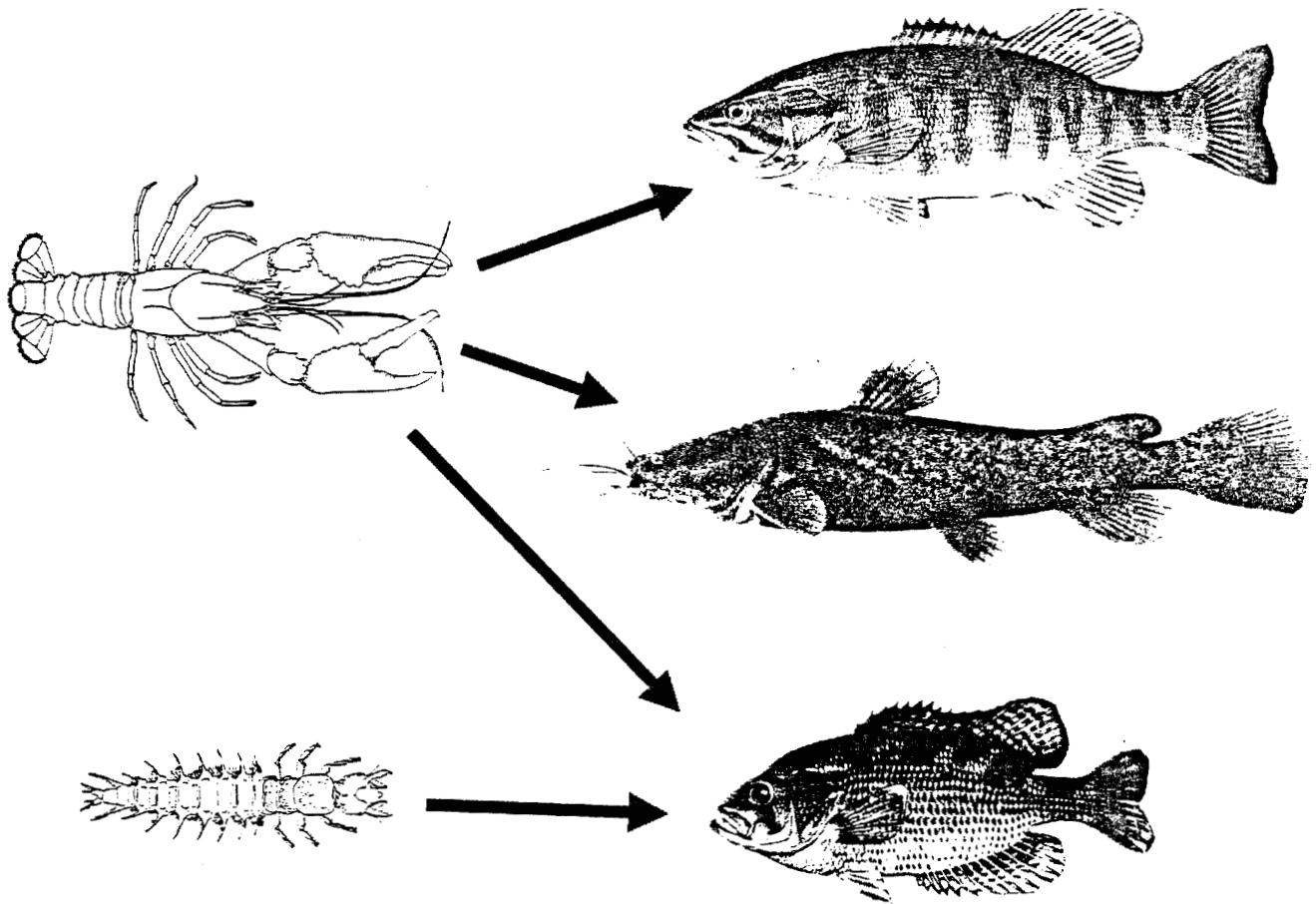


Impacts of Commercial Harvest of Invertebrate Baits on the Predator-Prey Interactions in the New River

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Job II-c. Predation by sport fishes on invertebrate bait species

Job II-d. Model of the interaction among invertebrate bait species, sport fishes, and commercial bait harvest

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Job II: Impacts of commercial harvest of invertebrate baits on the predator-prey interactions in the New River.

Job Number: II-a

Job Title: Population dynamics of invertebrate prey.

Objective: Determine the abundance, mortality, growth, annual production, and seasonal production of major invertebrate bait and prey species.

Period Covered: June 14, 1983 - July 21, 1986.

Status: Completed

Abstract:

The dynamics of the hellgrammite population (*Corydalus cornutus* larvae) and three crayfish populations (*Orconectes virilis*, *Cambarus sciotensis*, and *Orconectes sanbornii sanbornii*) were assessed in the New River, West Virginia, between Bluestone Dam and Sandstone Falls. Quadrat sampling, qualitative collections, and laboratory analytical procedures were used to estimate abundance, age and growth, and production.

Mean abundance of hellgrammites was 1.3/m², and, as expected, abundance in riffles (1.4/m²) was greater than in pools (0.1/m²). Larvae were more numerous in the lower portion of the reach (2.0/m²) than immediately below the dam (1.0/m²). Annual production (age 1 and 2 larvae only) in the reach was 3.1 g/m² (wet weight). Production in riffles and pools was 6.0 and 0.3 g/m², respectively; surface areas of riffles (197 ha) and pools (211 ha) were nearly equal. Annual mean biomass of age 1 and 2 larvae in the reach was 1.3 g/m², and the production / mean biomass ratio was 2.41. Larvae of about 6 mm head capsule width or greater were considered marketable by bait dealers. The estimated annual mean abundance of marketable-sized hellgrammites in the study reach was 4.65 million larvae. Anglers and commercial bait dealers harvested about 8% of the annual production of age 1 and 2 hellgrammites.

Crayfish mean abundance was 2.7/m², and abundance in riffles (2.8/m²) was greater than in pools (1.2/m²). Densities were slightly greater in the lower portion of the reach (3.5/m²) than below the dam (2.7/m²). *O. virilis* was the most abundant (1.3/m²) in riffles; *C. sciotensis* dominated pools (1.1/m²), especially deeper (1 - 3 m) areas. Relative abundances of the three species in deep versus shallow (< 1 m) areas of a pool suggested habitat partitioning. Total annual crayfish production (age

1 and 2 crayfish only) in the reach was 10.4 g/m² (wet weight). Production in riffles and pools was 12.7 and 8.3 g/m², respectively. Annual mean biomass estimates (age 1 and 2 combined) for the reach were 0.7 g/m² for *O. virilis*, 2.3 g/m² for *C. sciotensis*, and 0.7 g/m² for *O. s. sanbornii*, and respective production / mean biomass ratios were 2.37, 2.89, and 3.05. Crayfish of about 20 mm carapace length were considered marketable by retailers, and the annual mean abundance of marketable-sized crayfish in the reach was 4.08 million animals. Approximately 4% of the annual production of age 1 and 2 crayfish was harvested by commercial retailers and anglers.

Introduction

Harvest of hellgrammites (dobsonfly larvae) and crayfish for bait from the New River in West Virginia is a common practice by anglers and commercially-licensed harvesters. The majority of the bait harvest occurs in the 16.4-km reach from Bluestone Dam to Sandstone Falls; the value of the commercial harvest alone is over \$100,000 per year. Since 48 people are licensed to harvest hellgrammites and crayfish, and 22 and 13% of all anglers harvest hellgrammites and crayfish, respectively (Job I-b report), the pressure on this resource is substantial enough to warrant study of the status of the bait stocks in the river.

Hellgrammites are top predators in the macroinvertebrate assemblage of the New River, because they prey on a variety of aquatic invertebrates (Davis 1903; Stewart et al. 1973; Merritt and Cummins 1984). Crayfish are polytrophic (Vannote and Ball 1972; Flint and Goldman 1975; Lorman and Magnuson 1978; Raymond W. Bouchard, personal communication) and, in effect, short-circuit the classical trophic food web by directly linking primary production and detritus to top predators (Momot et al. 1978). Crayfish may substantially structure the trophic dynamics of an aquatic system through their effects on plant biomass, predator consumption, and detrital processing (Lorman and Magnuson 1978). Furthermore, crayfish are the basis of substantial food and bait fisheries throughout North America (Huner 1978). Macroinvertebrate biomass in the New River below Bluestone Dam is extremely high due to high-quality seston imported from Bluestone Lake (Voshell 1985); benefits from this scenario can accrue to both hellgrammites (through carnivory) and crayfish (through omnivory).

No previous work has been done to determine abundance, mortality, growth, or production of hellgrammites or crayfish in the New River. Furthermore, the New River is one of the state's most popular streams for smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) fishing. Both of these species, as well as the relatively abundant flathead catfish (*Pylodictis olivaris*), feed heavily on crayfish (Minckley and Deacon 1959; Vannote and Ball 1972; Edmundson 1974; Coble 1975; Layher and Boles 1980; Probst et al. 1984) and may compete with man for this limited resource.

The objectives of this research were to: (1) develop sampling techniques for estimating abundances, (2) elucidate species composition and estimate age-specific abundances, mortality, growth, and production, (3) estimate caloric density, and (4) develop predictive equations of morphometric relationships of hellgrammites and crayfish in the New River, West Virginia.

Study Sites and Species

This research was conducted on the New River, West Virginia, between Bluestone Dam and Sandstone Falls, which is referred to hereafter as the study reach. Crayfish and hellgrammites were sampled quantitatively and qualitatively at six sites (Figure 1) within the study reach during 1983, 1984, and 1985. One site (Meadow Creek) below the study reach was sampled in 1983. The majority of crayfish and hellgrammite sampling occurred in two general areas within the reach, immediately below Bluestone Dam and in the vicinity of the "Study Pool" where sport fish dynamics were assessed. The Bluestone Dam site included from immediately below the dam to the first Hinton bridge (approximately 1.1 river kilometers). The Longbottom site was approximately eight river kilometers below the dam. The Upper and Lower Riffles were located about 4.1 and 1.6 river kilometers, respectively, upstream from Sandstone Falls; these two riffles bounded the Study Pool mentioned above. Sandstone Falls was 16.4 river kilometers below the dam, and sampling at this site occurred immediately above the falls. The last site, Meadow Creek, was about eight river kilometers below Sandstone Falls. Riffles and pools were somewhat evenly distributed throughout the study reach (Figure 2), and surface areas were 197 and 211 ha (Table 1), respectively. All sites sampled, except the Study Pool (a 2 - 3 m deep pool), were shallow riffle areas averaging less than 0.5 m deep at low flow. Substrate at all sites except Sandstone Falls and the Study Pool was gravel, cobble, and boulder, while that at the two other sites was predominantly gravel and bedrock. Patches of rooted aquatic vegetation, primarily *Justicia americana* (water willow), were present throughout the study stretch and were usually associated with the stream margins.

The dobsonfly larva *Corydalus cornutus* was the megalopteran insect studied in this research. *Nigronia* sp. occurred, but was insignificant in numbers and is too small to interest anglers and commercial bait retailers. Markham et al. (1980) reported the occurrence of six crayfish species in the West Virginia portion of the New River drainage, three species each of the genera *Orconectes* and *Cambarus*. Three species, *Orconectes virilis*, *Cambarus sciotensis*, and *Orconectes sanbornii sanbornii*, were regularly caught and were the focus of study; three other species were rarely caught.

Methods

Abundance

Two techniques were used to quantitatively sample crayfish and hellgrammites. In 1983 and 1984 (except 14 October 1984), a shock/kick method was employed. The gear for this consisted of a 2.44 X 1.22-m seine with either 0.8 or 1.6 mm mesh. The lead line of the seine was loosely tied to a 1.52-m diameter aluminum hoop which encompassed 1.815 m² of stream bed. The gear was held in place on the stream bed by one researcher while another thoroughly shocked within the hoop with a backpack electroshocker using either alternating current or pulsed, direct current electricity. Immediately after shocking, the substrate was kicked to dislodge crayfish and hellgrammites, and the larger rocks were removed to facilitate dislodging. Each sample was preserved with either 10% formalin or 100% 2-propanol in plastic bags for further laboratory analysis. At least 20 quadrats were sampled on each sampling date. A transect across the river was chosen and quadrats were sampled at approximately 5 m intervals. The gear was difficult to use in depths greater than about 0.75 m, therefore quadrats chosen in these areas were abandoned and new quadrats were chosen until a workable depth was encountered. A total of 230 quadrats were sampled on 11 dates at five sites in 1983 and 1984.

The shock/kick technique worked well with hellgrammites, but crayfish often recovered quickly from electrical shock and escaped the gear. Also, low flows in August, September, and October would occasionally fail to bag the seine and/or carry the animals into the seine, and sampling in deep water (> 1 m) precluded electroshocking. Consequently, on 9 and 14 October 1984 and all sampling dates in 1985, samples were collected by hand while snorkeling or using SCUBA. The same hoop as in the shock/kick technique was used to delimit quadrats, but without the seine. 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 carefully removed while crayfish and hellgrammites were captured by hand. Very few animals escaped from the quadrat, yet those that did were counted and recorded; nearly all escapees were crayfish. Each sample was preserved in 100% 2-propanol in plastic bags. At least 15 quadrats were sampled on each sampling date, and quadrat sites were chosen in the same manner as for the

shock/kick technique. A total of 140 quadrats on seven dates at four sites were sampled in 1984 and 1985. Overall then, 370 quadrats were sampled on 18 dates at seven sites during three field seasons.

Qualitative sampling was conducted, in addition to quadrat sampling, in 1984 on 9 October (Study Pool; depth of 1.5 m) and in 1985 on 5 May (Bluestone Dam), 13 June (Bluestone Dam), 14 June (Upper Riffle of the Study Pool), 30 July (Sandstone Falls), 2 August (Study Pool; depth < 1 m), 6 September (Longbottom), and 10 and 11 September (Study Pool; depths of 2 and < 1 m, respectively) to help elucidate individual cohorts by length-frequency analysis.

Age-specific estimates of abundance per square meter were calculated for hellgrammites and crayfish (each species) for each site by date. Cohorts were distinguished from size-frequency relationships (method of Momot 1967) in the quantitative and qualitative collections.

Identification and Measurements

All collected crayfish were identified in the laboratory to species, sex, and reproductive form (I or II, males only), and carapace length (CL - tip of rostrum to mid-posterior margin of carapace; mm) was measured. Identifications were made with the aid of a key (Hobbs 1976), illustrations (Hobbs 1974), and a reference collection verified by Horton H. Hobbs, Jr. of the Smithsonian Institution in Washington D. C. Females bearing eggs or young were noted. A 1983 subsample of *O. virilis* and subsamples of *C. sciotensis* and *O. s. sanbornii* from 1984 and 1985, each having a wide range of carapace lengths and a nearly equal number of males and females, were selected for additional measurements required in the development of morphometric relationships; total length (mm), carapace length (mm), and wet weight (g) were measured from crayfish with all appendages intact. Additionally, dry weight (g) and caloric density (cal/g dry weight) were measured for *O. virilis* collected in 1983. Carapace length and width (mm) of a non-regenerated chela were measured for each species from subsamples of 1985 collections.

The head capsule width (HCW; mm) of all collected hellgrammites was measured and recorded; sex is not readily distinguishable in the larval stage. In 1983, as for crayfish, a subsample was selected for additional measurements of wet weight (g), dry weight (g), and caloric density (cal/g dry weight).

All length measurements were done with vernier calipers to the nearest 0.05 mm. Wet weights and dry weights were measured to the nearest 0.01 g and 0.001 g, respectively. Caloric density determinations were made by grouping hellgrammites

and crayfish into size classes, followed by milling, pelleting, and bombing in an adiabatic bomb calorimeter; one animal alone was too small to form a complete pellet for bombing.

Mortality

Age 1 hellgrammite abundance estimates for 8 August 1984, 4 September 1985, and 14 October 1984 progressively declined and were assumed to be representative of age 1 abundance in any single year. Under this assumption, an instantaneous daily mortality rate was calculated using least squares regression. This mortality rate was used to approximate abundances of age 1 hellgrammites on other dates for production computations.

Age-specific estimates of hellgrammite and crayfish abundance were highly variable within and among sample dates, 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 instantaneous mortality rates from catch curves, hence no estimates of annual mortality were calculated.

Production

Estimates of annual production (g/m²/yr live weight) for hellgrammites and crayfish were calculated for age 1 and 2 animals residing in riffles. A qualitative assessment of hellgrammites and crayfish sold by four bait retailers in Hinton, West Virginia (see "Exploitation" below) revealed that the sizes sold corresponded with age 1 and 2 animals of all four species. Young-of-year animals were not fully recruited to the capture gear, precluding reasonable abundance estimates. *O. virilis* and *C. sciotensis* can live to age 3, but none of the former and only 16 of the latter were caught during quantitative sampling. Age 3 *O. virilis* and *C. sciotensis* likely contribute little to the total annual production of their respective populations due to low biomass and slow growth.

Production was calculated using the Ricker (instantaneous growth) method (Ricker 1975), where, for a given time interval, production is the product of instantaneous growth in weight and mean biomass. Growth in weight was estimated using length-frequency information. Collections of sufficient sample size to elucidate cohorts and from the same time of year were pooled, length-frequency histograms constructed (0.75 mm HCW intervals for hellgrammites; 2 mm CL intervals for crayfish), and cohort modes identified (Momot 1967). For each age group (cohort), the mean weight was estimated by calculating the wet weight corresponding to the

midpoint of each length interval using the appropriate length-weight equation, and calculating a mean, weighted by the frequency of occurrence in each interval. The instantaneous growth rate for a time interval, then, was the natural logarithm of the ratio between the mean weights at the end and beginning of the time interval. Mean biomass for a time interval was calculated from the corresponding abundance and mean weight estimates for the interval.

Production estimates were calculated only for the growing season, 22 March to 22 November (water temperatures ≥ 10 C; see Table 37 and Figure 7 in Job II-c report for annual temperature regime). Production intervals within the growing season were determined by the availability of abundance and/or mean weight estimates. When only one estimate was available for a particular date, the other estimate was approximated under certain assumptions (see below). Both abundance and mean weight were approximated for each species only for the dates of 22 March and 22 November, the bounds of the growing season; all other dates had at least one of the required estimates.

Two factors complicated the estimation of hellgrammite production. First, abundance immediately below Bluestone Dam was unusually low in 1985 relative to previous years, and, second, growth was faster for hellgrammites residing immediately below the dam. Abundance was "normal" again starting at approximately 1 km below the dam, and growth at the Longbottom site, the midpoint in the study stretch, was similar to that in study pool area riffles (Upper and Lower Riffles, and Sandstone Falls). This suggested that hellgrammites exhibited similar abundance and growth throughout most of the study reach, exclusive of about the first kilometer below the dam. Hence, abundance estimates and HCW-frequency of larvae residing in study pool area riffles was used to estimate production for riffle areas throughout the study reach. In addition, thirty quadrats were sampled along a longitudinal transect in the Study Pool on 9 October 1984 using SCUBA to facilitate the estimation of abundance and production in pools, assuming growth was equal to that of larvae in riffles.

Age 1 hellgrammite abundance estimates for 8 August 1984, 4 September 1985, and 14 October 1984, when assumed representative of any one year, were used to calculate an instantaneous daily mortality rate from which age 1 abundances were estimated for 22 March, 19 June, and 30 July. Similarly, age 1 abundance for 22 November and age 2 abundances for 22 March and 1 August were estimated from a mortality rate calculated from age 1 abundance on 14 October 1984 and age 2 abundance on 23 June 1985. Complete emergence from the river on 1 August was assumed for all remaining larvae.

Age 1 hellgrammite mean weight on 22 March was assumed to be equal to the 22 November mean weight estimate for age 0 larvae, assuming no growth or weight

loss during the winter (temperatures $< 10^{\circ}\text{C}$). The November estimate was calculated by linear extrapolation from age 0 mean weight estimates for 1 September (pool of 29 August 1983 and 4 September 1985 samples) and 14 October 1984. Age 1 mean weight on 22 November and age 2 mean weight on 22 March were linearly interpolated from the age 1 mean weight on 14 October 1984 and the age 2 mean weight on 23 June 1985, again assuming no winter growth or weight loss.

For each of the three crayfish species, sample CL-frequency distributions were similar among sample areas (Bluestone Dam area riffles, the Longbottom riffle, and Study Pool area riffles) during each of the times of year sampled. Consequently, for each species and age group, mean abundance estimates and CL-frequency data (for estimating mean weights) from the same time of year were each pooled to provide a general estimate of abundance and mean weight.

Age-specific crayfish abundances were pooled by calculating a mean abundance, weighted by the number of quadrats corresponding to each constituent mean, and assigning an equivalent date. Equivalent dates correspond 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 either linearly interpolated from adjacent estimates, if such estimates declined with time, or assumed equal to the previous or subsequent estimate, if adjacent estimates did not decline with time.

Equivalent dates for crayfish mean weights correspond 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). Similar to abundance, mean weight estimates on 22 March, 12 August, and 22 November were either linearly interpolated (assuming no growth or weight loss during temperatures $< 10^{\circ}\text{C}$) or assumed equal to the previous estimate.

For hellgrammites and crayfish, age 1 and 2 production estimates for the study reach were calculated by estimating production for pools, and then averaging the production in riffles and pools weighted by the total surface area of each. Production in pools was estimated for each age group by multiplying production in riffles (g/m^2) by a scalar, the ratio of abundance in the Study Pool on 9 October 1984 to the mean of abundances at the Bluestone Dam and Lower Riffle sites on 13 and 14 October 1984 (only abundance at the Lower Riffle site was used for hellgrammites).

Riffles and pools within the study reach were delineated on topographic maps with the aid of aerial photographs and on-site inspection. Surface areas were measured from the maps with a Tektronix digitizer. Annual mean biomass, required for the calculation of production / mean biomass ratios, was estimated for ages 1 and 2 animals (combined) from abundance and mean weight information used to calculate production.

Exploitation

A qualitative survey of four bait dealers in Hinton, West Virginia was conducted to determine the minimum sizes of hellgrammites and crayfish that were acceptable for sale. Age groups and sizes vulnerable to capture for bait were then identified, and annual means of abundance and biomass of marketable-sized animals residing in riffles were calculated from abundance and mean weight information, respectively, used to calculate production. The abundance of age 1 hellgrammites in the Study Pool on 9 October 1984 relative to that in the Lower Riffle on 14 October 1984 was used to proportionally adjust the age 1 abundances (used for production) to provide an estimate of pool-dwelling age 1 hellgrammites. This adjuster was assumed applicable also to the estimation of age 2 larval abundance in pools. The biomass exploited for bait was estimated using annual harvest information (Jobs I-a and I-b report).

Results

Species

Two megalopteran insect species were caught, the dobsonfly larva *Corydalus cornutus* and *Nigronia* sp. *C. cornutus* larvae (hellgrammites) were the focus of study; *Nigronia* sp. was insignificant in number and is too small to interest bait harvesters.

Six crayfish species were caught, three species each of the genera *Orconectes* (*O. virilis*, *O. sanbornii sanbornii*, and *O. spinosus*) and *Cambarus* (*C. sciotensis*, *C. bartonii*, and *C. chasmodactylus*). Three species were caught regularly and were the focus of study, *O. virilis*, *O. s. sanbornii*, and *C. sciotensis*; members of the other three species represented < 1% of total crayfish catch.

Life Histories

C. cornutus exhibited a two-year life cycle (semivoltine; Table 2) in the New River, West Virginia between Bluestone Dam and Sandstone Falls. The "typical" surviving larva, or hellgrammite, hatched from the egg in late July, grew until late November, resumed growth from late March until late November of its second year, and emerged from the river to pupate the following spring after continuing growth in late March. Emergence was asynchronous, occurring from about late May to late July.

O. virilis and *O. s. sanbornii* had three- and two-year life cycles, respectively (Tables 3 and 4). Young of both species hatched in May, but *O. virilis* and *O. s. sanbornii* 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 (Table 5), but the young hatched in early autumn and the senescent adults died in mid-summer of their fourth year.

Morphometric Relationships and Caloric Density

Linear relationships between selected body measurements from hellgrammites (Table 6) and crayfish (Table 7) were all highly significant ($P < 0.001$) and relatively precise ($R^2 > 0.80$). Mean caloric density (cal/g dry weight) of hellgrammites was 5362, 5415, and 5441 for small- (1.4 - 5.1 HCW), medium- (5.4 - 7.5 HCW), and large-sized larvae (9.2 - 11.7 HCW), respectively, with an overall mean of 5406 (Table 8). Small- (11.4 - 19.7 CL), medium- (24.5 - 30.6 CL), and large-sized (32.2 - 38.2 CL) *O. virilis* had mean caloric densities of 3420, 3598, and 3057, respectively, and the overall mean was 3358 (Table 9).

