.0696
5	1 - 175	0.8909	0.0016	0.0379	0.0696
	176 - 294	0	0	0.3500	0.6500
	295 - 365	0.8909	0.0016	0.0379	0.0696
6	1 - 175	0.8909	0.0016	0.0379	0.0696
	176 - 294	0	0	0.3500	0.6500
	295 - 365	0.8909	0.0016	0.0379	0.0696

¹ Approximately 40 age 0, 97 age 1, 128 age 2, 22 age 3, 11 age 4, 6 age 5, and 2 age 6 fish contained diet items.

² Day 1 is 1 June, the day of annulus formation; day 176 is 23 November, the day water temperature drops below 10 °C; day 295 is 22 March, the day water temperature equals or rises above 10 °C.

Table 14. The proportion of preserved wet weight of each prey type in the diet of rock bass that were caught in Brooks Pool of the New River, West Virginia.

Age/Cohort ¹	Days Represented ²	Wet Weight Proportion by Prey Type			
		Crayfish	Hellgrammites	Insects	Fish
0	1 - 365	0	0	1.0000	0
1	1 - 175	0.0500	0	0.9500	0
	176 - 294	0	0	1.0000	0
	295 - 365	0.0500	0	0.9500	0
2	1 - 175	0.5606	0.1237	0.3153	0.0004
	176 - 294	0	0	1.0000	0
	295 - 365	0.5606	0.1237	0.3153	0.0004
3	1 - 175	0.8105	0.1203	0.0692	0
	176 - 294	0	0	1.0000	0
	295 - 365	0.8105	0.1203	0.0692	0
4	1 - 175	0.8105	0.1203	0.0692	0
	176 - 294	0	0	1.0000	0
	295 - 365	0.8105	0.1203	0.0692	0
5	1 - 175	0.8105	0.1203	0.0692	0
	176 - 294	0	0	1.0000	0
	295 - 365	0.8105	0.1203	0.0692	0

¹ Approximately 40 age 0, 20 age 1, 163 age 2, 40 age 3, 17 age 4, and 4 age 5 fish contained diet items.

² Day 1 is 1 June, the day of annulus formation; day 176 is 23 November, the day water temperature drops below 10 °C; day 295 is 22 March, the day water temperature equals or rises above 10 °C.

Table 15. The proportion of preserved wet weight of each prey type in the diet of flathead catfish that were caught in Brooks Pool of the New River, West Virginia.

Age/Cohort ¹	Days Represented ²	Wet Weight Proportion by Prey Type			
		Crayfish	Hellgrammites	Insects	Fish
0	1 - 365	0	0	1.0000	0
1	1 - 161	0.2000	0	0.7000	0.1000
	162 - 280	0	0	0.8750	0.1250
	281 - 365	0.2000	0	0.7000	0.1000
2	1 - 161	0.7295	0.0336	0.0109	0.2260
	162 - 280	0	0	0.0460	0.9540
	281 - 365	0.7295	0.0336	0.0109	0.2260
3	1 - 161	0.7005	0.0848	0.0340	0.1807
	162 - 280	0	0	0.1584	0.8416
	281 - 365	0.7005	0.0848	0.0340	0.1807
4	1 - 161	0.7910	0.0065	0.1641	0.0384
	162 - 280	0	0	0.8104	0.1896
	281 - 365	0.7910	0.0065	0.1641	0.0384
5	1 - 161	0.9768	0	0	0.0232
	162 - 280	0	0	0	1.0000
	281 - 365	0.9768	0	0	0.0232
6	1 - 161	0.9768	0	0	0.0232
	162 - 280	0	0	0	1.0000
	281 - 365	0.9768	0	0	0.0232
7	1 - 161	0.9768	0	0	0.0232
	162 - 280	0	0	0	1.0000
	281 - 365	0.9768	0	0	0.0232
8	1 - 161	0.9768	0	0	0.0232
	162 - 280	0	0	0	1.0000
	281 - 365	0.9768	0	0	0.0232

¹ No age 0, 1 age 1, 33 age 2, 31 age 3, 29 age 4, 7 age 5, 3 age 6, 4 age 7, and no age 8 fish contained diet items.

² Day 1 is 15 June, the day of annulus formation; day 162 is 23 November, the day water temperature drops below 10 °C; day 281 is 22 March, the day water temperature equals or rises above 10 °C.

Table 16. Mean water temperatures (°C) used in the bioenergetics models to estimate the annual consumption by smallmouth bass, rock bass, and flathead catfish in Brooks Pool of the New River, West Virginia.