Abundance

Mean abundance (all ages) of hellgrammites, calculated from date-specific estimates (Table 10), was 1.317/m². As expected, abundance in riffles (1.412/m²) was greater than in the Study Pool (0.128/m²). Hellgrammites were more abundant in Study Pool area riffles (2.004/m²) than in Bluestone Dam area riffles (1.009/m²). At Longbottom, an intermediate site, larval abundance was 1.295/m² on 16 August 1983. Downstream from Sandstone Falls at the Meadow Creek site, their abundance was 0.771/m² on 2 September 1983. Early instar (young-of-year) larvae were under-represented in samples collected at times of the year when they were present in the river (August to December; Table 10); age 1 larvae were assumed to be fully recruited to the sampling gear.

Crayfish (all species and ages) were more abundant than hellgrammites; overall densities, derived from date-specific estimates (Tables 11, 12, and 13), were 2.704/m². Abundance in riffles (2.835/m²) was greater than in the Study Pool (1.231/m²). Densities were slightly higher in Study Pool area riffles (3.503/m²) than in Bluestone Dam area riffles (2.727/m²). Abundances at the Longbottom site and the Meadow Creek site were 0.110/m² and 1.737/m², respectively.

O. virilis was the most abundant crayfish species sampled (1.178/m² overall and 1.268/m² in riffles) followed by *O. s. sanbornii* (0.850/m² overall and 0.925/m² in riffles) and *C. sciotensis* (0.676/m² overall and 0.642/m² in riffles). However, these estimates can be misleading since *C. sciotensis* was more abundant (1.065/m²) in the Study Pool than either *O. virilis* (0.166/m²) or *O. s. sanbornii* (0/m²).

Crayfish abundance was variable among species at each of the areas sampled (Figure 3). *O. s. sanbornii* was the most abundant (1.753/m²) crayfish species in Bluestone Dam area riffles and the least abundant (0.244/m²) species in Study Pool area riffles. *C. sciotensis* was the least abundant (0.375/m²) species in Bluestone Dam

riffles, and was intermediate in abundance ($1.043/\text{m}^2$) in Study Pool riffles. *O. virilis* had intermediate abundance ($0.599/\text{m}^2$) at the Bluestone Dam site and the highest abundance ($2.216/\text{m}^2$) in Study Pool riffles. *C. sciotensis* and *O. virilis* had equal estimates of abundance ($0.055/\text{m}^2$) at the Longbottom site, where *O. s. sanbornii* was not captured. *O. virilis* had greater abundance ($1.186/\text{m}^2$) than *C. sciotensis* ($0.551/\text{m}^2$) at the Meadow Creek site, where *O. s. sanbornii* was not captured. Greater abundance estimates resulted for *O. virilis* ($1.268/\text{m}^2$) than for *O. s. sanbornii* ($0.925/\text{m}^2$) or *C. sciotensis* ($0.642/\text{m}^2$) when all riffle-specific information was pooled. *C. sciotensis* was more abundant ($1.065/\text{m}^2$) than *O. virilis* ($0.166/\text{m}^2$) or *O. s. sanbornii* ($0/\text{m}^2$) in the Study Pool on 9 October 1984.

The relative abundance of each species in four qualitative collections from the Study Pool was 18% *O. virilis*, 65% *C. sciotensis*, and 17% *O. s. sanbornii*. *C. sciotensis* dominated two collections from deeper (1.5 and 2 m) locations in the pool (7% *O. virilis*, 86% *C. sciotensis*, and 7% *O. s. sanbornii*; $N = 116$), but relative abundance was more evenly distributed in two collections from shallower (< 1 m) locations (23% *O. virilis*, 55% *C. sciotensis*, and 22% *O. s. sanbornii*; $N = 232$).

Production

Annual production (age 1 and 2 animals combined) in riffles for hellgrammites ($6.035 \text{ g}/\text{m}^2/\text{yr}$) was nearly half that for crayfish ($12.684 \text{ g}/\text{m}^2/\text{yr}$ all species considered), although hellgrammite production (Table 14) was greater than for any single crayfish species (Tables 15, 16, and 17). Of the three crayfish species, *C. sciotensis* had the highest estimates of production ($4.919 \text{ g}/\text{m}^2/\text{yr}$), followed by *O. s. sanbornii* ($4.478 \text{ g}/\text{m}^2/\text{yr}$) and *O. virilis* ($3.287 \text{ g}/\text{m}^2/\text{yr}$). *O. s. sanbornii* had the highest estimate ($4.074 \text{ g}/\text{m}^2/\text{yr}$) for age 1 annual production, and *C. sciotensis* had the highest age 2 estimate ($2.545 \text{ g}/\text{m}^2/\text{yr}$). The estimate of age 1 production for *O. virilis* ($0.811 \text{ g}/\text{m}^2/\text{yr}$) appeared unusually low, likely due to underestimation of abundance.

Hellgrammite production in pools was an estimated 5.7% of that in riffles for ages 1 and 2 combined, resulting in a production estimate for the study reach of $3.092 \text{ g}/\text{m}^2/\text{yr}$. Annual mean biomass (ages 1 and 2 combined) of larvae in riffles (197 ha) was $2.505 \text{ g}/\text{m}^2$, and that in pools (211 ha) was $0.142 \text{ g}/\text{m}^2$, resulting in a value for the study reach (408 ha) of $1.283 \text{ g}/\text{m}^2$. Therefore, the production/mean biomass ratio ($P/\bar{B}$) was 2.410.

Respective estimates of crayfish production for age 1 and 2 animals in pools were 30% and 0% of that in riffles for *O. virilis*, and 166% and 161% of that in riffles for *C. sciotensis*; no production was estimated to occur in pools by *O. s. sanbornii*. Annual production estimates (ages 1 and 2 combined) representative of the study

reach were 1.713 g/m² for *O. virilis*, 6.533 g/m² for *C. sciotensis*, and 2.162 g/m² for *O. s. sanbornii*; a total of 10.408 g/m²/yr was produced by the three predominant crayfish species. Respective estimates of annual mean biomass (ages 1 and 2 combined) in riffles and pools were 1.311 and 0.172 g/m² for *O. virilis*, 1.709 and 2.777 g/m² for *C. sciotensis*, and 1.469 and 0 g/m² for *O. s. sanbornii*. Estimates for the study reach, then, were 0.722 g/m² for *O. virilis*, 2.261 g/m² for *C. sciotensis*, and 0.709 g/m² for *O. s. sanbornii*, and respective $P/\bar{B}$ ratios for the three species were 2.373, 2.889, and 3.049.

Exploitation

The qualitative survey of four bait dealers in Hinton, West Virginia revealed that the hellgrammite harvest corresponded to age 1 and 2 animals, and that larvae with head capsule widths (HCW) of about 6 mm or greater were marketable. Therefore, age 1 larvae on approximately 1 August and thereafter were assumed to be of acceptable size for sale as bait, and all age 2 animals were acceptable. In any single year, then, hellgrammite harvest in the spring and early summer (March through July) was comprised of age 2 larvae, and that during the remainder of the harvest season (August through October) consisted of age 1 larvae.

Annual mean abundance of marketable-sized age 1 and 2 hellgrammites in riffles was 2.226/m² and that in pools was 0.126/m². The estimated mean abundance of vulnerable-sized hellgrammites in the study reach (408 ha), then, was 4,651,080 larvae, 4,385,220 in riffles (197 ha) and 265,860 in pools (211 ha). The estimated annual harvest of hellgrammites between Bluestone Dam and Sandstone Falls was 806,940 larvae in 1983, 709,512 by commercial interests (Job I-a report) and 97,428 by anglers (Job I-b report). Therefore, the estimated instantaneous rate of fishing mortality on hellgrammites was 0.17.

Annual mean biomass of marketable-sized age 1 and 2 hellgrammites in riffles was 2.883 g/m², and that in pools was 0.163 g/m². In the study reach, mean biomass of marketable hellgrammites was an estimated 6,024 kg, 5,680 kg in riffles and 344 kg in pools. The estimated 1983 annual harvest in terms of biomass in the study reach was 1,045 kg, 919 kg by commercial interests and 126 kg by anglers, assuming an annual mean individual weight of 1.295 g. The total hellgrammite biomass harvested in the study reach is equivalent to about 8% of the annual age 1 and 2 hellgrammite production.

Crayfish harvest was found to correspond to age 1 and 2 animals also, and that crayfish with carapace lengths (CL) of about 20 mm or greater were marketable. Thus, *O. virilis* and *O. s. sanbornii* of ages 1 and 2 were assumed marketable

throughout the harvest season, and age 1 *C. sciotensis* on approximately 1 August and thereafter and all age 2 animals were deemed marketable through the season.

Annual mean abundance of marketable-sized age 1 and 2 crayfish (all species) in riffles was 1.208/m² and that in pools was 0.805/m². The estimated annual mean abundance of marketable-sized crayfish in the study reach was 4,078,310 crayfish, 2,379,760 in riffles and 1,698,550 in pools. The annual harvest of crayfish in the study reach was estimated to be 216,696 crayfish in 1983, 156,960 by commercial interests (Job I-a report) and 59,736 by anglers (Job I-b report). Thus, the estimated instantaneous rate of fishing mortality on crayfish was 0.05.

Annual mean biomass of marketable-sized crayfish in riffles was 8.158 g/m², and that in pools was 5.562 g/m². In the study reach, mean biomass of marketable crayfish was an estimated 27,807 kg, 16,071 kg in riffles and 11,736 kg in pools. The estimated 1983 annual harvest in terms of biomass in the study reach was 1,612 kg, 1,168 kg by commercial interests and 444 kg by anglers, assuming an annual mean individual weight (all species) of 7.441 g per individual. The total crayfish harvest in the study reach is equivalent to about 4% of the annual age 1 and 2 crayfish production.

Discussion

Species

The crayfish assemblage in the New River, West Virginia has changed in recent years. Markham et al. (1980) found four species in 1979 from a total of five sites located between Bluestone Dam and Sandstone Falls. *Orconectes 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 information in Edmundson (1974). Occurrence of *Cambarus sciotensis* (3), *O. spinosus* (1), and *O. obscurus* (2) was rare. The latter of the four species was not found in this research. Markham et al. (1980) used a 1.3-m deep seine and presumably sampled in riffles; therefore, the species *O. sanbornii sanbornii* and a relatively greater number of *C. sciotensis* should have been caught if the crayfish species assemblage in 1979 was the same as 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); both species were likely introduced by releases from anglers and/or bait dealers.

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 (for example, Michigan) have 2- or 3-year life cycles (Chandler 1956; Knight and Simmons 1975), and those in the New River have a 2-year life cycle, suggesting 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. Within a 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), and pre-emergence larvae attain a larger size than those reported from other studies.

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.

Relative abundances of hellgrammites in five Texas streams were about equal (Brown and Fitzpatrick 1978) or much greater (Short et al. 1987) than that in the New River. But, the New River is 5 - 30 times wider than these streams, and thus absolute abundance per unit stream length is much greater in the New River, providing the basis of a substantial bait fishery. Additionally, a two-year life cycle facilitates the capture of marketable-sized hellgrammites throughout the sport fishing season, an advantage that would not necessarily be available with a univoltine population.

Hellgrammite annual production in the New River is less than reported in other detailed studies. Two reasons for this difference relate to underrepresentation of young-of-year larvae in the catch and lower growth rates due to thermal regime. New River hellgrammite abundance was similar to that reported by Brown and Fitzpatrick (1978) in a Texas stream, but growth and, therefore, production ($15.1 \text{ g/m}^2/\text{yr}$; converted to live weight using a coefficient from Waters 1977) in Texas were likely greater. Growth rate differences are likely due to differing thermal regimes between Texas and West Virginia. Degree-days ($> 0^\circ \text{C}$) in four Texas streams in which hellgrammite populations were studied ranged from 7,499 to 8,107 (Short et al. 1987), while those in the New River were about 5,389. Short et al. (1987) attributed the variation in hellgrammite production in four south Texas streams to differing thermal regimes; hellgrammite production in these streams varied from 9.72 to $79.14 \text{ g/m}^2/\text{yr}$ (after conversion to live weight). Compared to New River hellgrammite production, production in at least three of these streams was greater, reflecting higher standing crops and growth rates.

Production/mean biomass ($P/\bar{B}$) ratios reflect the higher growth rates in the southern populations; $P/\bar{B}$ ranged 8.6 to 11.9 in five Texas streams (Brown and Fitzpatrick 1978; Short et al. 1987). $P/\bar{B}$ in the New River for age 1 and 2 larvae was about 2.4, but this value would be somewhat greater if fast growing age 0 larvae are considered. Compared to the Texas populations, $P/\bar{B}$ for the New River population would likely be lower, reflecting a lower standing crop and a slower growth rate.

The annual harvest of hellgrammites by commercial ventures and anglers is substantial (0.8 million) in an absolute sense, but is only about 17% of the annual mean abundance of marketable-sized larvae. The exploitation rate would be a smaller percentage, since mortality often proceeds in a negative exponential manner. Furthermore, only 8% of the annual age 1 and 2 production is harvested annually. This suggests that the population could sustain greater exploitation, although the importance of hellgrammites to predators requires consideration (see Job II-c report). A considerable pool of energy resides in the hellgrammite component of the New River system, and could provide substantial benefits to sport fish and man.

Crayfish

The life histories of *O. virilis* and *O. s. sanbornii* residing in the New River, West Virginia between Bluestone Dam and Sandstone Falls agree with life histories reported by Fielder (1972), Momot (1967), Momot and Gowing (1977a, 1977b, 1983), and Momot (1978). Published life history information about *C. sciotoensis* was not found. Of the three species, published information on population dynamics was found for *O. virilis* only.

Momot (1967, 1978) and Momot and Gowing (1977a) elucidated the population dynamics of lake-resident populations of *O. virilis* in three northern Michigan and two northern Ontario lakes. Age 1 and 2 abundance estimates in the Michigan lakes were greater than those for New River, while those from the Ontario lakes were slightly lower than found in this study. A crayfish species may, in general, attain greater biomass in lentic versus lotic systems (Momot et al. 1978); supporting evidence is presented by Hopkins (1967a, 1967b). Jones and Momot (1983) postulated that food availability (and presumably quality) may be the primary limiting factor of crayfish abundance in most aquatic environments, since crayfish must process substantial quantities of food materials to acquire sufficient energy for tissue maintenance and growth. However, predation may be a more important limiting factor to prey abundance in general (Bowlby and Roff 1986) and to New River crayfish abundance in particular. New River fish predators preyed heavily on crayfish (Job II-c report).

The species composition of quantitative and qualitative crayfish collections from the Study Pool suggested that habitat partitioning was occurring among the three crayfish species. *C. sciotensis* clearly dominated deeper (1 - 3 m), mid-stream locations (87% and 86% relative abundance in quantitative and qualitative collections, respectively), but relative abundances in qualitative collections from 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 co-exist 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 from abundance information was not possible for the reasons stated above. 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. Additionally, the abundance of adults had no noticeable effect on young-of-year mortality. 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 three Michigan (Momot 1967; Momot and Gowing 1977a) and two Ontario populations (Momot 1978) indicated similar growth rates for age 0 and 1 crayfish, but somewhat higher rates for older 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. Length-frequency data (and assigned ages) from New River *O. s. sanbornii* agreed well with like information reported by Fielder (1972) for a northeastern Ohio stream population. 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*, a New Zealand crayfish species.

Production estimates were found in the literature for *O. virilis*, but none were found for the other two species. Combined estimates of annual production of age 1 and 2 *O. virilis* residing in three Michigan lakes (Momot and Gowing 1977a) were much greater than like estimates from New River *O. virilis*. Similar combined estimates from two Ontario lakes (Momot 1978) were less than those from this research. Considering that the estimate for age 1 New River *O. virilis* is likely an underesti-

mate, combined age 1 and 2 annual production may be equivalent to that of the Michigan lakes. Age 2 *O. virilis* production in the New River was, on average, slightly less than that in two of the Michigan lakes, and equivalent to that in one lake. Differences in production between the *O. virilis* population in the New River and those populations studied by Momot and Gowing (1977a) and Momot (1978) are likely due to differences in age-specific abundances.

Few researchers have determined annual crayfish production in streams, and one has reported age-specific estimates. Annual production of *C. bartonii* (the only species present) in a North Carolina mountain stream was 6.4 g/m²/yr (after conversion to live weight using coefficients in 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/m²/yr. Two estimates of 235.8 and 241.7 g/m²/yr (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 (presented at the 117th Annual American Fisheries Society meeting) reported a total crayfish production of 48 g/m²/yr (after conversion to live weight assuming 83% moisture content; Waters 1977) for two species (*Orconectes luteus* - 25.8 g/m²/yr; *O. punctimanus* - 22.2 g/m²/yr) living in a small stream in south-central Missouri. The annual 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/m² (Vannote and Ball 1972), and production for only ages 1 and 2 was 33.7 g/m²/yr, which was greater than that from the New River.

Nine $P/\bar{B}$ estimates calculated for age 1 and 2 (combined) *O. virilis* from age-specific information in Momot and Gowing (1977a) ranged from 1.0 to 1.4, and two like estimates calculated from data in Momot (1978) were 1.0 and 1.4. $P/\bar{B}$ for New River age 1 and 2 *O. virilis* was greater (2.4), but is likely an overestimate due to underestimated age 1 abundances. Growth and $P/\bar{B}$ should be slightly greater on average for New River crayfish species than for their more northern counterparts. Momot et al. (1978) noted remarkably similar $P/\bar{B}$ estimates for four species (representing three genera) in four different environments, suggesting that production could be [more easily] estimated from mean biomass estimates.

Wild crayfish populations are exploited commercially and for recreation for food and bait throughout the United States and Canada (Huner 1978); more than 20,000 kg of *O. virilis* and *O. rusticus* are harvested annually in Wisconsin for bait, food, and scientific purposes, half of which may be used as bait. Brandt and Schreck (1975) qualitatively evaluated the effect of harvest of *O. spinosus* and *Cambarus bartonii* populations in a West Virginia stream, concluding that these stocks were relatively resilient to moderate exploitation. Studies which rigorously evaluated the impact of crayfish bait fisheries were not found. Momot and Gowing (1977b) experimentally

exploited *O. virilis* populations in two Michigan lakes and concluded that both exploitation by man and predation by trout did not result in the removal of the maximum available biomass from the production of a given cohort.

Short-lived crayfish species (such as those in this research) can be expected to respond to increased predation or exploitation through limited increases in fecundity (Momot 1984) and subsequent numbers of young. Exploitation of two previously unexploited, lake-resident populations of *O. virilis* in Michigan resulted in a doubling of fecundity (Momot and Gowing 1977b, 1977c). Exploitation in the New River is well-established, and fecundity-related change in the crayfish populations there have likely stabilized. Mean number of attached eggs per female for age 2 and 3 *O. virilis* in Michigan ranged from 17.7 - 144.9; the number of attached eggs on three New River *O. virilis* ranged from 453 - 509.

Annual commercial and angler harvest of crayfish is less than for hellgrammites, but is large (0.2 million) nonetheless. Annual harvest is about 5% of the annual mean abundance of marketable-sized crayfish; again, the exploitation rate would be a smaller percentage. Only 4% of the annual age 1 and 2 production is harvested annually, suggesting that higher exploitation may be acceptable once fish predator demands are evaluated (see Job II-c report). Similar to hellgrammites, a large energy potential exists in the crayfish component of the New River ecosystem.

River cooters (*Pseudemys concinna*) and queen snakes (*Regina septemvittata*) are among other vertebrates in the New River Gorge known to feed on crayfish (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, but should not be ignored.

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Tables

Table 1. Surface areas (ha) of riffles and pools within the study reach of the New River, West Virginia (refer to Figure 2 for riffle and pool locations).

<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>	31.8		
Total	197.0		211.1

Table 2. Pooled length-frequency distributions of head capsule widths (HCW) measured from *Corydalis cornutus* larvae collected from Study Pool-area riffles, and used to calculate age-specific mean weights required for the estimation of production.

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 3. Pooled length-frequency distributions of carapace lengths (CL) measured from *Orconectes virilis* collected between Bluestone Dam and Sandstone Falls, and used to calculate age-specific mean weights required for the estimation of production.

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 4. Pooled length-frequency distributions of carapace lengths (CL) measured from *Orconectes sanbornii sanbornii* collected between Bluestone Dam and Sandstone Falls, and used to calculate age-specific mean weights required for the estimation of production.

CL Midpoint (mm)	Equivalent Date ^a				
	5 May ^b	20 Jun ^c	1 Aug ^d	7 Sep ^e	12 Oct ^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 5. Pooled length-frequency distributions of carapace lengths (CL) measured from *Cambarus sciotensis* collected between Bluestone Dam and Sandstone Falls, and used to calculate age-specific mean weights required for the estimation of production.

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

^a Equivalent 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).

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

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

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

^e Age 0 is CL < 8, age 1 is 18 ≤ CL < 26, age 2 is 26 ≤ CL < 44, and age 3 ≥ 48.

Table 6. Morphometric relationships between head capsule width (HCW; mm), wet weight (WW; g), and dry weight (DW; g) for *Corydalis cornutus* larvae residing in the New River, West Virginia in 1983; N = 45.

Predictive Equation	R ²	Mean Square Error	P
$\log_{10} WW = -2.306 + 2.698 \bullet \log_{10} HCW$	0.885	0.04436	0.0001
$\log_{10} DW = -3.249 + 3.079 \bullet \log_{10} HCW$	0.912	0.06316	0.0001
$DW = -0.018 + 0.299 \bullet WW$	0.921	0.01048	0.001

Table 7. Morphometric relationships between carapace length (CL; mm), wet weight (WW; g), dry weight (DW; g), and chela width (CW; mm) each for *Orconectes virilis*, *Cambarus sciotensis*, and *Orconectes sanbornii sanbornii* residing in the New River, West Virginia; $P < 0.0001$ for all regressions.

Predictive Equation	N	R ²	Mean Square Error
<i>Orconectes virilis</i>			
$\log_{10} WW = -3.808 + 3.156 \bullet \log_{10} CL$	40	0.950	0.01352
$\log_{10} DW = -4.228 + 3.067 \bullet \log_{10} CL$	40	0.961	0.00995
$DW = -0.062 + 0.292 \bullet WW$	40	0.952	0.11028
$CL = 8.11 + 2.61 \bullet CW$	87	0.954	5.74047
<i>Cambarus sciotensis</i>			
$\log_{10} WW = -3.787 + 3.173 \bullet \log_{10} CL$	15	0.996	0.00154
$CL = 8.63 + 1.90 \bullet CW$	129	0.953	4.66564
<i>Orconectes sanbornii sanbornii</i>			
$\log_{10} WW = -4.115 + 3.366 \bullet \log_{10} CL$	15	0.996	0.00189
$CL = 11.93 + 1.96 \bullet CW$	97	0.790	3.22239

Table 8. Caloric density (cal/g dry weight) of *Corydalus cornutus* larvae collected from the New River, West Virginia on 15 and 16 August 1983.

Size Class	Head Capsule Width Range (mm)	N ^a	N ^b	Caloric Density (cal/g DW)	Standard Deviation
Small	1.4 - 5.05	25	2	5361.68	18.11
Medium	5.4 - 7.5	10	3	5414.97	24.20
Large	9.2 - 11.65	10	4	5441.08	28.48
All	1.4 - 11.65	45	9	5405.91	33.04

^a Number of specimens dried and ground for pelleting.

^b Number of pellets bombed.

Table 9. Caloric density (cal/g dry weight) of *Orconectes virilis* collected from the New River, West Virginia on 29 August 1983.

Size Class	Head Capsule Width Range (mm)	N ^a	N ^b	Caloric Density (cal/g DW)	Standard Deviation
Small	11.4 - 19.7	20	4	3420.22	53.59
Medium	24.5 - 30.6	10	4	3598.28	51.52
Large	32.2 - 38.2	10	4	3056.61	50.24
All	11.4 - 38.2	40	12	3358.37	225.57

^a Number of specimens dried and ground for pelleting.

^b Number of pellets bombed.

Table 10. Site-specific abundance estimates of age 0, 1, and 2 *Corydalis cornutus* larvae residing in the New River, West Virginia in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
			2	0	0	0
Study Pool	9 Oct 84	30	0	1	0.033	0.018
			1	6	0.200	0.110
			2	0	0	0

Table 10. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
Meadow Creek	2 Sep 83	20	0	0	0	0
			1	15	0.750	0.413
			2	13	0.650	0.358

Table 11. Site-specific abundance estimates of age 0, 1, and 2 *Orconectes virilis* residing in the New River, West Virginia in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
Study Pool	9 Oct 84	30	0	2	0.067	0.037
			1	7	0.233	0.129
			2	0	0	0

Table 11. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
Meadow Creek	2 Sep 83	20	0	28	1.400	0.772
			1	14	0.700	0.386
			2	1	0.050	0.028

Table 12. Site-specific abundance estimates of age 0, 1, 2, and 3 *Cambarus sciotensis* residing in the New River, West Virginia in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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 12. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
			3	0	0	0
Study Pool	9 Oct 84	30	0	10	0.333	0.184
			1	17	0.567	0.312
			2	30	1.000	0.551
			3	1	0.033	0.018
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
			3	0	0	0
	18 Jul 83	20	0	0	0	0
			1	5	0.250	0.138
			2	0	0	0
			3	0	0	0
Sandstone Falls	1 Aug 83	20	0	0	0	0
			1	5	0.250	0.138
			2	0	0	0
			3	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
	2 Sep 83	20	0	0	0	0
			1	15	0.750	0.413
			2	5	0.250	0.138
			3	0	0	0

Table 13. Site-specific abundance estimates of age 0, 1, and 2 *Orconectes sanbornii sanbornii* residing in the New River, West Virginia in 1983, 1984, and 1985.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
Study Pool	9 Oct 84	30	0	0	0	0
			1	0	0	0
			2	0	0	0

Table 13. Concluded.

Site	Date	Number of Quadrats	Age	Number Caught	Mean Number/Quadrat	Mean Number/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
Meadow Creek	2 Sep 83	20	0	0	0	0
			1	0	0	0
			2	0	0	0

Table 14. Annual production (g/m²/yr) estimates for age 1 and 2 *Corydalis cornutus* larvae residing in Study Pool-area riffles of the New River, West Virginia.

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

Table 15. Annual production (g/m²/yr) estimates for age 1 and 2 *Orconectes virilis* residing in riffles of the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Date ^a	Mean Number/m ²	Mean Weight (g)	Biomass (g/m ²)	Mean Biomass (g/m ²)	Growth Rate	Production (g/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 ^g	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 ^g	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						

^a 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 15. 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 16. Annual production (g/m²/yr) estimates for age 1 and 2 *Cambarus sciotoensis* residing in riffles of the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Date ^a	Mean Number/m ²	Mean Weight (g)	Biomass (g/m ²)	Mean Biomass (g/m ²)	Growth Rate	Production (g/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).

Table 16. Concluded.

- ^d Assumed to be the same as the previous abundance estimate.
- ^e Linearly interpolated from 14 October and 24 June abundance estimates of age 2 and age 3 crayfish, respectively.
- ^f Linearly interpolated from 14 October and 24 June mean weights, assuming no growth or weight loss during temperatures < 10 C.
- ^g 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).
- ^h Linearly interpolated from 29 July and 5 September mean weights.

Table 17. Annual production (g/m²/yr) estimates for age 1 and 2 *Orconectes sanbornii* residing in riffles of the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Date ^a	Mean Number/m ²	Mean Weight (g)	Biomass (g/m ²)	Mean Biomass (g/m ²)	Growth Rate	Production (g/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.

Table 17. Concluded.

- ^a 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 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.

Figures

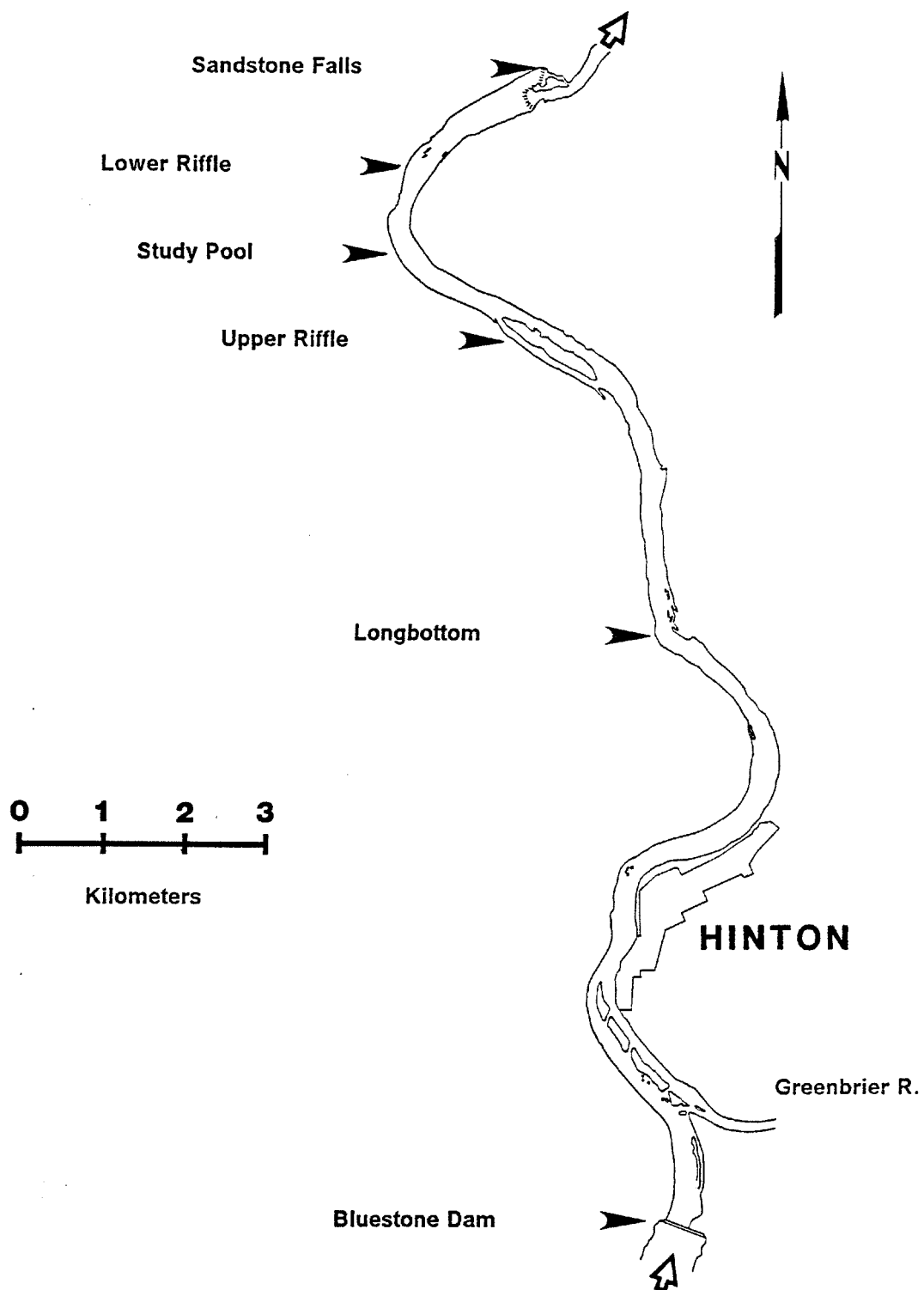


Figure 1. Map of the study reach showing the location (arrows) where crayfish and hellgrammites were sampled during 1983, 1984, and 1985 in the New River, West Virginia.

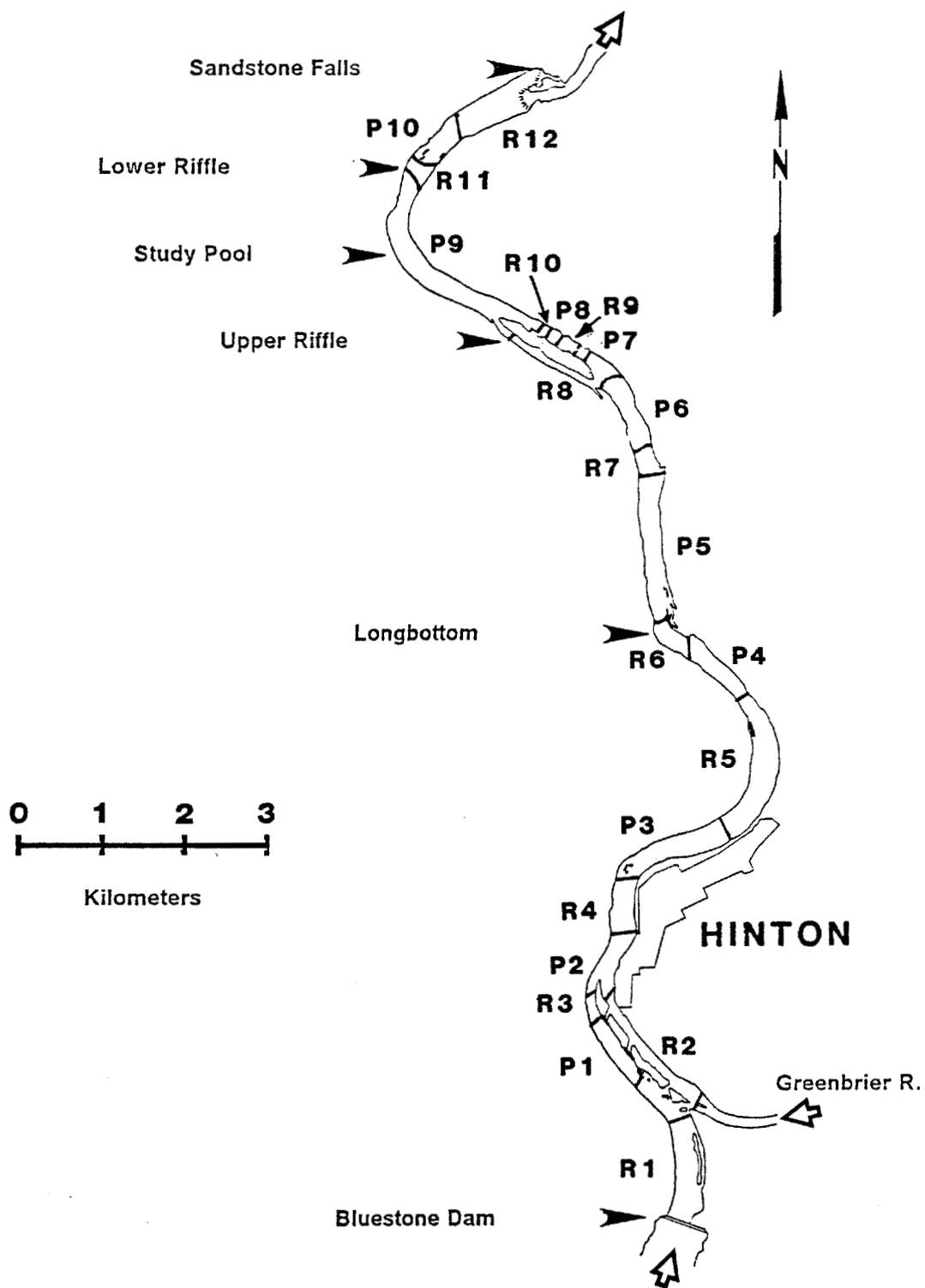
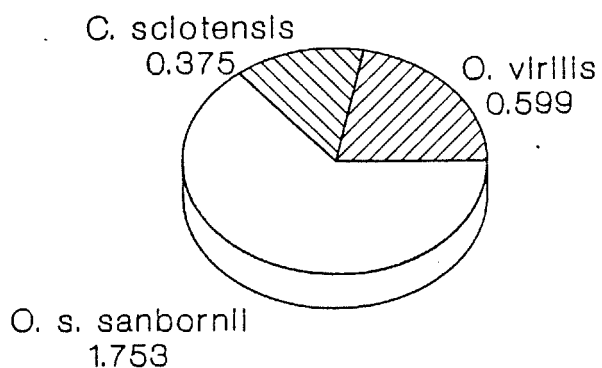
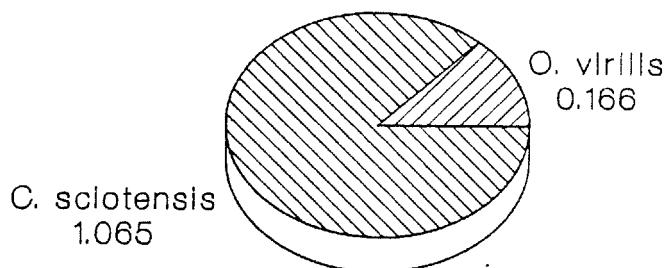


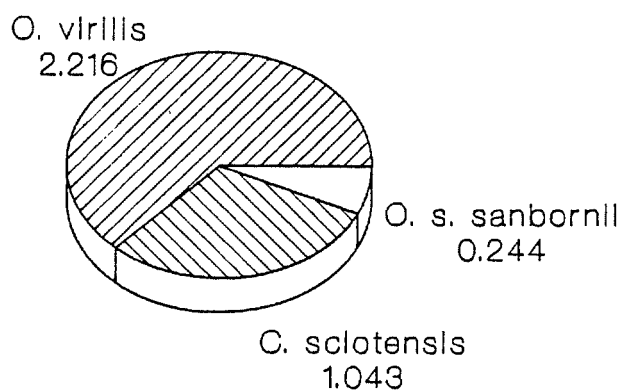
Figure 2. Locations of riffles (R1 - R12) and pools (P1 - P10) in the study reach of the New River, West Virginia.



Bluestone Dam Riffles



Study Pool



Study Pool Riffles

Figure 3. Mean crayfish abundance (number/m²) by species in Bluestone Dam-area riffles, the Study Pool, and Study Pool-area riffles of the New River, West Virginia.

Job II: Impacts of commercial harvest of invertebrate baits on the predator-prey interactions in the New River, West Virginia.

Job Number: II-b

Job Title: Population dynamics of sport fishes.

Objective: Determine the abundance, mortality, growth, annual production, and seasonal production of smallmouth bass, rock bass, and flathead catfish.

Period Covered: June 14, 1983 - July 21, 1986

Status: Completed

Abstract:

The dynamics of the smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and flathead catfish (*Pylodictis olivaris*) populations were determined through mark-recapture abundance estimates, estimation of total annual mortality, age and growth analyses, and the estimation of production for fish residing in a single, large pool (62 ha) of the New River, West Virginia. Estimated abundances on 1 June of smallmouth bass (ages 0 - 6) and rock bass (ages 0 - 5), and on 15 June of flathead catfish (ages 0 - 8) were 3,587, 4,292, and 540/ha, respectively. Total annual mortality was 80% for smallmouth bass (ages 2 - 5), 77% for rock bass (ages 2 - 5), and 56% for flathead catfish (ages 4 - 9). Annual mean biomass for the three predator fishes was 43.5 kg/ha; annual mean biomass was the highest for smallmouth bass (24.3 kg/ha), then rock bass (13.8 kg/ha) and flathead catfish (5.4 kg/ha). Total annual production by the three species was 66.3 kg/ha/yr; smallmouth bass had the highest production (40.6 kg/ha/yr), double that by rock bass (20.1 kg/ha/yr) and more than seven times that by flathead catfish (5.6 kg/ha/yr). Young-of-year for all three species contributed most to production with progressively less being contributed by older age groups. All three species exhibited negative production (loss of weight) during the winter period (temperatures < 10 C), as modeled in bioenergetics simulations.

Population "performance" characteristics (abundance, mortality, growth, biomass, and production) for smallmouth bass and rock bass were exceptional, excluding mortality, in comparison to other stream-dwelling populations in North America. Total annual mortality was very high; fishing mortality likely contributes substantially to the total, and may lower the quality of at least the smallmouth bass fishery. All performance characteristics for flathead catfish were favorable. These

three species alone represent a considerable predation force in the New River, West Virginia.

Introduction

This research was designed to estimate abundance, mortality, and growth of the numerically dominant fish predators in the New River, West Virginia. These estimates were necessary as input to the calculation of fish production and consumption of prey (Job II-c report) in the study reach between Bluestone Dam and Sandstone Falls. The dominant predators in this stretch are smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and flathead catfish (*Pylodictis olivaris*). Lobb (1986), in describing habitat use by fishes in the New River, West Virginia, conducted electrofishing collections in a reach which included approximately the lower 75% of the reach studied in this research. Total catch by number of all fishes was dominated by rock bass (20.6%) and smallmouth bass (19.4%); other predators were caught less frequently, such as flathead catfish (1.0%), spotted bass (0.7%), redbreast sunfish (0.5%), white crappie (0.2%), and largemouth bass (0.1%). Other fishes included at least seven shiner species (35.5% by number), six other cyprinids (15.4%), five darter species (3.0%), one sucker species (2.1%), and two other sunfish species (1.7%). This research found that flathead catfish were more abundant than indicated by the catch of Lobb (1986). Smallmouth bass, rock bass, and flathead catfish feed heavily on crayfish and, to a lesser extent, on hellgrammites in the New River (Job II-c report), and therefore may compete with each other and bait harvesters for this limited resource.

The objectives of this research component were 1) to estimate the abundance, mortality, age and growth, biomass, and production of smallmouth bass, rock bass, and flathead catfish in the New River, West Virginia, between Bluestone Dam and Sandstone Falls, and 2) to compare these population "performance" measures with those of other stream-resident populations. The relative "health" of the sport fisheries associated with these species was addressed, and estimates of input parameters required for the estimation of prey consumption by predators were provided.

Study Site

Smallmouth bass, rock bass, and flathead catfish population parameters were estimated in the second pool (hereafter called the Study Pool) upstream from Sandstone Falls (Figure 1; Job II-a report). This pool was selected on the basis of access, clear definition by riffles, and representativeness (included 15.1% of the total study reach). Brooks Island partially extended into the upper portion of the pool. The left ascending bank was overhung by deciduous trees and was virtually undeveloped except for a railroad approximately 30 - 50 m from the river. The right ascending bank was moderately developed by private-land owners and was dominated by beds of emergent hydrophytes (primarily *Justicia americana*). Surface area was 61.65 ha with maximum, minimum, and mean widths of 287, 154, and 228 m, respectively. Length of the pool was 2.7 km. Maximum and mean depth were approximately 4 and 2 m, respectively, at moderate flow. The bottom substrate was predominately sand, gravel, and bedrock with scattered boulders, submerged ledges (or outcrops), and depositional areas.

Methods

Abundance and Mortality

The modified Schnabel abundance estimator was used to estimate age-specific abundances of smallmouth bass, rock bass, and flathead catfish residing in the Study Pool. 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, using 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 new 5.5-m electrofishing boat similarly equipped.

Approximately four days were required to thoroughly electrofish the area of the Study Pool; each four-day block 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 tip of Brooks Island; fishing continued in the same fashion for the left ascending bank, upper riffle, and left side of Brooks Island. Finally, areas not associated with the stream margins (mid-pool habitat) and vulnerable to electrofishing were fished to complete the mark-recapture period. Fish were retained in a live well until approximately 100 - 150 fish were caught. Batches of about 25 - 30 fish were lightly anesthetized with tricaine methanesulfonate (MS-222) to lessen the stress of handling. Anesthetized fish were fin clipped (and tagged in 1984), a scale sample or a pectoral spine was collected for age identification, and total length (mm) and live weight (g) were measured. The fish were then released alive into shallow areas where recovery could be monitored. Very little immediate mortality was observed, but fish that died were eliminated from the procedure.

Fish were fin-clipped (left pelvic) in 1984 and tagged with metal, individually-numbered strap tags affixed to the edge of the opercle. Approximately 95% tag loss ensued, therefore tagging was abandoned in favor of fin-clipping only. In 1985, fish were fin-clipped only.

Estimates of age-specific abundance for all age groups of each species were desired for comparison with other studies and as input to the consumption estimation procedure (Job II-c report); however, acceptable estimates from the Schnabel method were possible for only particular age groups of smallmouth and rock bass, and only the flathead catfish population as a whole could be estimated. Estimates for the other age groups of bass were calculated from the acceptable estimates using an appropriate mortality rate. For example, acceptable estimates were achieved for only ages 2 and 3 smallmouth bass 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 3 was estimated from the age-specific mean abundances, and was converted to an instantaneous daily mortality rate. Abundance on 1 June (the approximate time of annulus formation) was then estimated by back-calculation using the daily rate. Young-of-year smallmouth bass abundance and mortality was estimated from transect abundance information reported by Lobb (1986) for the Study Pool. Abundances of ages 1, 4, 5, and 6 smallmouth bass were estimated from the age 2 and 3 abundances with a 70% annual mortality rate, which was an extension of the rate for age 2 fish.

Acceptable abundance estimates resulted for only ages 2, 3, and 4 rock bass in 1984 and 1985. Means were calculated for these ages, and the same procedure as with smallmouth bass was used to estimate abundance for ages 0, 1, and 5. Ninety five percent annual mortality was assumed for young-of-year fish, and the mortality rate of age groups adjacent to ages 1, 4, and 5 was used.

Reliable age-specific abundance estimates were not achieved in 1984 and 1985 for flathead catfish. Recaptures were of age 2, 3, and 4 fish, 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 and 1,329 were calculated for 1984 and 1985, respectively. The average, 1,712, and a 56% annual mortality rate, calculated from a catch curve of ages 2 - 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 and rock bass was estimated from age-specific abundance estimates from the two consecutive years. Catch curve annual mortality estimates (least-squares regression procedure; Ricker 1975) were calculated for each of the three species from pooled catch-at-age data collected in 1984 and 1985.

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 and rock bass were made on acetate slides using a roller press. Catfish spines were thin-sectioned with a diamond-blade saw. Scale impressions and spine sections were subsequently aged by examining an enlarged projection, and scale (spine) radius and annular measurements were made for determination of mean lengths-at-age using the Fraser-Lee method of back calculation. One technician and the primary author separately aged 426 smallmouth bass scales and 490 rock bass scales from 1984 with nearly 100% agreement, therefore all remaining scales and spines were aged by the latter. This age information was used in the calculation of age-specific abundances and catch curve mortality estimates for all three species, and in the derivation of smallmouth and rock bass seasonal growth equations to be used in an age assignment procedure.

A method of assigning ages based on lengths and using probability was employed for smallmouth and rock bass due to the large number of bass handled 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 to estimate the age of a fish from its length. The growth model (Moreau 1987)

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

was fit to mean length-at-age estimates (length-at-age data pooled for 1984 and 1985) for the two bass species using a computer-implemented nonlinear fitting 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 lengths and weights were used to develop length-weight predictive equations for each species. Total lengths and live 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), and were used to develop predictive length-weight equations.

Production and Biomass

The bioenergetics procedure for estimating consumption (Job II-c report) involved the calculation of age-specific daily abundances and daily specific growth in weight, enabling the estimation of age-specific production on a daily basis. Daily production was summed for each of three time periods totaling one year. The first period was from the recognized time of annulus formation (1 June for smallmouth and rock bass, and 15 June for flathead catfish) to the end of the growing season (23 November - when water temperatures drop below 10 C), the second period was from the end of the growing season to the beginning of the next growing season (22 March - when water temperatures rise above 10 C), and the third period included the beginning of the growing season to the time of next annulus formation. Annual production was the sum of production from the three periods.

Age-specific daily biomass was also calculated in the bioenergetics procedure from abundance and mean weight. Annual mean biomass for each age group was calculated from daily biomass values occurring at each of 7-day intervals over a year.

Results

Abundance

A total of 5,945 smallmouth bass, rock bass, and flathead catfish were marked during this research, 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.

Direct estimates of age-specific abundances were possible for ages 1 - 3 smallmouth bass in 1984 (Table 18) and 1985 (Table 19), ages 1 - 4 rock bass in 1984 (Table 20), and ages 1 - 5 rock bass in 1985 (Table 21). No attempt was made to directly estimate young-of-year abundances, but an estimate of 98,332 young-of-year (calculated from underwater transect abundances reported by Lobb 1986) in the Study Pool, corresponding to 1 September 1985, was used to back-calculate young-of-year abundance on 1 June. Similar information reported by Lobb (1986) for rock bass and flathead catfish was not used; the secretive behavior of these species during daylight hours probably resulted in underestimates of abundance calculated from daytime enumeration along transects. A low recapture rate for flathead catfish precluded direct estimation of age-specific abundances. Only three and four catfish were recaptured in 1984 and 1985, respectively, all of which were ages 2 - 4 in both years. Assuming equal vulnerability to capture among ages 2 - 9 catfish, modified Schnabel abundance estimates were calculated for these ages as a group for 1984 (Table 22) and 1985 (Table 23).