Date	Day for Smallmouth Bass and Rock Bass	Mean Temperature	Day for Flathead Catfish	Mean Temperature ¹
1 Jun	1	20.8		
15 Jun	15	23.7	1	23.7
22 Jun	22	23.2	8	23.2
29 Jun	29	24.1	15	24.1
6 Jul	36	24.1	22	24.1
20 Jul	50	26.0	36	26.0
31 Aug	92	26.0	78	26.0
7 Sep	99	25.0	85	25.0
14 Sep	106	24.5	92	24.5
28 Sep	120	20.1	106	20.1
5 Oct	127	17.9	113	17.9
19 Oct	141	16.2	127	16.2
26 Oct	148	16.1	134	16.1
2 Nov	155	15.0	141	15.0
16 Nov	169	10.5	155	10.5
23 Nov	176	9.8	162	9.8
7 Dec	190	8.0	176	8.0
11 Dec			180	6.4
14 Dec	197	5.2	183	6.4
4 Jan	218	5.3	204	6.4
11 Jan	225	2.8	211	6.4
18 Jan	232	2.0	218	6.4
15 Feb	260	1.8	246	6.4
22 Feb	267	3.8	253	6.4
1 Mar	274	4.3	260	6.4
7 Mar			266	6.4
8 Mar	281	6.8	267	6.8
15 Mar	288	7.3	274	7.3
22 Mar	295	10.3	281	10.3
29 Mar	302	9.0	288	9.0
5 Apr	309	12.9	295	12.9
12 Apr	316	12.6	302	12.6
26 Apr	330	14.8	316	14.8
3 May	337	15.5	323	15.5
10 May	344	17.2	330	17.2
17 May	351	17.5	337	17.5
24 May	358	18.6	344	18.6
31 May	365	20.1	351	20.1
1 Jun			352	20.8
7 Jun			358	22.1
14 Jun			365	23.5

¹ For flathead catfish, a constant temperature of 6.4 °C was assumed for Days 180 to 266 due to computing problems.

Table 17. Modified Schnabel estimates of abundance of smallmouth bass living in Brooks Pool of the New River, West Virginia, in 1984. (Column heading notation from Ricker 1975.)

Period ¹	C_t	R_t	m	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	ΣR_t	\hat{N}	95% CI
Age I									
1	79	-	79	-	-	-	-	-	-
2	176	2	147	79	13904	13904	2	4635	-
3	290	16	259	226	65540	79444	18	4181	-
4	84	10	69	485	40740	120184	28	4144	[2903,6132]
Age II									
1	67	-	67	-	-	-	-	-	-
2	85	2	81	67	5695	5695	2	1898	-
3	63	1	62	148	9324	15019	3	3755	-
4	39	2	37	210	8190	23209	5	3868	[1827,8927]
Age III									
1	33	-	33	-	-	-	-	-	-
2	38	1	37	33	1254	1254	1	627	-
3	32	2	30	70	2240	3494	3	874	-
4	13	1	12	100	1300	4794	4	959	[428,2397]

¹ Capture period 1 was 13 June to 15 June, period 2 was 18 June to 22 June, period 3 was 26 June to 29 June, and period 4 was 10 July to 12 July.

Table 18. Modified Schnabel estimates of abundance of smallmouth bass living in Brooks Pool of the New River, West Virginia, in 1985. (Column heading notation from Ricker 1975.)

Period ¹	C_t	R_t	m	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	ΣR_t	\hat{N}	95% CI
Age I									
1	171	-	171	-	-	-	-	-	-
2	109	10	99	171	18639	18639	10	1694	-
3	70	8	62	270	18900	37539	18	1976	-
4	96	11	85	332	31872	69411	29	2314	[1629,3403]
Age II									
1	175	-	175	-	-	-	-	-	-
2	46	6	40	175	8050	8050	6	1150	-
3	69	10	59	215	14835	22885	16	1346	-
4	95	8	87	302	28690	51575	24	2063	[1409,3145]
Age III									
1	35	-	35	-	-	-	-	-	-
2	12	0	12	35	420	420	0	420	-
3	13	1	12	47	611	1031	1	516	-
4	23	1	22	59	1357	2388	2	796	[291,1990]

¹ Capture period 1 was 18 June to 27 June, period 2 was 2 July to 4 July, period 3 was 9 July to 12 July, and period 4 was 13 July to 17 July.

Table 19. Modified Schnabel estimates of abundance of rock bass living in Brooks Pool of the New River, West Virginia, in 1984. (Column heading notation from Ricker 1975.)

Period ¹	C_t	R_t	m	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	ΣR_t	\hat{N}	95% CI
Age I									
1	5	-	5	-	-	-	-	-	-
2	92	0	82	5	460	460	0	460	-
3	95	1	91	87	8265	8725	1	4363	-
4	17	1	16	178	3026	11751	2	3917	[1433,9793]
Age II									
1	73	-	73	-	-	-	-	-	-
2	331	2	328	73	24163	24163	2	8054	-
3	262	23	239	401	105062	129225	25	4970	-
4	152	20	130	640	97280	226505	45	4924	[3701,6701]
Age III									
1	73	-	73	-	-	-	-	-	-
2	107	2	105	73	7811	7811	2	2604	-
3	81	11	70	178	14418	22229	13	1588	-
4	80	10	70	248	19840	42069	23	1753	[1188,2697]
Age IV									
1	6	-	6	-	-	-	-	-	-
2	9	0	9	6	54	54	0	54	-
3	6	0	6	15	90	144	0	144	-
4	6	2	4	21	126	270	2	90	[33,225]

¹ Capture period 1 was 13 June to 15 June, period 2 was 18 June to 22 June, period 3 was 26 June to 29 June, and period 4 was 10 July to 12 July.