Rock bass appeared to be the most abundant sport fish in the New River in 1984 and 1985, followed by smallmouth bass and then flathead catfish. More precise estimates of rock bass abundance were possible in 1985 as a result of higher recapture rates. Age-specific estimates for June and November of the year (Tables 34, 35, and 36; Job II-c report), extrapolated from the direct estimates (see "Abundance and Mortality" in Methods for procedures), also suggested that rock bass were more numerous than smallmouth bass and flathead catfish.

Mortality

The total annual mortality rate estimate for the 1982 cohort of smallmouth bass was 79% from ages 2 to 3. Estimates of annual mortality for the 1980, 1981, and 1982 cohorts of rock bass were 77% from ages 4 to 5, 76% from ages 3 to 4, and 78% from ages 2 to 3, respectively. Catch curve (least squares regression) total annual mortality estimates from catch-per-age data (both years pooled; Table 24) 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 (Table 25; standard deviations ranging 9 - 16 mm), followed by smallmouth bass (Table 26; SD ranging 16 - 42 mm) and then flathead catfish (Table 27; SD ranging 17 - 69 mm). Mean square errors were relatively low for the seasonal von Bertalanffy growth equations, which were fit to smallmouth and rock bass mean lengths-at-annulus (Table 28). Coefficients of determination (R^2) were very high for the length-weight equations of all three species (Table 28), indicating precise predictability of weight from length.

Biomass

Annual mean biomass of the three predator fishes was 43.5 kg/ha. Totals of age-specific estimates of annual mean biomass (Table 29) in the Study Pool were highest for smallmouth bass (24.3 kg/ha), then rock bass (13.8 kg/ha) and flathead catfish (5.4 kg/ha). Young-of-year exhibited the highest mean annual biomass for smallmouth bass (7.8 kg/ha) and rock bass (4.2 kg/ha), while age 3 flathead catfish were the highest (1.0 kg/ha).

Production

Total production by the three species was 66.3 kg/ha/yr. The smallmouth bass population in the Study Pool had the highest production (40.6 kg/ha/yr; Table 30), double that by rock bass (20.1 kg/ha/yr; Table 31) and more than seven times that by flathead catfish (5.6 kg/ha/yr; Table 32). Estimates for each of the three species were highest for young-of-year with progressively less production for older age groups.

All three species, as modeled in bioenergetics simulations, exhibited negative production during the winter period (temperatures < 10 C).

Discussion

Comparison of population parameter estimates of New River sport fish species to reported estimates for other populations was complicated by several factors. First, ages or size ranges corresponding to estimates were not always reported or determined by others. Second, estimates reported by others pertained to different times of the year. Third, the populations being compared experienced different mortality rates. Fourth, estimation methods differed. And lastly, the estimation methods are inherently prone to substantial error. Therefore, comparison of estimates from the New River with those reported for other streams was based on contributing age groups (or reasonably inferred age groups if size range and growth information were reported), and estimates resulting from all methods were assumed to be directly comparable with no further interpretation of estimate bias. Estimates for which corresponding age groups were not explicitly reported or could not be reasonably inferred were not used for comparison with those from the New River unless obviously much greater; much smaller estimates could correspond to one or a few age groups.

Abundance for each species was considered to be the most critical population parameter estimated, because subsequent estimates of biomass, production, and consumption of prey (Job II-c report) depended on these estimates. Relatively accurate estimates were assumed to have been achieved for ages 2 and 3 smallmouth bass in 1984 and age 2 smallmouth bass in 1985, because the number of recaptures was four or more for each estimate (Tables 18 and 19); statistical bias can likely be ignored when this is the case (Ricker 1975). Likewise for rock bass, age groups 2 and 3 in 1984 and groups 2, 3, and 4 in 1985 were considered accurate. Although recapture numbers were low for age 3 smallmouth bass in 1985, age 4 rock bass in 1984, and age 2 and older flathead catfish (combined) in both years, estimates for these groups were used as a first approximation for further population analysis (see "Abundance and Mortality" in Methods for procedures). Recapture numbers were generally high for age 1 smallmouth and rock bass, but corresponding estimates of abundance appeared low and inconsistent with expected rates of mortality for these ages. This contention was supported by evidence from Lobb (1986), who conducted 45 daytime underwater transects in August-September 1985 to estimate abundance and habitat use by fish species residing in the Study Pool. Abundance of smallmouth bass juveniles (total length of 100 - 199 mm), which would have been mostly age 1

fish, was 13,409, an estimate which is more than five times the value resulting from the mark-recapture method. Likewise for rock bass young-of-year and juveniles (total length < 100 mm), which were likely age 1 fish due to the very secretive nature of young-of-year, abundance was 10,403, a value which was more than four times that resulting in this study.

Smallmouth Bass

Abundance

Estimated smallmouth bass abundance in the New River was greater than 40 of 45 individual estimates (and 11 of 12 means thereof) reported in 8 studies of 11 stream-dwelling smallmouth bass populations. Abundances of smallmouth bass (ages 0 - 6) in the New River were 3,587 and 963/ha on 1 June and 22 November, respectively (sum of age-specific abundances used in energetics simulations; see Table 34 in Job II-c report), and those for smallmouth bass (ages 1 - 6) were 254 and 142/ha on the same respective dates. Paragamian (1987) estimated the abundance of age 1 and older smallmouth bass in the Maquoketa River, Iowa in three seasons over five years; mean abundances in spring (late April-early May), summer (July), and autumn (late September-early October) were 206/ha (range of 84 - 542/ha), 129/ha (range of 78 - 237/ha), and 117/ha (range of 67 - 269/ha), respectively. Abundance (age 1 and older) in April-May of three years averaged 150/ha (range of 96 - 217/ha) and 1202/ha (range of 437 - 1830/ha) in two reaches of the Maquoketa River, Iowa (Paragamian 1984); two of these six estimates were also reported by Paragamian (1987). Smallmouth bass abundance (fish 175 mm total length and longer) in two reaches (time of year not reported) each of the Jacks Fork and Current Rivers, Missouri averaged 142/ha (range of 74 - 210/ha) and 44/ha (range of 39 - 49/ha, respectively (Covington et al. 1983). Mean abundance of ages 0 - 1 smallmouth bass for five sites in the Speed River, Ontario in September-October was 228/ha (range of 123 - 504/ha; Mahon et al. 1979). Abundance in May in the Red Cedar and Plover Rivers, Wisconsin was 132/ha (ages 1 - 8) and a mean of 118/ha (range of 45 - 164/ha; ages 1 - 9), respectively (Paragamian and Coble 1975). Abundance (approximately age 1 and older) in 11 consecutive years in autumn in Courtois Creek, Missouri averaged 59/ha (range of 34 - 96/ha; Fajen 1975a). Smallmouth bass abundance (ages 0 - 4) in a reach of the Red Cedar River, Michigan in August was an estimated 197 and 498/ha by electrofishing and rotenone poisoning, respectively (Vannote and Ball 1972). Larimore (1961) determined the abundance of all fish species in a 1.57 km reach of Jordan Creek, Illinois in August by electrofishing, then applying rotenone, and finally pumping out all pools within the reach; smallmouth bass (ages 0 and older) abundance was 67/ha. Paragamian and Coble (1975) summarized four additional studies

in which abundance estimates were reported for seven streams; estimates ranged from 1/ha in the Des Moines River, Iowa to 87/ha in Massie Creek, Ohio. Only one of these studies included the ages corresponding to each estimate.

Lobb (1986) independently estimated the abundance of various fish species, some by lifestage, in the Study Pool in August-September 1985 by daytime underwater enumeration of fish along transects. He attempted to sample each of eight habitat types in proportion to their total area in the pool. Smallmouth bass were more than eight times as abundant in snags than in the other seven habitat types combined. The abundance estimate of adult smallmouth bass (total length ≥ 200 mm; approximately age 2 and older) in the pool, considering all habitat types, was 10,403. The estimate of ages 2 - 6 bass from the current study was 4,630 smallmouth bass on 1 June and 2,580 on 22 November (Table 34; Job II-c report). This discrepancy may be an artifact of snags being over-represented in the total number of transects completed (2 of 45). Snags are probably much less than 1% of the habitat in the Study Pool.

Mortality

Total annual mortality of smallmouth bass in the New River (80% for ages 2 - 5) was greater than estimates reported for 15 of 18 exploited, stream-resident smallmouth bass populations. Annual mortality estimates for smallmouth bass in five Iowa streams ranged from 42% (ages 1 - 8) to 84% (ages 2 - 10); Paragamian 1984). Orth et al. (1983) reported an annual mortality rate of 61% for bass in Glover Creek, Oklahoma. Annual mortality for bass in the Buffalo River, Arkansas was an estimated 36% (Kilambi et al. 1977). Paragamian and Coble (1975) reported annual mortality rates of 55% (ages 2 - 8) and 65% (ages 1 - 6) for bass in the Red Cedar and Plover Rivers, respectively, in Wisconsin. Annual mortality estimates reported by Funk (1975a) for smallmouth bass in Courtois Creek, Missouri ranged from 54 - 80% (ages 2 - 5). Coble (1975) summarized annual mortality rates for bass in five additional streams reported in the literature; rates ranged from 55 - 66%. Fajen (1975b) used year-class data reported by others for three stream populations to calculate mortality rates of 51, 52, and 63% (ages not reported). Fajen (1975b) also estimated annual mortality from data reported by others for a lightly exploited stream population, and mortality was 11% (ages 1 - 11); mortality for ages 3 - 7 was 39%.

Fishing is usually the greatest mortality factor in exploited smallmouth bass populations. Fishing mortality exceeded natural mortality in the Red Cedar River, Wisconsin and in five of six other populations reviewed by Paragamian and Coble (1975); they concluded that exploited smallmouth bass populations typically experi-

enced total annual mortality rates of 50% or greater, most due to fishing, and that standing stock and catch were mostly comprised of relatively young fish.

Total annual mortality in an unexploited smallmouth bass population in Little Saline Creek, Missouri was 11% (Fajen 1975b). Assuming this rate is a reasonable approximation of natural mortality for smallmouth bass in the New River and that natural and fishing mortality occur simultaneously, the exploitation rate of New River bass would be about 74%; therefore, annual harvest of age 2 and older bass would be about 71 bass/ha, which is less than 104 bass/ha calculated from harvest information in Pierce et al. (1981). This harvest is high compared to other studies. A harvest of about 21 smallmouth bass per hectare was calculated from information in Paragamian and Coble (1975) for the Red Cedar River, Wisconsin. Harvest of smallmouth bass in three years in two reaches of the Maquoketa River, Iowa averaged 33 fish/ha (range of 20 - 46 fish/ha) and 44 fish/ha (range of 24 - 72 fish/ha; Paragamian 1984). Smallmouth bass harvest in a reach of Courtois Creek, Missouri over ten years averaged 37 fish/ha (range of 29 - 49 fish/ha; Fleener 1975).

Growth

Growth in length of New River smallmouth bass was greater than the average for 27 stream-dwelling populations in 11 states (Figure 4). Carlander (1977) reviewed mean length-at-annulus information reported in other studies for numerous stream-dwelling smallmouth bass populations; an unweighted mean of reported length-at-annulus means, corresponding to each of the first six annuli, was calculated, and lengths of 87, 168, 232, 287, 326, and 369 mm, respectively, were the result. Lengths-at-annulus for New River bass were 9 - 24% longer than the corresponding average lengths calculated above. Eleven of the 34 "populations" (included individually are multiple studies of the same stream and analyses for different reaches within the same stream) had at least one mean length-at-annulus greater than those of New River smallmouth bass, but only three of the 34 had at least four lengths-at-annulus greater than those of New River bass.

Biomass

Estimated smallmouth bass annual mean biomass in the New River (24.3 kg/ha) was greater than 33 of 43 individual estimates (and 10 of 15 means thereof) reported in 12 studies of 13 stream-dwelling smallmouth bass populations. In some cases, annual mean biomass for the New River was directly compared to estimates repre-

sentative of a particular time of year. Paragamian (1987) estimated the mean biomass (ages 1 - 5) of smallmouth bass in the Maquoketa River, Iowa for two time intervals in each of five years; mean biomass estimates in spring-summer (late April-July) and summer-autumn (July-early October) were 16.7 kg/ha (range of 10.5 - 33.0 kg/ha) and 15.5 kg/ha (range of 12.5 - 23.5 kg/ha), respectively, and the mean annual biomass was 16.1 kg/ha (range of 11.6 - 28.2 kg/ha). Biomass (ages 1 and older) in April-May of three years averaged 4.6 kg/ha (range of 1.0 - 9.1 kg/ha) and 33.0 kg/ha (range of 15.7 - 45.2 kg/ha) in two reaches of the Maquoketa River, Iowa (Paragamian 1984). Smallmouth bass biomass (fish of 175 mm total length and longer) in two reaches each (time of year not reported) of the Jacks Fork and Current Rivers, Missouri averaged 28.5 kg/ha (range of 14.0 - 43.0 kg/ha) and 10.5 kg/ha (range of 10.0 - 11.0 kg/ha), respectively (Covington et al. 1983). Mean biomass of age 0 - 1 smallmouth bass for five sites in the Speed River, Ontario in September-October was 3.5 kg/ha (range of 1.2 - 8.1 kg/ha; Mahon et al. 1979). Biomass in May in the Red Cedar and Plover Rivers, Wisconsin was 15.0 kg/ha (ages 1 - 8) and a mean of 17.5 kg/ha (range of 3.7 - 29.2 kg/ha; ages 1-9), respectively (Paragamian and Coble 1975). Biomass (approximately age 1 and older) in 11 consecutive years in autumn in Courtois Creek, Missouri averaged 8.5 kg/ha (range of 4.4 - 15.5 kg/ha; Fajen 1975a). Smallmouth bass biomass (ages 0 - 4) in a reach of the Red Cedar River, Michigan in August was an estimated 20.9 kg/ha by rotenone poisoning (Vannote and Ball 1972). Larimore (1961) determined the biomass of all fish species in a 1.57 km reach of Jordan Creek, Illinois in August by electrofishing, then applying rotenone, and finally pumping out all pools within the reach; smallmouth bass (ages 0 and older) biomass was 1.9 kg/ha. Paragamian and Coble (1975) and Funk (1975b) summarized ten additional studies in which biomass estimates were reported for 17 streams; estimates ranged from 0.2 kg/ha in the Whitewater River, Indiana to 82.9 kg/ha (ages 0 - 3) in Livingston Branch, Wisconsin. Two of these studies reviewed by Paragamian and Coble (1975) included the ages corresponding to each estimate.

Production

Smallmouth bass annual production in the New River was greater than all 13 individual estimates (and all three means thereof) reported for three stream-dwelling smallmouth bass populations. Annual production contributed by ages 0 - 6 bass in the New River was 40.6 kg/ha, and $P/\bar{B}$ was 1.67. Mean annual production (ages 0 - 1) of two sites in the Speed River, Ontario was 0.5 kg/ha (range of 0.3 - 0.6 kg/ha; Mahon et al. 1979), and mean $P/\bar{B}$ was 7.53 (range of 7.43 - 7.63) reflecting the young age composition. Annual production (approximately age 1 and older) in Courtois Creek, Missouri in ten consecutive years averaged 18.0 kg/ha (range of 11.5 - 25.1 kg/ha/yr; Funk 1975a); mean $P/\bar{B}$ of 2.17 was calculated using a corresponding mean biomass estimate from Fajen (1975a). Annual production by smallmouth bass (ages

0 and older) in the Red Cedar River, Michigan was 13.6 kg/ha (Vannote and Ball 1972), and $P/\bar{B}$ was 0.91.

Rock Bass

Abundance

Rock bass abundance in the New River was greater than all 22 individual estimates (and all six means thereof) reported in five studies for six stream-dwelling rock bass populations. Abundances of ages 0 - 5 bass in the New River were 4,292 and 1,376/ha on 1 June and 22 November, respectively (sum of age-specific abundances used in energetics simulations; see Table 35 in Job II-c report), and those for ages 1 - 5 bass were 357 and 204/ha on those respective dates. Pajak (1985) estimated the abundance (age 0 and older) of rock bass in two Virginia streams; abundances in July, November, and the following June were an average 535, 175, and 452/ha, respectively, in Little Walker Creek, and 641, 254, and 337/ha, respectively, in Back Creek. Rock bass abundance (fish of 100 mm total length or longer) in two reaches each (time of year not reported) of the Jacks Fork and Current Rivers, Missouri averaged 469/ha (range of 168 - 770/ha) and 327/ha (range of 240 - 413/ha), respectively (Covington et al. 1983). Mean abundance of age 0 and older rock bass (only three of 62 bass caught were older than age 0) for three sites in the Speed River, Ontario in September-October was 315/ha (range of 89 - 713/ha; Mahon et al. 1979). Abundance (approximately age 1 and older) in 11 consecutive years in autumn in Courtois Creek, Missouri averaged 67/ha (range of 24 - 120/ha; Fajen 1975a). Rock bass abundance (age 0 and older) in a reach of the Red Cedar River, Michigan in August was an estimated 264 and 854/ha by electrofishing and rotenone poisoning, respectively (Vannote and Ball 1972). Larimore (1961) determined the abundance of all fish species in a 1.57 km reach of Jordan Creek, Illinois in August by electrofishing, then applying rotenone, and finally pumping out all pools within the reach; rock bass (ages 0 and older) abundance was 86/ha.

Rock bass adults (total length ≥ 100 mm; about age 2 and older) were almost 100 times as numerous in snags within the Study Pool than in seven other habitat types combined (Lobb 1986). The abundance of rock bass adults in the Study Pool, calculated from habitat-specific bass densities reported by Lobb (1986; see "Abundance" of smallmouth bass for details), was 79,143, a value which was much higher than 6,902 (corresponding to 1 June) or 3,752 (corresponding to 22 November) for ages 2 - 5 bass from the current study (Table 35; Job II-c report). Again, as for smallmouth bass, snags were over-represented as a habitat type, and thus led to over-estimation of adult bass numbers using the habitat-specific information.

Mortality

Reports of total annual mortality of rock bass are scant in the fisheries literature. Annual mortality of New River rock bass (77% for ages 2 - 5) was greater than estimates of 55% (ages 2 - 3) and 72% (ages 4 - 5) in an Ohio streams report reviewed by Carlander (1977).

Growth

Growth in length of New River rock bass was greater than the average for 13 stream-resident populations in six states (Figure 5). Carlander (1977) reviewed mean length-at-annulus information reported in other studies of stream-dwelling rock bass populations; an unweighted mean of reported length-at-annulus means, corresponding to each of the first six annuli, were calculated from this information, and lengths of 48, 94, 142, 174, 195, and 205 mm, respectively, resulted. Lengths-at-annulus for New River bass were 18 - 31% longer than the corresponding average lengths calculated above. Only two of the 13 populations had at least one mean length-at-annulus greater than those of New River rock bass.

Biomass

Rock bass annual mean biomass in the New River (13.8 kg/ha) was greater than 15 of 22 individual estimates (and three of seven means thereof) reported in five studies for seven stream-dwelling rock bass populations. In some cases, annual mean biomass for New River rock bass was directly compared to estimates representative of a particular time of year. Estimates of mean biomass of rock bass (ages 0 and older) for two sites each in Little Walker and Back Creeks, Virginia were 34.6 kg/ha (range of 26.0 - 43.1 kg/ha) and 34.1 kg/ha (range of 20.3 - 47.8 kg/ha), respectively (Pajak 1985). Rock bass biomass (fish of 100 mm total length and longer) in two reaches each (time of year not reported) of the Jacks Fork and Current Rivers, Missouri averaged 32.0 kg/ha (range of 12 - 52 kg/ha) and 32.5 kg/ha (range of 19.0 - 46.0 kg/ha), respectively (Covington et al. 1983). Mean biomass of age 0 and older rock bass for three sites in the Speed River, Ontario in September-October was 1.4 kg/ha (range of 0.1 - 3.9 kg/ha; Mahon et al. 1979). Biomass (approximately age 1 and older) in 11 consecutive years in autumn in Courtois Creek, Missouri averaged 4.6 kg/ha (range of 1.9 - 8.3 kg/ha; Fajen 1975a). Larimore (1961) determined the biomass of all fish species in a 1.57 km reach of Jordan Creek, Illinois in August, and rock bass biomass (ages 0 and older) was 2.9 kg/ha.

Production

Rock bass annual production in the New River was greater than all five individual estimates (and both means thereof) reported in two studies of two stream-dwelling rock bass populations. Annual production contributed by ages 0 - 5 bass in the New River was 20.1 kg/ha, and $P/\bar{B}$ was 1.46. Estimates of mean annual production by rock bass (ages 0 and older) at two sites each in Little Walker and Back Creeks, Virginia were 10.3 kg/ha (range of 8.3 - 12.2 kg/ha) and 10.4 kg/ha (range of 8.1 - 12.7 kg/ha), respectively (Pajak 1985); mean $P/\bar{B}$ in Little Walker Creek was 0.30 (range of 0.28 - 0.32), and that in Back Creek was 0.34 (range of 0.27 - 0.40). Annual production by age 0 rock bass in the Speed River, Ontario was 2.4 kg/ha (Mahon et al. 1979), and $P/\bar{B}$ was 1.13.

Flathead Catfish

Estimates of abundance, mortality, biomass, and production were not found in the fisheries literature for stream-dwelling flathead catfish populations with the exception of Fajen (1975a), who reported a biomass estimate of 0.1 kg/ha for one of 11 years in which sampling was conducted in Courtois Creek, Missouri. In addition, Lobb (1986) conducted daytime underwater enumeration of flathead catfish and other species along 45 transects in the Study Pool in August-September 1985; from this information, abundance estimates of 231 and 77 young-of-year (total length < 100 mm) and "adults" (total length $\geq$ 100 mm; age 1 and older), respectively, resulted. These are probably underestimates due to the secretive behavior of flathead catfish during daylight hours. Numerous age and growth studies have been conducted on stream and reservoir populations of flathead catfish. Growth comparisons with the findings of many of these studies are complicated by their use of an erroneous method of age estimation. Inspection of spine sections for age determination was conducted by many investigators in a region of the spine where the first through fifth annuli were potentially absent due to spine resorption (Turner 1977) resulting in underestimated age and overestimated growth. Turner (1977) reviewed four age and growth studies of stream-dwelling flathead catfish populations in which the error was realized. Growth in length of New River flathead catfish was less than the average for two stream-dwelling populations in two states (Figure 6). An unweighted mean of reported length-at-annulus means, corresponding to each of the first nine annuli, was calculated, and lengths of 93, 192, 297, 383, 465, 526, 578, 628, and 700 mm, respectively, were the result. The mean length for only the first annulus of New River flathead catfish was longer than the corresponding average calculated above. All six "populations" (included individually are multiple studies of the same stream and analyses for different reaches within the same stream) showed superior growth in length in all but the first annulus (one population was superior at all annuli).

Overview

Population "performance" characteristics (abundance, mortality, growth, biomass, and production), excluding mortality, for smallmouth and rock bass were exceptional. Total annual mortality for these species was very high, especially for smallmouth bass mortality relative to that in other stream-resident populations. Fishing mortality likely contributes substantially to the total, and may lower the overall quality of the sport fishery, at least for smallmouth bass. The lack of detailed investigations of stream-dwelling flathead catfish populations precluded comparisons, but all performance characteristics were favorable, especially mortality which was relatively moderate.

The smallmouth bass, rock bass, and flathead catfish populations in the New River represent a considerable predation force, especially that of the two basses in regard to other stream populations. The link between predators and prey is detailed in Job II-c of this report.

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Tables

Table 18. Modified Schnabel abundance estimates for smallmouth bass residing in the Study Pool in 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 19. Modified Schnabel abundance estimates for smallmouth bass residing in the Study Pool in 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 20. Modified Schnabel abundance estimates for rock bass residing in the Study Pool in 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 21. Modified Schnabel abundance estimates for rock bass residing in the Study Pool in 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 21. Concluded.

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 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 22. Modified Schnabel abundance estimates for age 2 and older flathead catfish residing in the Study Pool in 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 23. Modified Schnabel abundance estimates for age 2 and older flathead catfish residing in the Study Pool in 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 24. Catch-at-age of smallmouth bass, rock bass, and flathead catfish from the Study 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.

Table 25. Mean lengths-at-annulus and associated information for rock bass in the Study Pool in the New River, West Virginia (1984 and 1985 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 26. Mean lengths-at-annulus and associated information for smallmouth bass in the Study Pool in the New River, West Virginia (1984 and 1985 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 27. Mean lengths-at-annulus and associated information for flathead catfish in the Study Pool in the New River, West Virginia (1984 and 1985 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 28. Length-weight and seasonal von Bertalanffy growth equations for smallmouth bass, rock bass, and flathead catfish residing in the Study Pool in the New River, West Virginia, in 1984 and 1985.

Predictive Equation	N	R ²	Mean Square Error
Smallmouth Bass			
1984 : $\log_{10} W = -4.859 + 2.979 \bullet \log_{10} L$	566	0.989	0.00330
1985 : $\log_{10} W = -4.993 + 3.040 \bullet \log_{10} L$	165	0.994	0.00159
All : $\log_{10} W = -4.891 + 2.994 \bullet \log_{10} L$	731	0.990	0.00293
Growth : $L_t = 2600 \bullet (1 - e^{-0.0297 \bullet (t+0.7082)+0.0087 \bullet \sin(6.2832 \bullet (t-0.5498))})$	18	-	37.09290
Rock Bass			
1984 : $\log_{10} W = -4.775 + 3.035 \bullet \log_{10} L$	659	0.992	0.00111
1985 : $\log_{10} W = -4.722 + 3.016 \bullet \log_{10} L$	263	0.991	0.00150
All : $\log_{10} W = -4.766 + 3.033 \bullet \log_{10} L$	922	0.992	0.00126
Growth : $L_t = 320 \bullet (1 - e^{-0.2618 \bullet (t)+0.1279 \bullet \sin(6.2832 \bullet (t-0.5446))})$	20	-	24.71080
Flathead Catfish			
1984 : $\log_{10} W = -5.118 + 3.040 \bullet \log_{10} L$	271	0.994	0.00177
1985 : $\log_{10} W = -5.340 + 3.128 \bullet \log_{10} L$	145	0.997	0.00090
All : $\log_{10} W = -5.188 + 3.068 \bullet \log_{10} L$	416	0.995	0.00154

Table 29. Annual mean biomass (kg/ha, kcal/ha) by age group of smallmouth bass, rock bass, and flathead catfish in the Study Pool in the New River, West Virginia.

Age/Cohort	Smallmouth bass		Rock bass		Flathead catfish	
	kg/ha	kcal/ha	kg/ha	kcal/ha	kg/ha	kcal/ha
0	7.776	7776	4.187	4187	0.876	876
1	5.967	5967	3.303	3303	0.746	746
2	4.873	4873	3.730	3730	0.983	983
3	2.888	2888	1.922	1922	1.002	1002
4	1.620	1620	0.512	512	0.772	772
5	0.816	816	0.111	111	0.510	510
6	0.367	367	-	-	0.300	300
7	-	-	-	-	0.150	150
8	-	-	-	-	0.080	80
Total	24.307	24307	13.765	13765	5.419	5419

Table 30. Smallmouth bass production (kg/ha/season, kg/ha/yr) by age group in the Study Pool in the New River, West Virginia.

Age/Cohort	Season ¹			Total
	Summer-Fall	Winter	Spring	
0	23.412	-1.083	0.373	22.702
1	9.478	-0.583	0.386	9.281
2	4.667	-0.269	0.179	4.577
3	2.216	-0.123	0.082	2.175
4	1.219	-0.056	0.037	1.200
5	0.509	-0.023	0.015	0.501
6	0.183	-0.009	0.005	0.179
Total	41.684	-2.146	1.077	40.615

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 31. Rock bass production (kg/ha/season, kg/ha/yr) by age group in the Study Pool in the New River, West Virginia.

Age/Cohort	Season ¹			Total
	Summer-Fall	Winter	Spring	
0	9.722	-1.076	0.376	9.022
1	5.557	-0.972	0.661	5.246
2	4.416	-0.753	0.516	4.179
3	1.572	-0.266	0.151	1.457
4	0.244	-0.062	0.036	0.218
5	0.023	-0.012	0.007	0.018
Total	21.534	-3.141	1.747	20.140

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 32. Flathead catfish production (kg/ha/season, kg/ha/yr) by age group in the Study Pool in the New River, West Virginia.

Age/Cohort	Season ¹			Total
	Summer-Fall	Winter	Spring	
0	2.237	-0.170	0.052	2.119
1	1.010	-0.086	0.063	0.987
2	0.969	-0.095	0.071	0.945
3	0.824	-0.067	0.050	0.807
4	0.433	-0.037	0.027	0.423
5	0.227	-0.022	0.016	0.221
6	0.098	-0.012	0.009	0.095
7	0.019	-0.005	0.004	0.018
8	0.007	-0.003	0.002	0.006
Total	5.824	-0.497	0.294	5.621

¹ Summer-Fall is 15 June to 22 November, winter is 23 November to 21 March, and spring is 22 March to 14 June.

Figures

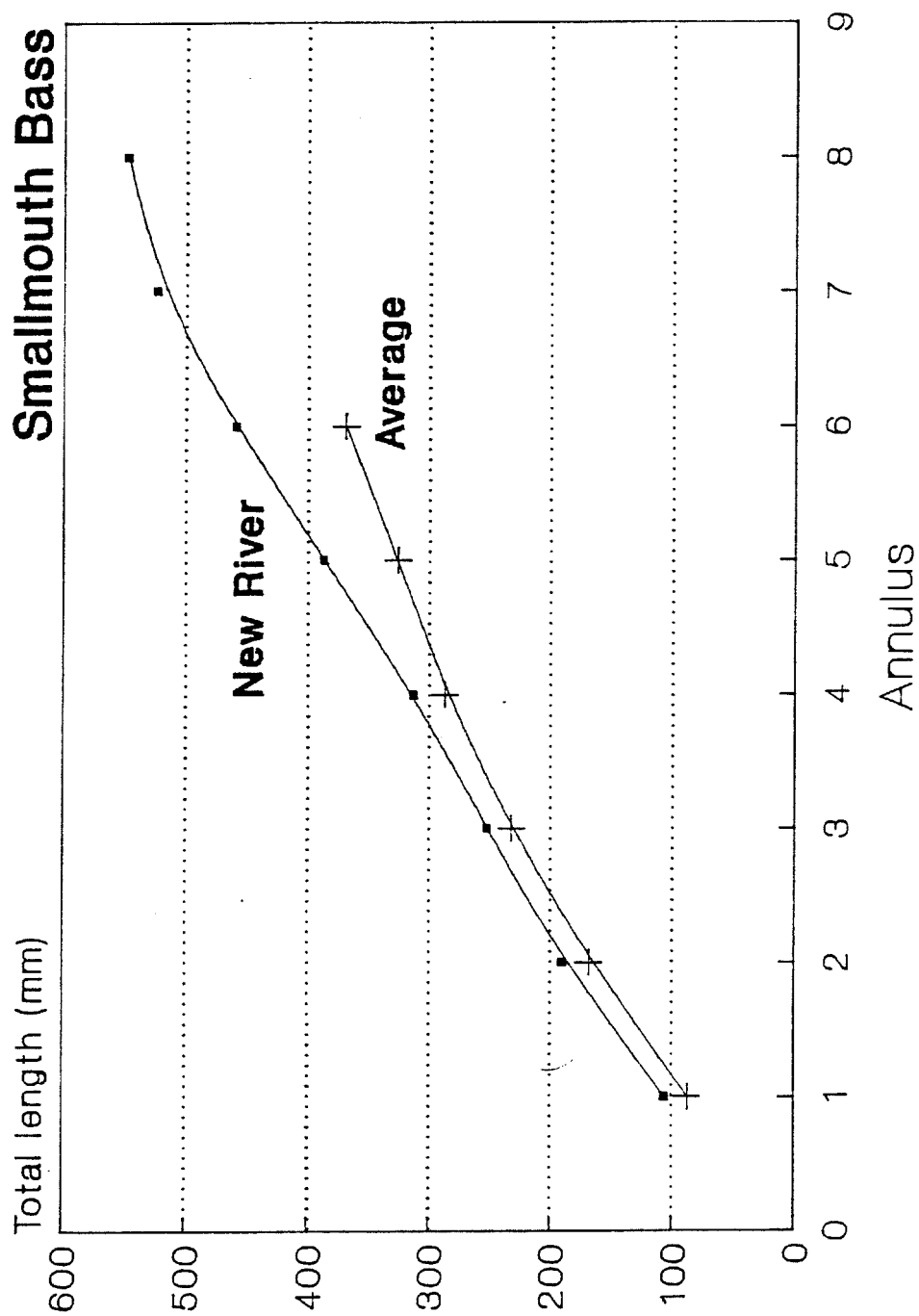


Figure 4. Comparison between mean total lengths-at-annulus (mm) of smallmouth bass from the New River, West Virginia, and the average of mean total lengths-at-annulus reported by Carlander (1977) for 27 stream-resident smallmouth bass populations in 11 states.

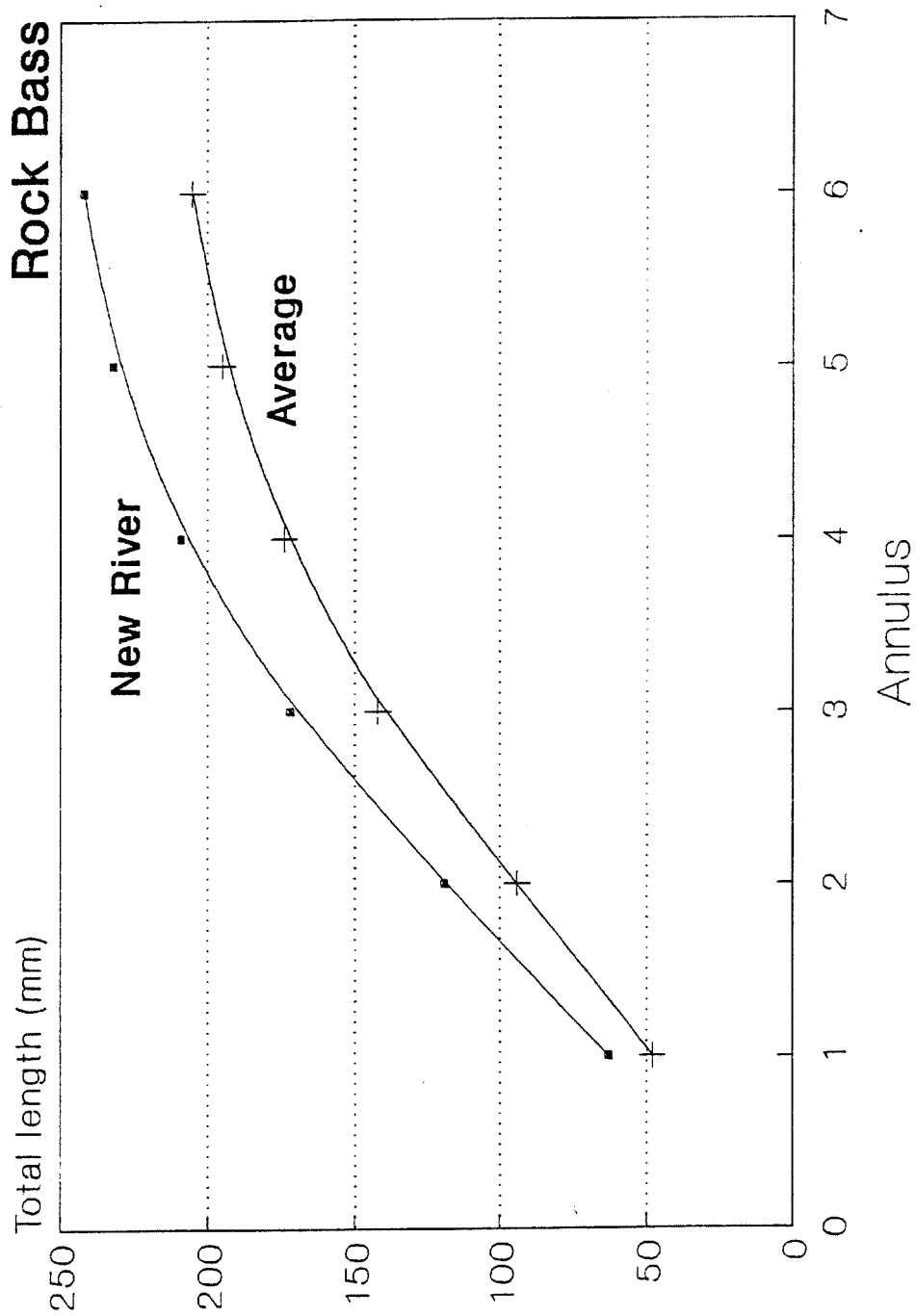


Figure 5. Comparison between mean total lengths-at-annulus (mm) of rock bass from the New River, West Virginia, and the average of mean total lengths-at-annulus reported by Carlander (1977) for 13 stream-resident rock bass populations in six states.

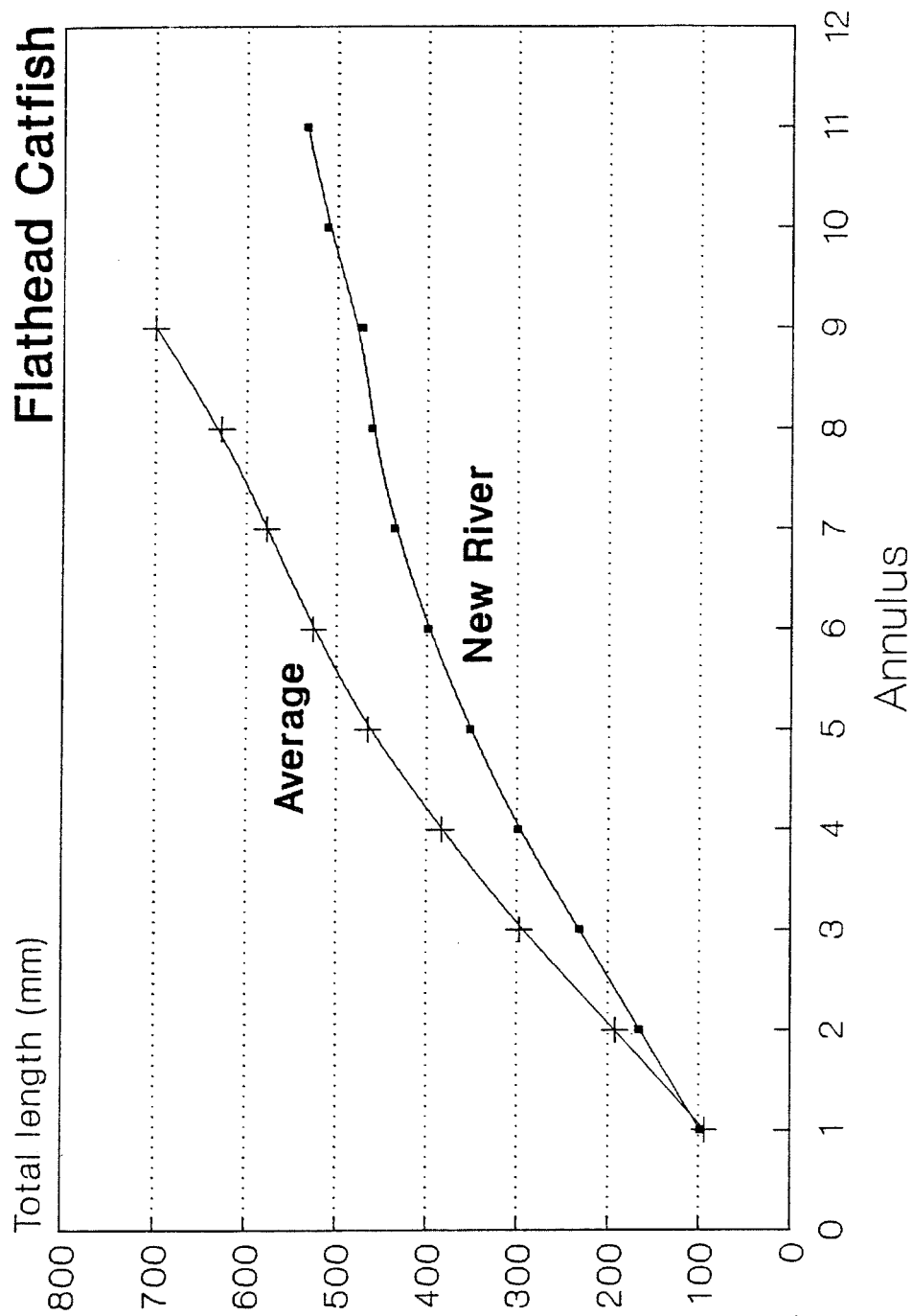


Figure 6. Comparison between mean total lengths-at-annulus (mm) of flathead catfish from the New River, West Virginia, and the average of mean total lengths-at-annulus reported by Turner (1977) for 2 stream-resident flathead catfish populations in 2 states.

Job II: Impacts of commercial harvest of invertebrate baits on the predator-prey interactions in the New River.

Job Number: II-c

Job Title: Predation by sport fishes on invertebrate bait species.

Objective: Determine the consumption of crayfish and hellgrammites by smallmouth bass, rock bass, and flathead catfish.

Period Covered: June 14, 1983 - July 21, 1986

Status: Completed

Abstract:

The diet composition for smallmouth bass, rock bass, and flathead catfish was characterized by stomach contents analysis, and bioenergetics simulations were used to estimate annual consumption of prey by these species. The diet by wet weight of the three predators was dominated by insects and crayfish. Insects were most prevalent in the stomachs of young-of-year fish, and became less important with increasing age of fish. However, crayfish became more prevalent in the diet with increasing age of the predator, and comprised more than 80% of the diet of adult fish. Hellgrammites and fish were relatively unimportant in the diet of these fish species.

Vulnerability of crayfish to predation increased substantially at 15 - 17 mm carapace length (30 - 34 mm total length), as shown by size-frequency of crayfish in the diet of the three predators. Hellgrammite vulnerability was less clear, but a minimum size of about 5.6 mm head capsule width was suggested. Crayfish species composition in the diet of the three species was 45% *Orconectes virilis*, 45% *Cambarus sciotensis*, and 10% *Orconectes sanbornii sanbornii*. Individually, rock bass ate similar proportions of the three crayfish species, but smallmouth bass preyed on *O. virilis* less (37%) and *C. sciotensis* more (57%), while flathead catfish exhibited the opposite tendency (66% *O. virilis* and 29% *C. sciotensis*).

The total annual consumption of crayfish, hellgrammites, insects, and fish by the three predators was 53.1, 4.2, 134.4, and 8.7 kg/ha, respectively, a total of 200.4 kg/ha/yr with a caloric equivalent of 244,495 kcal/ha/yr. Insects were the single most important prey to the smallmouth and rock bass populations, amounting to 69% of total consumption for each species. To the flathead catfish population, insects (43% of total consumption) and crayfish (45% of the total) were equivalently the most important prey. The smallmouth bass population consumed the most crayfish (24.4 kg/ha), insects (69.5 kg/ha), and fish (7.0 kg/ha) annually, while the rock bass popu-

lation consumed the most hellgrammite biomass (3.9 kg/ha). Insects and crayfish were major energetic pathways to the three predator populations. Substantial overlap in energy resources occurred among the three species. Energy resource overlap, calculated with Shoener's Index, was the highest (0.93) between smallmouth and rock bass; overlap between smallmouth bass and flathead catfish was 0.76, and that between rock bass and flathead catfish was 0.74.

The equivalent of 23, 21, and 7% of the annual age 1 and 2 crayfish production was consumed by smallmouth bass, rock bass, and flathead catfish, respectively, and about 4% was harvested for bait. Similarly for hellgrammites, rock bass consumed 13% of the annual age 1 and 2 production, while flathead catfish (1%) and smallmouth bass (< 1%) consumed much less; harvest accounted for about 8% of that production.

Introduction

This portion of the project was designed to provide the direct link between the three dominant fish predators and their prey, most notably crayfish and hellgrammites, the focus of an extensive bait fishery in the New River, West Virginia (Job I-a and -b report). Smallmouth bass, rock bass, and flathead catfish feed heavily on crayfish (Minckley and Deacon 1959; Vannote and Ball 1972; Edmundson 1974; Coble 1975; Layher and Boles 1980; Probst et al. 1984), and the popularity of hellgrammites among anglers on the New River suggests that hellgrammites are a preferred food of sport fish. Therefore, the high abundance of crayfish and hellgrammites in the New River suggests that these prey items are important energy sources for predatory fishes.

This project component is essential for evaluating the effect of crayfish and hellgrammite harvest on the fish predators, and therefore on the sport fishery. Increases in crayfish and hellgrammite harvest could reduce the food resources available for sport fishes, leading to lower fish growth, production, and/or abundance. Reductions in harvest may result in increases in these parameters. The extent of harvest effects depends on the magnitude of crayfish and hellgrammite consumption by the fish predator populations. In addition, changes in the abundance of predators, such as occurs under different fishing regulations, could reduce or increase the availability of invertebrates for commercial harvest.

The objectives were to: (1) characterize the diet composition of each of the three predator fishes by age group, and (2) estimate age-specific consumption of prey by each of the three predator fishes, thereby determining the principal energetic pathways to each species.

Methods

Consumption Estimation

The bioenergetics approach to estimating food consumption by fish (Weininger 1978; Kitchell and Breck 1980; Stewart 1980; Stewart et al. 1981; Cochran and Rice 1982; Kerr 1982; Stewart et al. 1983; Rice and Cochran 1984; Stewart and Binkowski 1986) was used to estimate the annual consumption of each prey type by each predator. Six groups of information for each predator species were required; the latter five are site-specific and are required for each time interval modeled within the year:

- 1) a mass balance equation, and algorithms and parameter estimates therewith, representing fish energetics and physiology,
- 2) live weight estimates for the beginning and end of the time interval,
- 3) ambient water temperatures during the interval,
- 4) caloric densities (calories/gram wet weight) of predator and prey,
- 5) wet weight diet composition (proportions) by prey type, and
- 6) estimates of abundance and daily mortality rates (for cohort-level modeling).

For the purposes of this research, cohort-specific estimates of consumption were generated to evaluate the dependence of each age group on their respective prey. Age assignment occurred at the time of annulus formation, 1 June for smallmouth and rock bass, and 15 June for flathead catfish. Furthermore, a growing season (water temperatures ≥ 10 C) and a winter period (temperatures < 10 C) were defined, since 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 1977; Momot 1978), and hellgrammites (Brown and Fitzpatrick 1978); inactivity below 10 C was assumed for flathead catfish. Therefore, the simulation year for each cohort of smallmouth and rock bass began during the growing season on 1 June (Day 1), proceeded to the be-

ginning of the winter period (23 November; Day 176), continued to the beginning of the next growing season (22 March; Day 295), and culminated on the day before annulus formation (31 May; Day 365). The simulation year for flathead catfish was similar to that of the basses, but was lagged by 14 days due to later annulus formation.

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 growth. The ability to estimate these fates allows estimation of consumption by

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

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 (g/g/d) enabling calculation of absolute estimates of each component for a specific-sized 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 as in most studies. Estimates for the parameters within each algorithm are shown in Table 33 for each of the three predator species.

Consumption

The specific rate of consumption (C) is modeled as a function of three subcomponents;

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

$C_{\max}$ is the maximum specific consumption rate for a fish of a given weight and is calculated as

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

where

a_1 = the intercept for maximum consumption (g/g/d),

b_1 = the slope for maximum consumption dependence on weight, and

W = fish weight (g).

The $C_{\text{adj}}(T)$ function is a temperature-dependent adjuster of $C_{\max}$. The algorithm chosen as the $C_{\text{adj}}(T)$ function is that of Thornton and Lessem (1978), which uses the logistic equation to approximate biological rates which behave in a sigmoid manner. The adjuster is calculated as

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

where

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

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

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

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

θ = the ambient 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 upper and lower maximum-rate temperatures,

θ_4 = the upper minimum-rate temperature, and

γ_1, γ_2 = the specific rate coefficients,

where

$$\gamma_1 = \frac{1}{\theta_2 - \theta_1} \cdot \log_e((K_2 \cdot (1 - K_1)) / (K_1 \cdot (1 - K_2))) \quad , \text{ and}$$
$$\gamma_2 = \frac{1}{\theta_4 - \theta_3} \cdot \log_e((K_3 \cdot (1 - K_4)) / (K_4 \cdot (1 - K_3))) \quad .$$

P is a proportionality constant representing prey availability, and ranges from zero to one. P adjusts consumption to fit growth, and is iteratively chosen to allow the beginning and ending weights for a time interval to conform with the solution of the mass balance equation.