Table 20. Modified Schnabel estimates of abundance of rock bass living in Brooks Pool of the New River, West Virginia, in 1985. (Column heading notation from Ricker 1975.)

Period ¹	C_t	R_t	m	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	ΣR_t	\hat{N}	95% CI
Age I									
1	129	-	129	-	-	-	-	-	-
2	213	12	201	129	27477	27477	12	2114	-
3	296	55	241	330	97680	125157	67	1841	-
4	212	45	167	571	121052	246209	112	2179	[1813,2616]
Age II									
1	388	-	388	-	-	-	-	-	-
2	348	25	323	388	135024	135024	25	5193	-
3	477	81	396	711	339147	474171	106	4432	-
4	295	89	206	1107	326565	800736	195	4085	[3553,4696]
Age III									
1	139	-	139	-	-	-	-	-	-
2	89	10	79	139	12371	12371	10	1125	-
3	118	26	92	218	25724	38095	36	1030	-
4	88	24	64	310	27280	65375	60	1072	[836,1373]
Age IV									
1	51	-	51	-	-	-	-	-	-
2	34	3	31	51	1734	1734	3	434	-
3	36	7	29	82	2952	4686	10	426	-
4	18	5	13	111	1998	6684	15	418	[259,711]

Table 20. Concluded.

<u>Period¹</u>	<u>C_t</u>	<u>R_t</u>	<u>m</u>	<u>M_t</u>	<u>C_tM_t</u>	<u>Σ(C_tM_t)</u>	<u>ΣR_t</u>	<u>N̂</u>	<u>95% CI</u>
Age V									
1	6	-	6	-	-	-	-	-	-
2	2	0	2	6	18	18	0	18	-
3	5	1	4	8	40	58	1	29	-
4	2	2	0	12	24	82	3	21	[8,51]

¹ Capture period 1 was 18 June to 27 June, period 2 was 2 July to 4 July, period 3 was 9 July to 12 July, and period 4 was 13 July to 17 July.

Table 21. Modified Schnabel estimates of abundance of age 2 and older flathead catfish living in Brooks Pool of the New River, West Virginia, in 1984. (Column heading notation from Ricker 1975.)

Period ¹	C_t	R_t	m	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	ΣR_t	\hat{N}	95% CI
1	8	-	8	-	-	-	-	-	-
2	100	2	98	8	800	800	2	267	-
3	59	0	59	106	6254	7054	2	2351	-
4	8	1	7	165	1320	8374	3	2094	[854,5234]

¹ Capture period 1 was 13 June to 15 June, period 2 was 18 June to 22 June, period 3 was 26 June to 29 June, and period 4 was 10 July to 12 July.

Table 22. Modified Schnabel estimates of abundance of age 2 and older flathead catfish living in Brooks Pool of the New River, West Virginia, in 1985. (Column heading notation from Ricker 1975.)

Period ¹	C_t	R_t	m	M_t	$C_t M_t$	$\Sigma(C_t M_t)$	ΣR_t	\hat{N}	95% CI
1	49	-	49	-	-	-	-	-	-
2	23	1	22	49	1127	1127	1	564	-
3	44	1	43	71	3124	4251	2	1417	-
4	21	2	19	114	2394	6645	4	1329	[593,3323]

¹ Capture period 1 was 18 June to 27 June, period 2 was 2 July to 4 July, period 3 was 9 July to 12 July, and period 4 was 13 July to 17 July.

Table 23. Catch-at-age of smallmouth bass, rock bass, and flathead catfish caught in Brooks Pool of the New River, West Virginia, in 1984 and 1985.

Age	Smallmouth Bass			Rock Bass			Flathead Catfish		
	1984 ^a	1985 ^b	Pooled	1984 ^a	1985 ^b	Pooled	1984 ^c	1985 ^d	Pooled
0							2	0	2
1	196	31	227	52	28	80	31	10	41
2	123	78	201	228	126	354	45	48	93
3	59	14	73	112	50	162	82	35	117
4	5	4	9	10	16	26	72	29	101
5	0	2	2	3	2	5	14	20	34
6							13	3	16
7							7	4	11
8							1	5	6
9							1	0	1
10							2	1	3
11							1	0	1

^a Captured from 13 to 15 and 18 to 20 June 1984.

^b Captured from 18 to 20 June 1985.

^c Captured from June to September 1984.

^d Captured from June to October 1985.

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