Values for a_1 and b_1 for smallmouth bass were borrowed from the largemouth bass (*Micropterus salmoides*) model derived by Rice et al. (1983) from information presented by Niimi and Beamish (1974). Estimates for rock bass were assumed equivalent to values derived for yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) by Kitchell et al. (1977). "Best-judgement" estimates of a_1 and b_1 for flathead catfish were chosen on the basis of estimates for 12 species presented in Hewett and Johnson (1987).

Values for $K_1 - K_4$ 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 nature of the logistic equation; 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 temperatures at which maximum consumption occurs; θ_2 may equal θ_3 in some fish species. The final temperature preference of a fish species closely corresponds with the optimum temperature for growth and consumption (Brett 1956; Kitchell et al. 1977; Jobling 1981). Smallmouth bass temperature preference information in the literature (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) was reviewed, and respective estimates for θ_2 and θ_3 of 29 and 31 C for young-of-year, and 26 and 28 C for juveniles and adults were chosen. A similar review of the rock bass literature (Neill and Magnuson

1974; Reutter and Herdendorf 1974; Cherry et al. 1977) produced respective estimates for θ_2 and θ_3 of 29 and 31 C for young-of-year, and 27 and 29 C for juveniles and adults. Gammon (1973) hypothesized that the final temperature preference of flathead catfish adults ranged from 31.5 to 33.5 C. Values of 31 and 32 C were assumed for θ_2 and θ_3 , respectively, for juveniles and adults; 33 and 34 C was arbitrarily assumed for young-of-year. The upper avoidance temperature was used to approximate θ_4 . Review of upper avoidance temperatures reported in Cherry et al. (1975), Stauffer et al. (1976), and Cherry et al. (1977) resulted in θ_4 estimates of 35 C for young-of-year and 33 C for juveniles and adults for smallmouth and rock bass. For flathead catfish, values of 37 and 35 C were assumed for young-of-year and older fish, respectively.

Respiration

The specific rate of respiration (R) is also modeled as a function of three sub-components;

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

$R_{\max}$ is the maximum specific standard respiration rate for a fish of a given weight and the general equation is

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

where

a_2 = the intercept for maximum standard respiration (g O₂/g/d),

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

W = fish weight (g).

The $R_{\text{adj}}(T)$ function, similar to $C_{\text{adj}}(T)$ 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 $R_{\text{adj}}(T)$, and is as follows:

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

where

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

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

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

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

T = the ambient temperature,

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

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

Q = 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 that are a result of activity.

Estimates of a_2 and b_2 used by Rice et al. (1983) for largemouth bass and derived by Rice (1981) from data in Beamish (1970) were assumed applicable to smallmouth bass. Estimates of a_2 and b_2 for yellow perch and walleye models developed by Kitchell et al. (1977) were used for rock bass. "Best-judgement" estimates of a_2 and b_2 for flathead catfish were chosen based on the estimates for 12 species presented in Hewett and Johnson (1987). A value of 2.1 for Q has been used by Kitchell et al. (1974; 1977) and Kitchell and Breck (1980); this estimate was applied 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); A was estimated as 1.30 for water temperatures greater than or equal to 10 C, and 1.05 for temperatures less than 10 C. Young-of-year smallmouth bass were assumed to have twice as much activity at all times of year. For rock bass and flathead catfish, activity was assumed to be half that for 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), and the specific rate (S) is 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,

C = specific rate of consumption, and

F = specific rate of egestion.

The proportion of assimilated energy lost to apparent specific dynamic action (SDA) was 0.174 using information from Pierce and Wissing (1974) and Wissing (1974) for bluegills fed mayfly nymphs. 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 (wet weight), and

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

For all three sport fish, 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

this estimate agrees with that of Kelso (1972). The estimate for hellgrammites and insects was chosen based on the work by Elliott (1976) with brown trout (*Salmo trutta*) fed insects of different ration sizes over a range of temperatures. The estimate for fish as prey 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 excreted (all prey).

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

Live Weight Estimates

Estimates of live weight (g; Tables 34, 35, and 36), to which the mass balance equation is fit, were derived from the analysis of age and growth for each predator (Job II-b report). Mean lengths-at-annulus for each cohort were input to a length-weight equation (Table 28; Job II-b report) to estimate live weight on Day 1; each of these cohort-specific live weights became, for the previous cohort, the weight for Day 365 as well as for Day 176 (smallmouth and rock bass) or 162 (flathead catfish), the latter two being the first day of the winter period for the respective species. The assumption was made that the annulus was not completed until weight lost over the winter period was restored to the level just prior to the winter period. A weight of 1 g was assumed for young-of-year smallmouth bass (starting Day 1), rock bass (starting Day 29), and flathead catfish (starting Day 50); these weights were estimated from June and July weight-frequency information.

Since the level of activity (A) is different between the winter period and the growing season, a weight estimate was required for day 295 (smallmouth bass and rock bass) or day 281 (flathead catfish). To estimate this weight, a weighted mean A was calculated using the estimates of A from the two adjacent periods and weighting by the number of days in each period. The iterative fitting procedure (adjusting con-

sumption with P to observed growth) was conducted, using the weights from the beginning of the winter period and the day of annulus formation, and the weighted mean A. The resulting P was then input as a permanent value, and the simulation was run again to predict the weight on Day 295 or 281 (see "Estimating Consumption with Energetics" below for simulation details).

Ambient 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 for input to bioenergetics simulations. Continuously-recording thermographs measured temperature from June 1984 to December 1985 and March to June 1986. In addition, published daily temperature data (Water Resources Data for West Virginia 1979, 1980, 1984) corresponding to 1977 - 1979 and 1982 - 1983 was used. A date-specific mean temperature was calculated at seven-day intervals covering a year's time. The computer software (Hewett and Johnson 1987) used to simulate fish bioenergetics of each species allowed input of temperatures for only 36 dates within the year, and temperatures on days between each input date were linearly interpolated; given this, input dates and corresponding temperatures (Table 37) were thus chosen to represent as accurately as possible the annual temperature regime in the study reach. For flathead catfish, a constant temperature of 6.4 C was assumed for Days 180 through 266 due to computing limitations; this error in winter thermal regime was expected to not significantly affect consumption estimates for flathead catfish, because little feedings occurs at temperatures below 10 C.

Caloric Densities

Caloric densities of 1000 cal/g wet weight for fish, 900 cal/g for crayfish, 1569 cal/g for hellgrammites, and 1350 cal/g for insects were used in the bioenergetics simulations. These estimates were chosen on the basis of calorimetry results (Tables 8 and 9; Job II-a report) and information in Cummins and Wuycheck (1971), Kelso (1972), Vannote and Ball (1972), and Brown and Fitzpatrick (1978).

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 for bioenergetics simulations. Fish were captured with an electrofishing boat (see "Methods" in Job II-b report 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 activity periods of the previous evening and early morning (Reynolds and Casterlin 1976). All captured flathead catfish were sampled for diet items due to a low catch rate. Four prey types were recognized: crayfish, hellgrammites, other insects, and fish. Stomach contents were removed by inserting an acrylic tube (Van Den Avyle and Roussel 1980) of appropriate diameter down the esophagus and into the stomach, and then withdrawing the tube with the contents. A clawed retriever (Dimond 1985) was occasionally used to extract crayfish. In this manner, fish could be released alive. Contents were preserved with either 10% formalin or 100% 2-propanol in plastic bags. The contents of young-of-year smallmouth and rock bass stomachs were examined in the field throughout the 1985 field season, because these groups were expected to feed exclusively on insects. Since only two young-of-year flathead catfish were caught in the two years, an all-insect diet was assumed (Minckley and Deacon 1959). Only the 1985 diet data was used for flathead catfish, because only seven of 36 fish sampled for diet contents 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 wet weight of each prey type in the diet was estimated for each cohort of each predator species (Tables 38, 39, and 40). Small sample sizes for older fish necessitated pooling of information for age 3 and older smallmouth and rock bass, and age 5 and older flathead catfish. Activity is known to cease below temperatures near 10 C for crayfish (Momot 1967; Fast and Momot 1973; Momot and Gowing 1977; Momot 1978) and hellgrammites (Brown and Fitzpatrick 1978). During this time, these animals presumably undergo a dormancy within the substrate of the river, and, in this research, were assumed to be unavailable to predators. Therefore, during the winter period, only insects and fish were considered available prey. Proportions during winter were calculated relative to those used during the growing season; for example, if both insects and fish contributed 25% during the growing season, then in winter, each group comprised 50% of the diet.

Abundance and Mortality Estimates

Age-specific estimates of abundance and daily mortality rates were estimated for the three fish species in the Study Pool (Job II-b report) and used as input (Tables 34, 35, and 36) to the estimation of consumption by each age group.

Estimating Consumption with Energetics

Each cohort of each predator species was modeled separately using 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 end 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. Each cohort was modeled for a one year time period, but since activity (A) and prey availability (P) differ between the growing season and the winter period, three simulation intervals (Tables 34, 35, and 36) were necessary to represent a year of life. The first interval started with the day of annulus formation (the "birthday" of the fish) and went to the last day of the growing season on 22 November; the second interval or winter period (temperatures below 10 C) was from 23 November to 21 March; and the third interval completed the year, proceeding from 22 March (the start of the growing season; temperatures ≥ 10 C) to the day before annulus formation. A daily time step was used, since one day is a recognized cycle in the life of a fish and is sufficiently small enough for one year simulations.

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 assumed to be constant within a simulation interval. Since the consumption subcomponent is adjusted by P, the energy required to produce observed growth was estimated. During each simulated day of the iteration routine, growth was calculated in terms of grams of food per gram of fish per day; daily growth in weight is the product of this specific rate and the weight of the fish on that day. The weight on the next day was calculated by converting the daily growth increment to calories with the caloric density of the prey (since the prey supplies the energy for growth), adding the growth calories to the total caloric content of the fish on that day, and dividing the total by the caloric density of the fish on the next day. The procedure was continued through the last day of the simulation 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 estimate of P was input to

the energetics model, and the simulation was run a final time to estimate consumption by prey type on each day.

Energy Resource Overlap

Shoener's index (1970) was used to quantify the overlap in energy resources between two species as follows:

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

where

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

n = the number of energy resources, that is, 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).

Further Diet Characterization

A more detailed analysis of the stomach contents of the three predator fishes was conducted in addition to that done for consumption estimation (see "Diet Composition" above). Crayfish were identified to species, sex, and form (I or II, male only), when possible. Carapace length (CL; mm) was measured on relatively intact crayfish, but on those exhibiting advanced digestion, the width (mm) of a chela was measured from which carapace length could be back-calculated using predictive equations (Job II-a report). 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. Data from both 1984 and 1985 was pooled for each species in this analysis.

Results

Water Temperature

Water temperature measured immediately below Bluestone Dam was the warmest (26.8 C) in early August, and was the coldest in mid-February (1.8 C; Figure 7). Temperatures rose above 10 C on about 22 March (the first day of the growing season), and fell below 10 C on 23 November (the first day of the winter season). Biota in the New River experience about 5,389 degree-days per year.

Diet Composition

The diet by wet weight of the three predator species was dominated by insects and crayfish (Tables 38, 39, and 40). Insects were most prevalent in the stomachs of young-of-year fish, and became progressively less important with increasing age of fish. Conversely, crayfish became more prevalent with increasing age of the predator. Hellgrammites and fish were relatively unimportant in the diet of the three species. 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).

The size-frequency relationship of carapace lengths (CL) of crayfish in the diet of the three species suggested a minimum threshold size of vulnerability to predation of 15 - 17 mm CL (Figure 8). Therefore, fish predators consumed age 1 and 2 *Cambarus sciotensis* (Figures 9 and 10), *Orconectes virilis* (Figures 11 and 12), and *Orconectes sanbornii sanbornii* (Figures 13, 14, and 15), with predation commencing on young-of-year of the latter two species in approximately early August. In the diet of the three predators, *O. virilis* and *C. sciotensis* were equally important (45%), while *O. s. sanbornii* represented only 10% of crayfish in the diet. The size-frequency relationship of hellgrammite head capsule widths (HCW) suggested a minimum threshold to predation of 5.6 mm HCW (Figure 16), which corresponded to age 1 and 2 animals (Figures 17, 18, and 19).

Smallmouth Bass

Smallmouth bass had the second highest proportions of crayfish in the diet of the three predator fishes. Crayfish was most prevalent in the diet of age 3 - 6 bass (89% by wet weight; Table 38) with progressively lower proportions in age 2 (59%), age 1 (21%), and young-of-year (0%) bass. Hellgrammites were the least important to smallmouth bass of the four prey types, comprising less than 1% of the diet of any age group. Conversely, other insects were very prevalent in the diets of young-of-year (100%), age 1 (63%), and age 2 (21%) bass; insects comprised less than 4% of the diet of older bass. Fish in the diet appeared marginally important, ranging from 19% in age 2 bass to 7% in ages 3 - 6 bass; young-of-year did not contain fish.

A minimum threshold size to predation of 17 mm CL was indicated by the size-frequency distribution of crayfish carapace lengths for crayfish in the diet of smallmouth bass (Figure 20). The relationship for hellgrammites was unclear due to a paucity of larvae in the diet. Identifiable crayfish in the diet of smallmouth bass (both years pooled) were 37% *O. virilis*, 51% *C. sciotensis*, and 12% *O. s. sanbornii*. Fish in the diet were six shiners (*Notropis* spp.), five young-of-year smallmouth bass, four darters (*Percina* spp., *Etheostoma* spp.), two young-of-year rock bass, one flathead catfish, and 24 unidentified fish. Total lengths of fish in the diet ranged from 28 - 103 mm, and fish in the diet for which only standard lengths were measurable ranged from 37 - 86 mm.

Rock Bass

Rock bass adults had the lowest proportion of crayfish (81% by wet weight) in their diets compared to adults of smallmouth bass and flathead catfish, but crayfish were the most important of the four prey types to older rock bass (ages 3 - 5; Table 39). Lower proportions occurred in the diet of age 2 (56%), age 1 (5%), and young-of-year (0%) rock bass. Hellgrammites were a larger proportion of the diet of rock bass relative to the other two predators, but were marginally important with respect to other prey. Similar to smallmouth bass, insects were prevalent in ages 0 - 2 rock bass, but assumed lesser importance in older bass. Fish were virtually nonexistent in the rock bass diet.

The distribution of crayfish carapace lengths for crayfish in the rock bass diet suggested a minimum threshold size to predation of 17 mm CL (Figure 21), similar to that for smallmouth bass; a maximum of 35 mm CL was also suggested by the distribution. A low predation rate on hellgrammites by bass precluded a similar assessment for hellgrammites. The crayfish species composition in the rock bass diet

(both years pooled) was 41% *O. virilis*, 48% *C. sciotensis*, and 11% *O. s. sanbornii*. One unidentified fish was found in the rock bass diet.

Flathead Catfish

Crayfish were proportionally most prevalent in the diet of flathead catfish compared to the other two species, and ranged from 98% in ages 5 - 8 catfish to 20% in age 2 catfish (Table 40). Hellgrammites appeared marginally important to ages 2 (3%) and 3 (8%) catfish, and were not found in age 1 or ages 5 - 8 flathead catfish. Insects were prevalent in only age 1 catfish, and were assumed to be the only prey of young-of-year. Insects were marginally prevalent in ages 2 - 4 catfish, and were not found in older fish (ages 5 - 8). Fish was second in importance to age 2 (23%) and 3 (18%) flathead catfish, while other age groups contained 10% or less of fish.

A minimum threshold size to predation of 15 mm CL was indicated by the distribution of carapace lengths of crayfish in the diet of flathead catfish (Figure 22). A similar assessment for hellgrammites was not possible due to a low predation rate on larvae by catfish. Species composition of crayfish in the flathead catfish diet (both years pooled) was 66% *O. virilis*, 29% *C. sciotensis*, and 5% *O. s. sanbornii*. Fish in the flathead catfish diet were five shiners, three young-of-year smallmouth bass, two young-of-year rock bass, two flathead catfish, and 11 unknown fish. Measurable total lengths of these fish ranged from 27 - 63 mm, and fish for which only standard lengths were measurable included only one flathead catfish which was 67 mm.

Consumption

The total annual consumption of crayfish, hellgrammites, insects, and fish by the three predator populations in the Study Pool was 53.1, 4.2, 134.4, and 8.7 kg/ha, respectively (Tables 41, 42, and 43), a total of 200.4 kg/ha/yr with a caloric equivalent of 244,495 kcal/ha/yr. The smallmouth bass population consumed the most crayfish (24.4 kg/ha), insects (69.5 kg/ha), and fish (7.0 kg/ha), while the rock bass population ate the most hellgrammite biomass (3.9 kg/ha). Insects were the single most important prey to the smallmouth and rock bass populations, amounting to 69% of total consumption for each species; insects (43% of total consumption) and crayfish (45% of the total) were equivalently the most important prey to the flathead catfish population.

Smallmouth Bass

The smallmouth bass population (ages 0 - 6) consumed an estimated 100.8 kg/ha/yr of prey with a caloric equivalent of 122,783 kcal/ha/yr. Eighteen percent of the annual energy intake was from crayfish, 0% from hellgrammites, 76% from insects, and 6% from fish (Table 41). Age-specific consumption estimates for smallmouth bass suggested that insects were the chief source of energy for young-of-year (100%) and age 1 (71%) bass. Ages 2 bass relied on insects to a lesser degree (28%) as an energy source, and depended more on crayfish (52% of energy intake). Ages 3 - 6 bass obtained 86% of their energy from crayfish; insects were relatively unimportant to these age groups. Fish was a moderately important energy source for age 1 (13%), age 2 (19%), and ages 3 - 6 (8%) bass; hellgrammites were not important sources of energy.

Gross growth efficiency (Table 44), the ratio of annual production (kg/ha/yr X 1000 kcal/kg) to annual consumption (kcal/ha/yr), suggested that about one third of ingested energy goes to growth. Growth efficiency ranged from 32% for young-of-year and age 3 bass to 36% for age 1 bass.

In the bioenergetics simulations, values of P (Table 34), which allowed predicted fish growth to match observed growth by adjusting consumption (see "Estimating Consumption with Energetics" in the Consumption Estimation section of Methods), ranged from 0.22 - 0.30 during summer-fall (1 June to 22 November), 0.07 - 0.12 during winter (23 November to 21 March), and 0.14 - 0.18 during spring (22 March to 31 May).

Rock Bass

An estimated 83.4 kg/ha/yr (103,701 kcal/ha/yr) was consumed by the rock bass population (ages 0 - 5) in the Study Pool. Crayfish, hellgrammites, insects, and fish supplied 19, 6, 75, and 0%, respectively, of the annual energy intake of the population (Table 42). Insects were the primary energy source of young-of-year (100% of energy intake) and age 1 (97%) bass; the importance of insects diminished for age 2 (39%) and ages 3 - 5 (11%) bass. Crayfish as an energy source was equivalent to that of insects for age 2 bass (44% of energy consumed), but was the greatest source of energy for ages 3 - 5 bass (71%). Hellgrammites provided 17 - 18% of the annual energy intake of rock bass, while fish supplied virtually no energy benefit.

Gross growth efficiency (Table 44) increased from 20% in young-of-year to 22% in age 1 rock bass, then progressively declined to 4% in age 5 bass. Values of P from

the bioenergetics simulations ranged from 0.25 - 0.38 during summer-fall, 0.21 - 0.39 during winter, and 0.28 - 0.49 during spring (Table 35).

Flathead Catfish

The flathead catfish population (ages 0 - 8) ingested an estimated 16.1 kg/ha/yr (18,011 kcal/ha/yr). The annual energy budget of the population was 36% crayfish, 3% hellgrammites, 52% insects, and 9% fish (Table 43). Similar to the other two predators, insects were the major energy source of young-of-year (100% of energy intake) and age 1 (78%) catfish. Insects diminished in importance for older catfish except age 4 fish (24%), and crayfish became progressively more important for age 2 (68%), age 3 (62%), age 4 (71%), and ages 5 - 8 (95%) catfish. As an energy source, fish was marginally important to age 2 (25%) and age 3 (20%) fish, and assumed a lesser importance for age 1 (8%) and ages 4 - 8 (4 - 6%). Energy was derived from hellgrammites by age 2 (5% of annual energy intake), age 3 (13%), and age 4 (1%) catfish.

Flathead catfish gross growth efficiency (Table 44) progressively declined from 33% in young-of-year to 9% in age 8 fish. Bioenergetics P values ranged from 0.09 - 0.31 in summer-fall, 0.09 - 0.17 in winter, and 0.11 - 0.16 in spring (Table 36).

Energy Resource Overlap

Considerable overlap in energy resources occurred among the three predator species. Energy resource overlap was the highest (0.93) between the smallmouth and rock bass populations. Overlap between smallmouth bass and flathead catfish was 0.76, and that between rock bass and flathead catfish was 0.74.

Discussion

Diet Composition

Much research effort has gone into the characterization of the diet of fishes, both qualitative and quantitative. Of the three species studied in this research, more work has been conducted on smallmouth bass than on rock bass or flathead catfish, but detailed diet analysis by age of the fish is lacking in the fisheries literature. An exception is the work of George and Hadley (1979), who investigated the diet of young-of-year smallmouth and rock bass through the growing season with respect to food and habitat partitioning.

Smallmouth Bass

The diet of smallmouth bass in the New River progressively changed with age from a reliance on aquatic and terrestrial insects by young-of-year to a dominance of crayfish in older bass. Young-of-year smallmouth bass in the upper Niagara River, New York, preyed on zooplankton (from Lake Erie), amphipods (*Gammarus* sp.), aquatic insects (chironomid larvae and adult caddisflies), and fish (George and Hadley 1979); the latter two prey types dominated the diet later in the year. Young-of-year smallmouth bass in East Koy Creek, New York, preyed primarily on aquatic insects (35.0% by volume) and fish (30.8%); crayfish (19.6%) and copepods (from an upstream reservoir; 11.7%) were second in importance (Lachner 1950). Most accounts of the diet of smallmouth bass report a dominance of crayfish in the diet of older bass (Vannote and Ball 1972; Scott and Crossman 1973; Miner 1978; Probst et al. 1984; Austen and Orth 1985), however there are exceptions. Surber (1941) found that fish were the dominant prey in the diet of smallmouth bass from the Shenandoah River, Virginia, and the diet of immature and adult smallmouth bass in the Buffalo River, Arkansas, was dominated by fish (Kilambi et al. 1977). Fish were relatively unimportant in the diet of New River smallmouth bass. During electrofishing, abundance of forage fish in the New River appeared low, and was reflected in the smallmouth bass diet. Diet composition of adult smallmouth bass appears to be, in

part, a function of prey availability. Smallmouth bass may prefer crayfish to fish, perhaps due to easier catchability, but if fish of appropriate size are relatively abundant, smallmouth bass may opportunistically prey on them to a greater extent, thereby attaining a more favorable benefit / cost relation in terms of energy. Surber (1941) found that smallmouth bass in the Shenandoah River, Virginia, consumed relatively more fish than smallmouth bass in two other streams of the same drainage, presumably due to a higher abundance of forage fish in the former relative to the latter. Shenandoah River bass also had noticeably higher visceral fat content than those from the other two streams. Surber (1941) hypothesized that relatively greater growth rates (not reported) and visceral fat content were a result of greater predation on fish by Shenandoah River bass relative to that by bass in the other two streams.

Hellgrammites were infrequent in the New River smallmouth bass diet, although larvae were relatively abundant (Job II-a report). A similar result was found for smallmouth bass in three streams (Surber 1941). In both cases, although larvae were abundant, they were apparently unavailable as prey due to their secretive behavior.

The species composition of crayfish in the diet of smallmouth bass in the Study Pool (37% *O. virilis*, 51% *C. sciotensis*, and 12% *O. s. sanbornii*) differed substantially from that in quantitative (13% *O. virilis* and 87% *C. sciotensis*; Figure 3; Job II-a report) and qualitative (7% *O. virilis*, 86% *C. sciotensis*, and 7% *O. s. sanbornii*) crayfish collections from deeper (1 - 3 m), mid-stream locations in the pool. However qualitative crayfish collections from shallower (< 1 m) locations associated with the stream margins, areas where smallmouth bass probably forage during crepuscular periods (when peak smallmouth bass activity occurs; Reynolds and Casterlin 1976), had species compositions (23% *O. virilis*, 55% *C. sciotensis*, and 22% *O. s. sanbornii*) more closely resembling that in the smallmouth bass diet. Probst et al. (1984) found that smallmouth bass in two small Missouri streams fed on each of two species of crayfish in approximate proportion to their relative abundances, which lends support to the conclusion that New River smallmouth bass are also unselective predators on suitable-sized crayfish.

The size-frequency relationship of carapace lengths (CL) of crayfish in the diet of smallmouth bass indicated a minimum threshold size of vulnerability to predation of about 17 mm CL (Figure 20). Smallmouth bass studied in two Missouri streams (Probst et al. 1984) exhibited a similar threshold at about 10 mm CL (20 mm total length), and ate crayfish up to a size of about 28 mm CL (55 mm total length). Predation on crayfish near the threshold may be limited by abundance and size of available prey. In the New River, older smallmouth bass were capable of detecting and ingesting aquatic insects, presumably from drifting insects of benthic origin. This suggests that most crayfish smaller than the threshold size can be detected by smallmouth bass, but are unavailable as prey due to habitat selection differences between the two groups. Predation of the largest crayfish may be limited by abun-

dance (of relatively few, older crayfish), mouth gape of the predator, and behavioral responses by the crayfish (Stein and Magnuson 1976). Furthermore, the energy gain from crayfish (kcal/g live weight) declines as crayfish size increases due to corresponding increases in the proportion of indigestible materials (Stein and Murphy 1976).

Rock Bass

The diet composition of New River rock bass (Table 39) changed from a predominance of insects in young rock bass to a crayfish-dominated diet in older rock bass. In addition, rock bass relied on hellgrammites more than the other two predator species, and fish were virtually absent in the rock bass diet. Young-of-year rock bass in the upper Niagara River, New York, relied on aquatic insects (mayfly nymphs, adult caddisflies) and amphipods (George and Hadley 1979). Rock bass (100 - 254 mm total length) in two Missouri streams also ate crayfish extensively (Probst et al. 1984), but fish were more important in the diet of Missouri rock bass than in New River rock bass, which may reflect a low abundance of forage fish in the New River. Rock bass (≥ 76 mm total length) in a Michigan stream also fed heavily on crayfish (Vannote and Ball 1972). Use of insects by rock bass in Missouri (Probst et al. 1984) was comparable to use by New River rock bass.

The species composition of crayfish in the rock bass diet (41% *O. virilis*, 48% *C. sciotensis*, and 11% *O. s. sanbornii*) was remarkably similar to that of smallmouth bass, more so than that reported by Probst et al. (1984) for rock and smallmouth bass in two Missouri streams. The crayfish species composition of the rock bass diet was more similar to that of crayfish collections from shallow stream margins than from deeper, mid-stream locations, and may be a reflection of foraging by rock bass in shallower locations. Probst et al. (1984) found that rock bass fed on two crayfish species in proportion to their relative abundance in two Missouri streams.

Minimum and maximum threshold sizes to predation of 17 and 35 mm CL, respectively, were suggested by the size-frequency distribution of crayfish carapace lengths in the diet of rock bass (Figure 21). Probst et al. (1984) showed that rock bass predation on crayfish was substantial at crayfish total lengths of 30 - 45 mm (carapace lengths of about 15 - 23 mm). Rock bass predation on crayfish near the lower threshold is probably related to the size and abundance of available prey, as speculated for smallmouth bass, and crayfish smaller than the threshold may be unavailable as prey. Predation on crayfish near the upper threshold is probably limited by rock bass size (that is, mouth gape) more than availability of prey near that size.

Flathead Catfish

The diet of flathead catfish in the New River (Table 40) shifted from a predominance of insects in age 1 catfish to a diet dominated by crayfish in age 2 and older catfish. The all-insect diet of young-of-year flathead catfish was reasonably assumed from other studies. Aquatic insects comprised 91% (by volume) and 96% of young-of-year flathead catfish in the Big Blue and Neosho Rivers, Kansas (Minckley and Deacon 1959); catfish of approximately age 1 decreased use of aquatic insects and increased use of fish and crayfish, while older catfish relied heavily on fish and crayfish. A more general assessment of the diet of flathead catfish in the Tombigbee, Alabama, and Tenshaw Rivers, Alabama, suggested that flathead catfish switched from an invertebrate-dominated diet to a fish-dominated diet after achieving a length of approximately 254 mm. In reservoirs, adult flathead catfish have been documented to feed heavily on fish and crayfish (Turner and Summerfelt 1970; Edmundson 1974; Layher and Boles 1980).

Crayfish species composition in the New River flathead catfish diet (66% *O. virilis*, 29% *C. sciotensis*, and 3% *O. s. sanbornii*) differed the most of the three predator species from that in collections from deeper areas. Flathead catfish likely consume crayfish in proportion to each species' relative abundance, because they have a larger mouth gape and attain a larger size than smallmouth and rock bass, and could thus be assumed to feed indiscriminately on crayfish. Flathead catfish probably also feed in shallower areas at night; in general, flathead catfish were only occasionally caught during the day in shallow areas, but substantially more were caught there at night. Nevertheless, the differences between crayfish species composition in shallow areas of the Study Pool and in the flathead catfish diet remains unexplained.

Crayfish of about 15 mm carapace length or greater were vulnerable to predation (Figure 22). Vulnerability at this size was perhaps due to abundance and size of available crayfish; as speculated for smallmouth and rock bass, smaller crayfish were probably unavailable as prey.

Consumption

The bioenergetics approach to estimating consumption was validated for largemouth bass by Rice and Cochran (1984); estimates from bioenergetics simulations compared favorably with independent estimates of consumption. Thus, consumption estimates for New River fish predators were considered reliable with respect to the estimation method employed. Direct measurement of consumption in

the field yields few, highly variable point estimates which are labor intensive to achieve (Kerr 1982; Rice and Cochran 1984; Hewett and Johnson 1987).

Error Sources in Bioenergetics Models

Recent models of fish energetics involve many variables, one or more of which, if in serious error, could seemingly preclude reasonable consumption estimates. Despite the utmost care in estimating physiological parameters in the laboratory, numerous site-specific parameters (abundance and mortality, temperature, growth, diet composition, and caloric density) must also be resolved with relative accuracy. Consumption by several populations of different fish species has been estimated with bioenergetics models by several researchers, some of whom have evaluated the effects of input parameter errors on consumption estimates. Although all the models have a common foundation, that is, consumption equals growth plus respiration, each employs somewhat different algorithms for the various components. Nevertheless, sensitivity analyses (Majkowski and Waiwood 1981; Rice et al. 1983; Stewart et al. 1983) and error analyses (Bartell et al. 1986) have yielded generally similar conclusions regarding which model variables most influence estimates of consumption. Most influential are those variables associated with the consumption and respiration subcomponents; in this research, such variables corresponded to θ_2 and K_2 for consumption, and b_2 and Q for respiration. Error analyses of effects of input errors on growth or consumption prediction using three bioenergetics model variants led Bartell et al. (1986) to emphasize the need to accurately determine consumption and respiration relations for a species regarding temperature and fish weight effects, the two driving variables of these functions. Errors in consumption and respiration are likely further enhanced when parameter estimates for a species are assumed equivalent to those derived for other species as done in this research and other studies. For New River predators, parameters associated with temperature were directly used or derived from published information in the literature, and were considered reasonably accurate estimates. Estimates of coefficients for $C_{\max}$ (a_1 and b_1) and $R_{\max}$ (a_2 and b_2) for largemouth bass (Rice et al. 1983) were assumed applicable to smallmouth bass, and also considered reasonably accurate. A different approach was used in selecting the values of these coefficients for rock bass and flathead catfish, because values for closely related species were not available as was the case for smallmouth bass. Two assumptions were considered in the selection process: 1) 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), and 2) the maximum respiration rate ($R_{\max}$) was directly related to the gill surface area per unit body weight (ability to supply oxygen; Pauly 1981). In regard to these assumptions, rock bass were considered to be similar to yellow perch for which estimates were derived by Kitchell et al. (1977), therefore the yellow perch estimates were used for rock bass.

Consumption and respiration coefficients developed for other species were not considered applicable to flathead catfish in regard to the above assumptions, so "best-judgement" values were chosen. The coefficient estimates for all three species were considered first approximations, and were likely the greatest source of error in consumption estimates for New River predators. With respect to the difficulty of estimating consumption by any method, this approach was considered the most appropriate.

Apparent specific dynamic action (SDA), egestion (F), and excretion (U) parameters are indirect sources of large error (Bartell et al. 1986), because they are calculated as proportions of consumption, a parameter potentially prone to large error. Fortunately, modeling SDA, F, and U as simple fractions of consumption is adequate (Yahl and Davenport 1979; Kitchell and Breck 1980; Bartell et al. 1986). Activity metabolism (A) behaves similarly, being a multiple of standard respiration, a parameter also prone to large error. Of the physiological parameters, accurate measurement of activity metabolism is the most difficult due to behavioral influences of the fish. Fortunately, well-documented behavior and activity of smallmouth bass by Klauda (1975) allowed derivation of a good first approximation of A. Reasonably assuming that rock bass and flathead catfish are less active species than smallmouth bass, confident estimates for these species were made. The range of values that physiological parameters can assume is limited by the constraint in the model that simulated growth must fit observed growth (Bartell et al. 1986). Therefore, the parameter estimates chosen for smallmouth bass, rock bass, and flathead catfish were considered useful approximations.

Site-specific variables can have an important influence on consumption estimates. Bartell et al. (1986) emphasized the need for an accurate representation of water temperature, since it is an important input variable to the consumption and respiration subcomponents. Water temperature in the New River, measured with continuously-recording thermographs and borrowed from official water resources publications (United States Geological Survey 1979, 1980, 1984), was considered very accurate for this research. Further, previous studies of consumption by fish populations in lakes necessarily assumed that individual fish sought temperatures closest to their thermal optima for consumption and growth due to thermal stratification. New River temperatures were assumed uniform from the surface to the stream bed due to continuous mixing at least in riffle areas.

Accurate estimates of growth, abundance, and mortality are necessary for cohort-level estimates of consumption (Majkowski and Waiwood 1981). Detailed age and growth analysis of New River predators (Job II-b report) was performed and was considered accurate for our purposes. Abundance and mortality estimates were considered accurate as well, given the size of the system studied.

Errors in diet composition and caloric density appear to be relatively unimportant with respect to errors of other parameters in predicting growth with bioenergetics models. In analyses of an alewife energetics model, Bartell et al. (1986) found that, in predicting alewife growth, diet composition uncertainty and a nearly three-fold difference in caloric density of four prey types were insignificant relative to error contributions from physiological parameters. Intuitively, when bioenergetics models are used to estimate consumption, errors in diet composition and caloric density can introduce substantial error into prey-specific estimates of consumption. Nevertheless, diet proportions for estimating consumption of the three New River predators were considered reliable. Diet samples were collected from smallmouth bass and rock bass in the morning to take advantage of peak activity periods occurring the previous evening and early morning (Reynolds and Casterlin 1976), and to minimize biases (to calculated proportions) caused by differential digestion rates of the different prey types. Compared to fish and insects, crayfish probably require more time to digest due to their relatively thick exoskeleton. Therefore, the greater the period between feeding by the fish and inspection of the fish diet, the greater becomes the error in inflating the percentage of crayfish in the diet of the predator and in not detecting the presence of fish or insects eaten during the same time. Morning collection of smallmouth and rock bass diet samples was an attempt to minimize this bias. Largemouth bass held in water temperatures of 23 - 26 C (equivalent to the highest average temperatures in the New River) completely digested five mosquitofish (*Gambusia affinis*) in an average of 17.5 hrs (range of 16 - 19 hrs; Hunt 1960). In the same study, complete digestion by warmouth (*Lepomis gulosus*) similarly fed averaged 26.2 hrs (range of 24 - 28 hrs). For both species, the average time of complete digestion of one fish is probably somewhat less, because Hunt (1960) also showed that Florida gar (*Lepisosteus platyrhincus*) completely digested one mosquitofish in about 40% of the time required to digest five mosquitofish. Largemouth bass completely digested bleak (*Alburnus alburnus*) in 19 hrs at water temperatures of 25 C (Molnar and Tolg 1962). Bluegill (*Lepomis macrochirus*) completely digested six prey organisms (crayfish, darters, chironomids, dragonfly naiads, mayfly naiads, and oligochaetes) in about 18 - 21 hrs at temperatures ranging from 18.1 - 22.0 C (Windell 1967); the crayfish were probably quite small given the size of the bluegills (average of 133 mm) and the relatively low percentage of chitin (1.07%) reported for crayfish. Thus, heavier use of fish or insects by smallmouth and rock bass would probably have been detected, because only about 12 hrs elapsed between feeding the previous evening and diet sampling the next morning. Given that flathead catfish feed nocturnally and assuming that insects and fish digest more rapidly than crayfish, proportions of crayfish in the flathead catfish diet may have been slightly positively biased, because catfish were caught and sampled throughout any given day.

Caloric density of New River crayfish (*O. virilis* only) and hellgrammites was estimated directly, and considered accurate. Estimates for fish (predators and prey)

and insects from the literature were considered reliable first approximations for application to the New River system. The assumptions of constant energy density has been used extensively, but can lead to substantial error in predictions if the species modeled exhibits an extreme annual cycle of energy density such as some salmonine and clupeoid fishes (Stewart and Binkowski 1986); the three New River predators and their prey were reasonably assumed to have relatively little variability in caloric density through the year.

Overall, errors in estimates of consumption for the three New River predators was probably moderate. However, the general magnitude of consumption for each species was determined, and should prove useful in evaluating the effect of predation on the crayfish and hellgrammite populations.

Predation and Energy Resources

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. Consumption of crayfish by smallmouth bass in a Michigan stream (assuming an all crayfish diet) was an estimated 60.6 kg/ha/yr (compared to 24.2 kg/ha/yr in the New River), and that by rock bass was roughly estimated as "probably twice that harvested by smallmouth bass" (Vannote and Ball 1972).

Age 1 and 2 crayfish were consumed extensively by all three predator populations in the New River. The equivalent of 23, 21, and 7% of the estimated annual age 1 and 2 crayfish production (Job II-a report) was consumed by smallmouth bass, rock bass, and flathead catfish, respectively, and 4% was harvested by man for bait. In addition, consideration of other sources of predation on crayfish (birds, amphibians, reptiles, mammals, and other fish) suggests that food resources could have been limiting to older predator fishes and that competition for these resources may have occurred, especially between smallmouth bass and rock bass. Smallmouth bass in a Michigan stream consumed an estimated 15% of the annual crayfish production (18% of the annual age 1 and 2 crayfish production; Vannote and Ball 1972); a value comparable to that of smallmouth bass in the New River.

Age 1 and 2 hellgrammites were consumed less extensively than crayfish by the three predator species, and were not considered an important food resource. Rock bass consumed an estimated 13% of the annual production, followed in importance by flathead catfish (1%) and smallmouth bass (< 1%). Harvest by man was approximately 8%. In addition, hellgrammites likely have few other predators besides fish due to their secretive behavior.

Gross growth efficiency in fish declines with increasing fish size or age (Kinne 1960; Paloheimo and Dickie 1966; Gerking 1971; Jones 1976; Webb 1978; Ursin 1979; Majkowski and Waiwood 1981; Adams et al. 1982; Stewart and Binkowski 1986). This pattern was apparent in age-specific growth efficiencies for rock bass and flathead catfish (Table 44), but growth efficiencies for smallmouth bass remained relatively constant, which suggests an error in one or more subcomponents of the smallmouth bass bioenergetics model. The error source was probably the exponent for maximum standard respiration (b_2), which controls the shape of the relationship between specific respiration rate and weight. The true value of b_2 for a fish species is expressed in the relationship between consumption (actually assimilated energy) and respiration; as fish size increases, progressively more assimilated energy is required for body maintenance and less for growth, thus producing a lower growth efficiency. As values of b_2 become larger (absolute value becomes smaller), estimates of maximum specific standard respiration rate for a given fish weight become greater. In this research, the value of b_2 , borrowed from the largemouth bass model (Rice et al. 1983), was probably an underestimate (too negative), producing a rather constant ratio between growth and consumption, and therefore growth efficiency, for all age groups. Such an error would result in underestimates of age-specific consumption rates, because lower respiratory energy losses were therefore modeled, producing a lower value of P (proportion of maximum consumption realized).

Energy resource overlap, estimated with Shoener's (1970) overlap index, was relatively high among the three fish predator populations in the New River. Substantial overlap (0.93) occurred between smallmouth and rock bass. In addition, overlap in sizes of crayfish eaten by smallmouth and rock bass was considerable (see "Diet Composition" for these species in Results). Probst et al. (1984) estimated diet composition overlap of smallmouth and rock bass (100 - 254 mm total length) in two Missouri streams using Shoener's index; diet overlap was 0.73 (March-July) and 0.72 (August-November). Unless food is limited, high overlap values do not necessarily indicate competition for food resources, and can result when prey is readily available. Probst et al. (1984) concluded similarly, and noted that diet overlap between fishes can be highest during high food abundance, supporting their argument with information from Gee and Northcote (1963), Nilsson (1967), and Zaret and Rand (1971); they concluded that smallmouth and rock bass in their streams did not segregate ecologically through food resource partitioning, but rather on the basis of habitat use. Lobb (1986) regarded these two species as habitat generalists, but did not attempt to quantify differences in habitat use relative to current velocity within a habitat type as did Probst et al. (1984). 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 smallmouth bass (see "Diet Composition" for smallmouth bass above) suggested that prey fishes were not abundant or available,

and may contribute to increased competition for crayfish between smallmouth bass and rock bass. Thus, ensuring adequate numbers of suitable-size crayfish is critical to the "health" of both predator populations and the fisheries they support.

Overview

Aquatic insects and crayfish were overwhelming in their importance as energy resources to smallmouth bass, rock bass, and flathead catfish. However, the abundance of both prey groups is potentially jeopardized by past, present, and future human activities. Two activities threaten to at least alter the aquatic macroinvertebrate assemblage below Bluestone Dam. First, in 1986, an insecticide was applied to the New River in an attempt to eliminate black fly larvae, and therefore control nuisance adult blackflies; Although the insecticide use was halted in 1987, application may occur again. Second, Bluestone Dam may be converted to hydroelectric capability (from run-of-river flood control), which could result in serious consequences for downstream biota. Predators currently have a greater demand for crayfish than do humans (bait retailers and anglers), but human demand can be expected to increase as the popularity of the New River for recreation increases. The effects of humans on the prey-predator interactions below Bluestone Dam are addressed more fully in the next section (Job II-d).

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Tables

Table 33. Parameter estimates used in the bioenergetics models for smallmouth bass (SMB), rock bass (RB), and flathead catfish (FHC).

Symbol	Parameter Description	Parameter Estimate		
		SMB	RB	FHC
Consumption				
a_1	Intercept for maximum consumption (g/g/d)	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 :	10	10	10
θ_2	Temperature for K_2 : Young-of-year Juveniles and adults	29	29	33
		26	27	31
θ_3	Temperature for K_3 : Young-of-year Juveniles and adults	31	31	34
		28	29	32
θ_4	Temperature for K_4 : Young-of-year Juveniles and adults	35	35	37
		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 /g/d)	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: Young-of-year Juveniles and adults	35	35	37
		33	33	35
T_{max}	Maximum temperature for standard respiration: Young-of-year Juveniles and adults	39	39	40
		38	37	38
SDA	Proportion of assimilated energy lost to SDA	0.17	0.17	0.17

Table 33. Concluded.

Symbol	Parameter Description	Parameter Estimate		
		SMB	RB	FHC
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 $\geq$ 10 C			
	Young-of-year	1.60	1.3	1.3
	Juveniles and adults	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

Table 34. Site-specific information and iteratively fit values of P for the estimation of smallmouth bass annual consumption.

Age/Cohort	Days Represented ¹	Starting Weight (g)	Final Weight (g)	Starting Abundance	Daily Mortality Rate	P
0	1 - 175	1	15	205332	0.0079711	0.21926
	176 - 294	15	13	50607	0.0079711	0.09647
	295 - 365	13	15	19526	0.0079711	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 35. Site-specific information and iteratively fit values of P for the estimation of rock bass annual consumption.

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 36. Site-specific information and iteratively fit values of P for the estimation of flathead catfish annual consumption.

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 37. Mean water temperatures used in the estimation of consumption by smallmouth bass, rock bass, and flathead catfish.

Date	Day for Smallmouth Bass and Rock Bass	Mean Temperature (C)	Day for Flathead Catfish	Mean Temperature (C) 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 limitations.

Table 38. Proportion (wet weight) of each prey type in the diet used to estimate consumption of smallmouth bass.

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 39. Proportion (wet weight) of each prey type in the diet used to estimate consumption of rock bass.

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 40. Proportion (wet weight) of each prey type in the diet used to estimate consumption of flathead catfish.

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 41. Smallmouth bass consumption (kg/ha/yr, kcal/ha/yr) on each prey type by each age group in the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Age/Cohort	Prey Type									
	Crayfish		Helgrammites		Insects		Fish		Total	
	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal
0	-	-	-	-	52.652	71080	-	-	52.652	71080
1	4.499	4049	-	-	13.406	18098	3.374	3374	21.279	25521
2	8.136	7322	0.053	83	2.938	3966	2.683	2683	13.810	14054
3	6.479	5831	0.012	19	0.290	392	0.535	535	7.316	6777
4	3.254	2929	0.006	9	0.144	194	0.266	266	3.670	3398
5	1.362	1226	0.002	3	0.063	85	0.111	111	1.538	1425
6	0.506	455	0.001	2	0.022	30	0.041	41	0.570	528
Total	24.236	21812	0.074	116	69.515	93845	7.010	7010	100.835	122783

Table 42. Rock bass consumption (kg/ha/yr, kcal/ha/yr) on each prey type by each age group in the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Age/Cohort	Prey Type									
	Crayfish		Hellgrammites		Insects		Fish		Total	
	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal
0	-	-	-	-	33.414	45109	-	-	33.414	45109
1	0.890	801	-	-	17.194	23212	-	-	18.084	24013
2	10.701	9631	2.361	3704	6.304	8510	0.008	8	19.374	21853
3	7.897	7107	1.172	1839	0.787	1062	-	-	9.856	10008
4	1.800	1620	0.267	419	0.179	242	-	-	2.246	2281
5	0.345	311	0.051	80	0.034	46	-	-	0.430	437
Total	21.633	19470	3.851	6042	57.912	78181	0.008	8	83.404	103701

Table 42. Rock bass consumption (kg/ha/yr, kcal/ha/yr) on each prey type by each age group in the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Age/Cohort	Prey Type									
	Crayfish		Hellgrammites		Insects		Fish		Total	
	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal
0	-	-	-	-	33.414	45109	-	-	33.414	45109
1	0.890	801	-	-	17.194	23212	-	-	18.084	24013
2	10.701	9631	2.361	3704	6.304	8510	0.008	8	19.374	21853
3	7.897	7107	1.172	1839	0.787	1062	-	-	9.856	10008
4	1.800	1620	0.267	419	0.179	242	-	-	2.246	2281
5	0.345	311	0.051	80	0.034	46	-	-	0.430	437
Total	21.633	19470	3.851	6042	57.912	78181	0.008	8	83.404	103701

Table 43. Flathead catfish consumption (kg/ha/yr, kcal/ha/yr) on each prey type by each age group in the New River, West Virginia between Bluestone Dam and Sandstone Falls.

Age/Cohort	Prey Type												Total	
	Crayfish		Hellgrammites		Insects		Fish							
	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal	kg	kcal
0	-	-	-	-	4.702	6348	-	-	-	-	-	-	4.702	6348
1	0.502	452	-	-	1.841	2485	0.263	263	-	-	-	-	2.606	3200
2	2.305	2074	0.106	167	0.037	50	0.776	776	-	-	-	-	3.224	3067
3	1.721	1549	0.208	327	0.092	124	0.487	487	-	-	-	-	2.508	2487
4	1.149	1034	0.009	15	0.263	355	0.062	62	-	-	-	-	1.483	1466
5	0.859	773	-	-	-	-	0.040	40	-	-	-	-	0.899	813
6	0.418	377	-	-	-	-	0.019	19	-	-	-	-	0.437	396
7	0.174	157	-	-	-	-	0.008	8	-	-	-	-	0.182	165
8	0.072	65	-	-	-	-	0.004	4	-	-	-	-	0.076	69
Total	7.200	6481	0.323	509	6.935	9362	1.659	1659	-	-	-	-	16.117	18011

Table 44. Annual production (AP; kcal/ha/yr), annual consumption (AC; kcal/ha/yr), and gross growth efficiency (GE; AP / AC) by age group for smallmouth bass, rock bass, and flathead catfish.

Age	Smallmouth Bass			Rock Bass			Flathead Catfish		
	AP	AC	GE	AP	AC	GE	AP	AC	GE
0	22702	71080	0.32	9022	45109	0.20	2119	6348	0.33
1	9281	25521	0.36	5246	24013	0.22	987	3200	0.31
2	4577	14054	0.33	4179	21853	0.19	945	3067	0.31
3	2175	6777	0.32	1457	10008	0.15	807	2487	0.32
4	1200	3398	0.35	218	2281	0.10	423	1466	0.29
5	501	1425	0.35	18	437	0.04	221	813	0.27
6	179	528	0.34				95	396	0.24
7							18	165	0.11
8							6	69	0.09

Figures

Figures

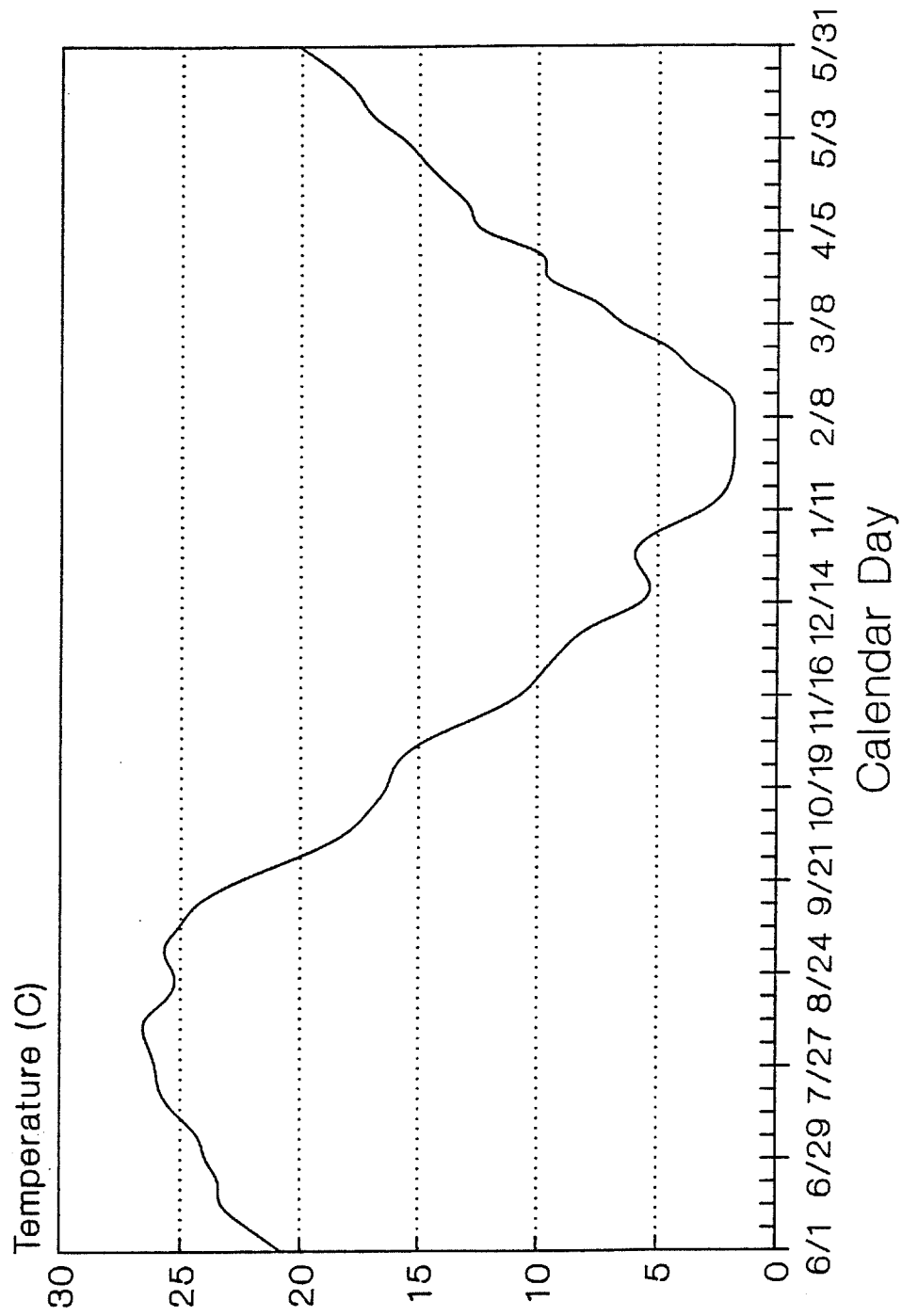


Figure 7. Annual temperature (C) profile of the New River, West Virginia, immediately below Bluestone Dam.

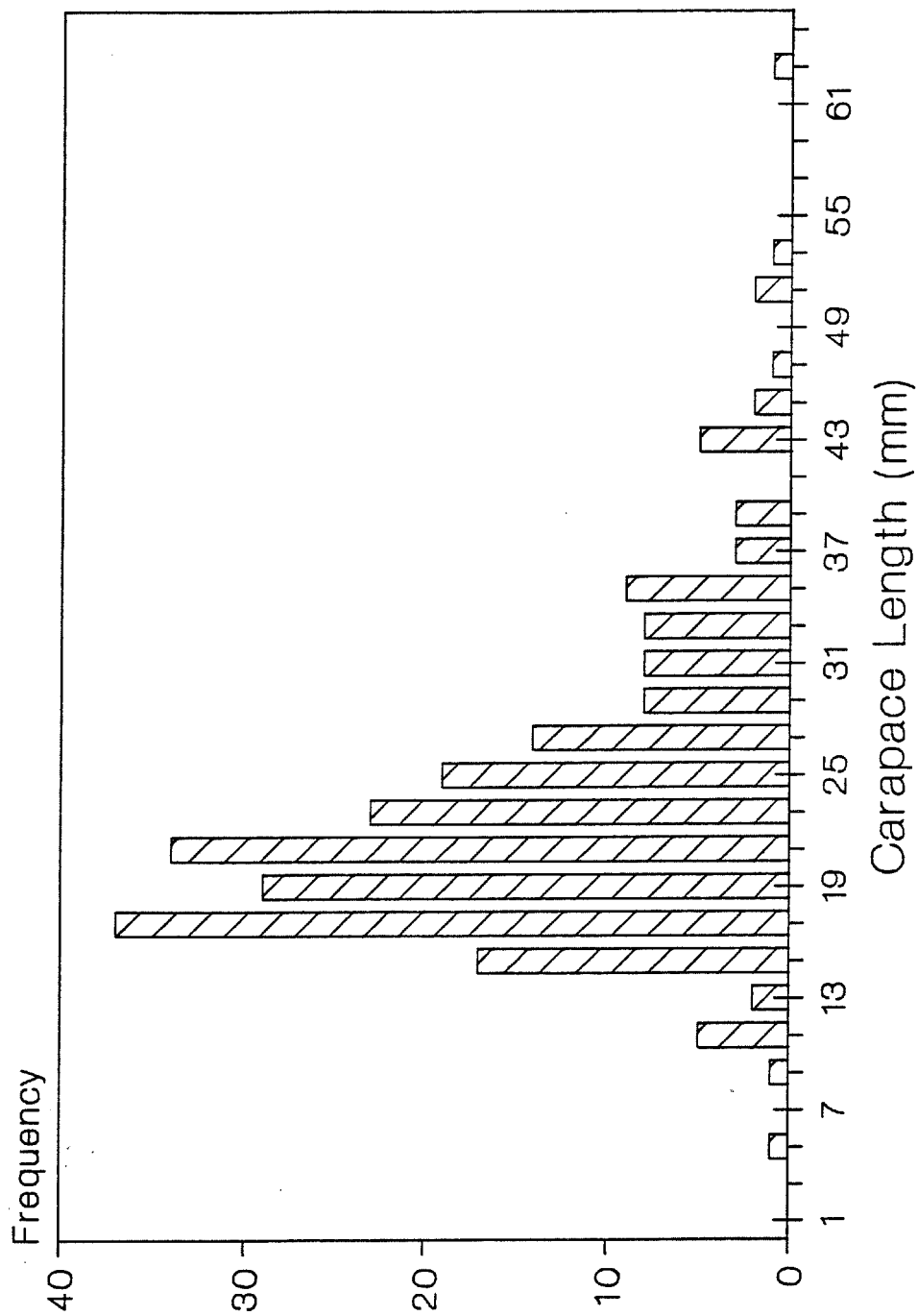


Figure 8. Frequency distribution of carapace lengths of all crayfish removed from the stomachs of smallmouth bass, rock bass, and flathead catfish captured from the Study Pool of the New River, West Virginia, in 1984 and 1985 (data pooled); N = 233.

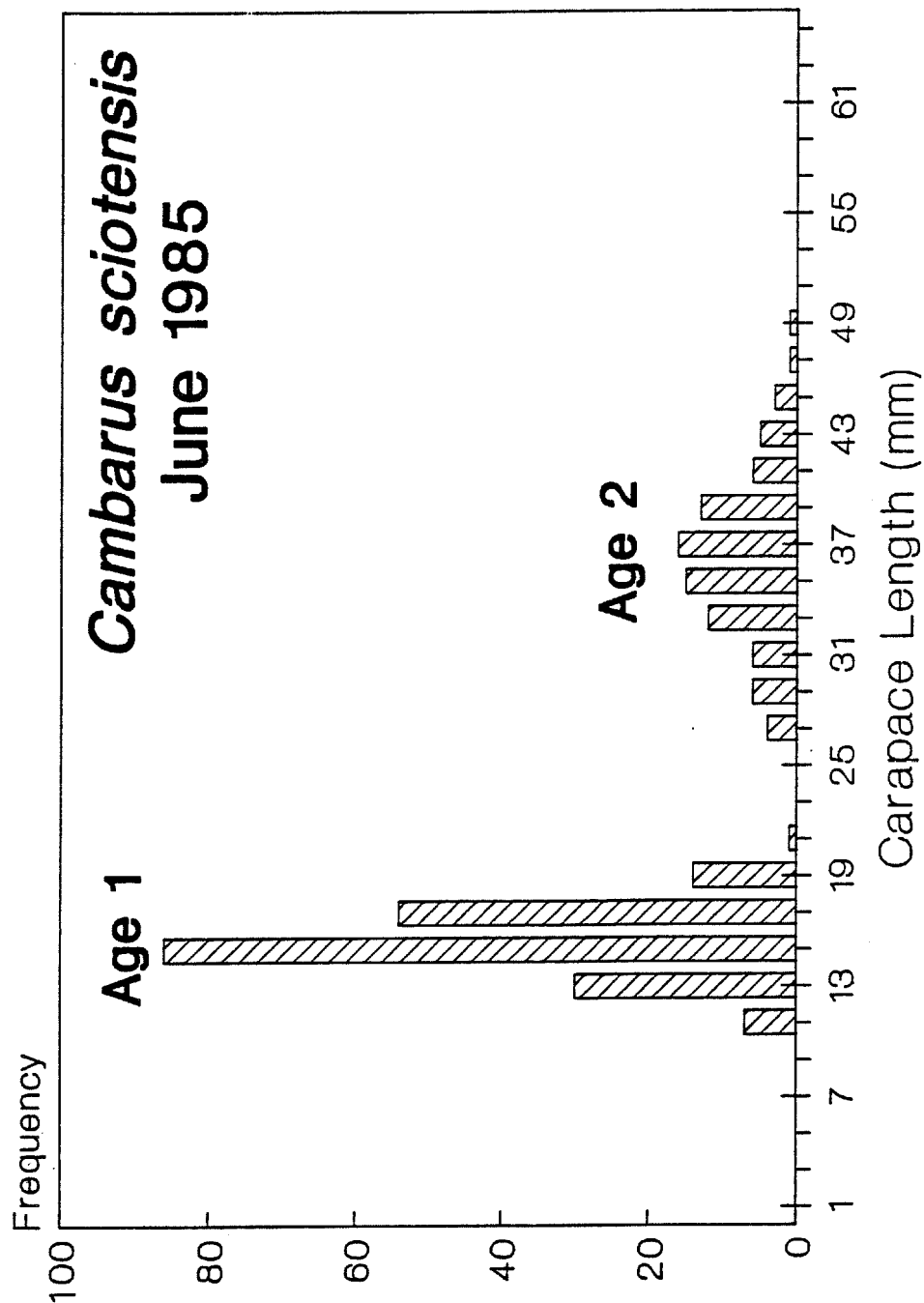


Figure 9. Frequency distribution of carapace lengths of *Cambarus sciotoensis* captured from the study reach of the New River, West Virginia, on 13, 14, 22, and 23 June 1985 (data pooled); N = 280.

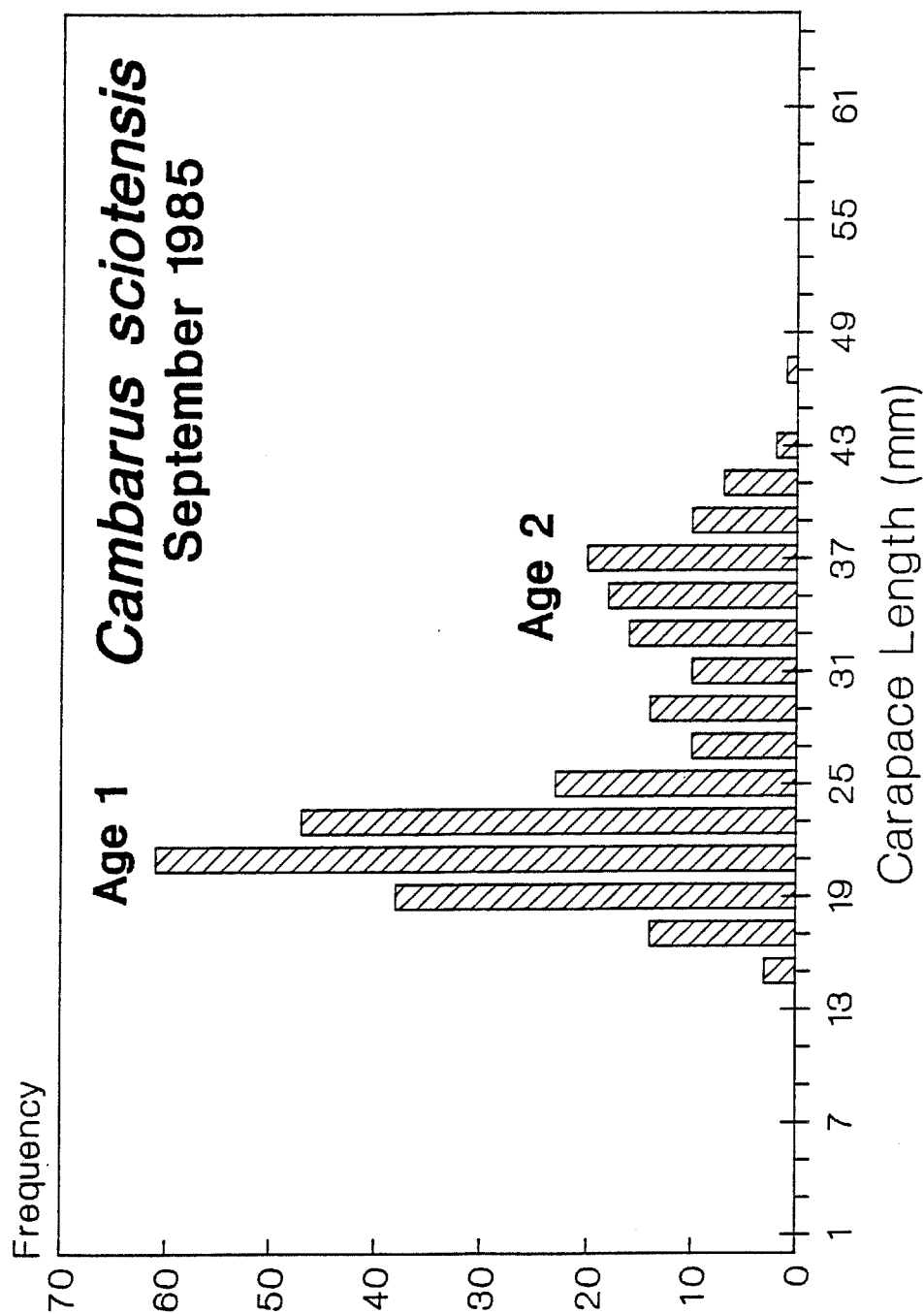


Figure 10. Frequency distribution of carapace lengths of *Cambarus sciotensis* captured from the study reach of the New River, West Virginia, on 4, 5, 6, 10, and 11 September 1985 (data pooled); $N = 294$.

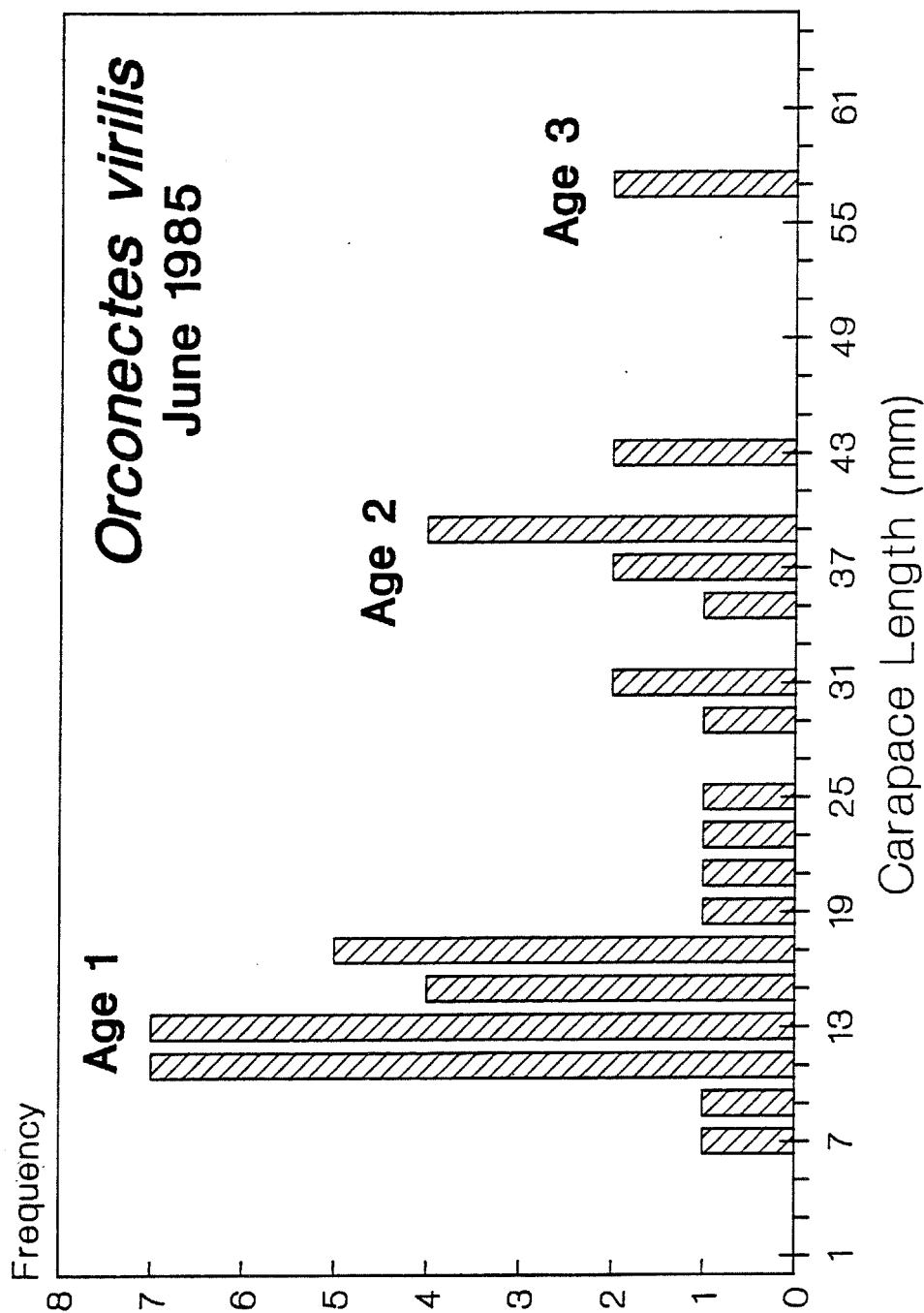


Figure 11. Frequency distribution of carapace lengths of *Orconectes virilis* captured from the study reach of the New River, West Virginia, on 13, 14, 22, and 23 June 1985 (data pooled); N = 43.

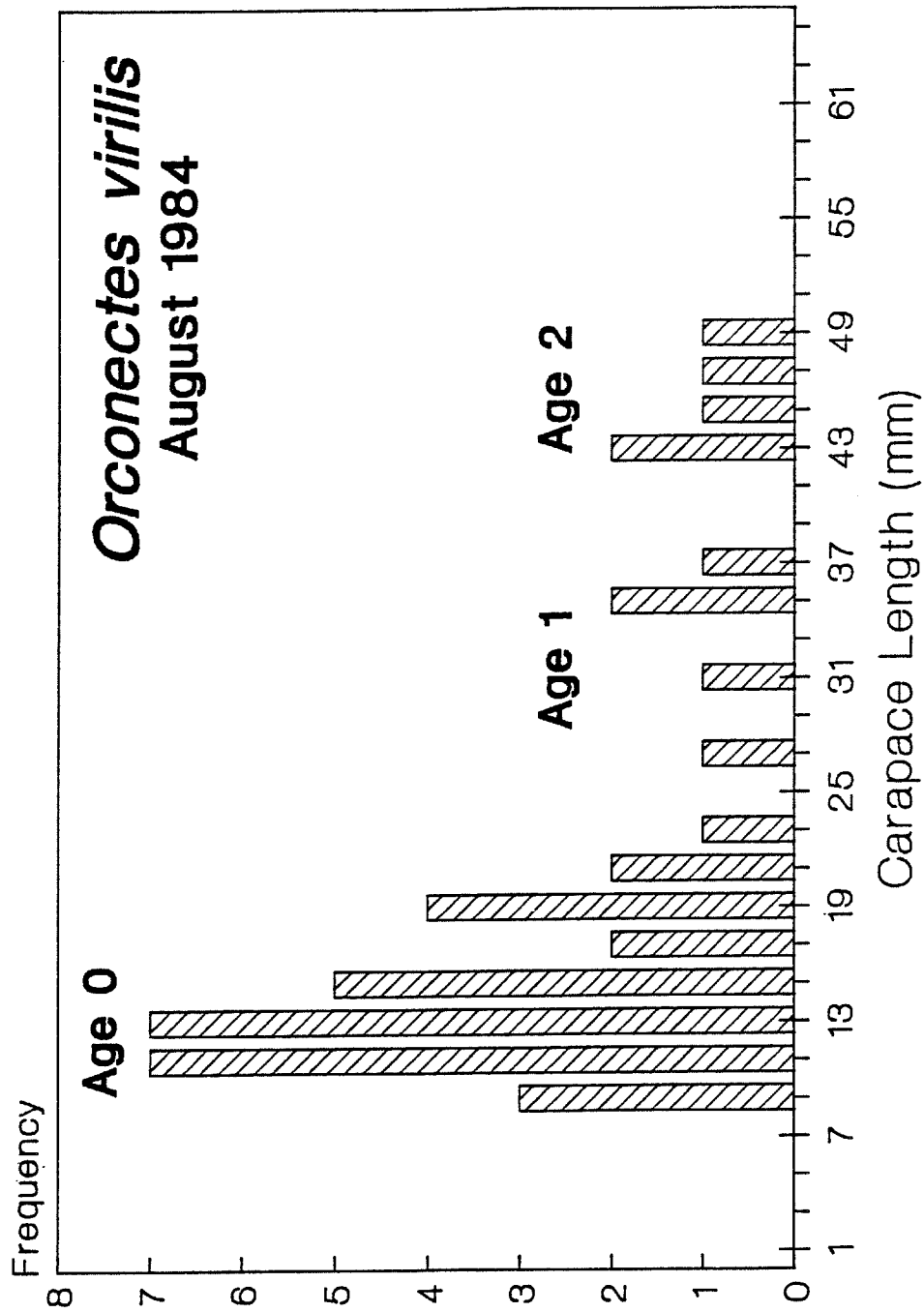


Figure 12. Frequency distribution of carapace lengths of *Orconectes virilis* captured from the study reach of the New River, West Virginia, on 7 and 8 August 1984 (data pooled); N = 41.

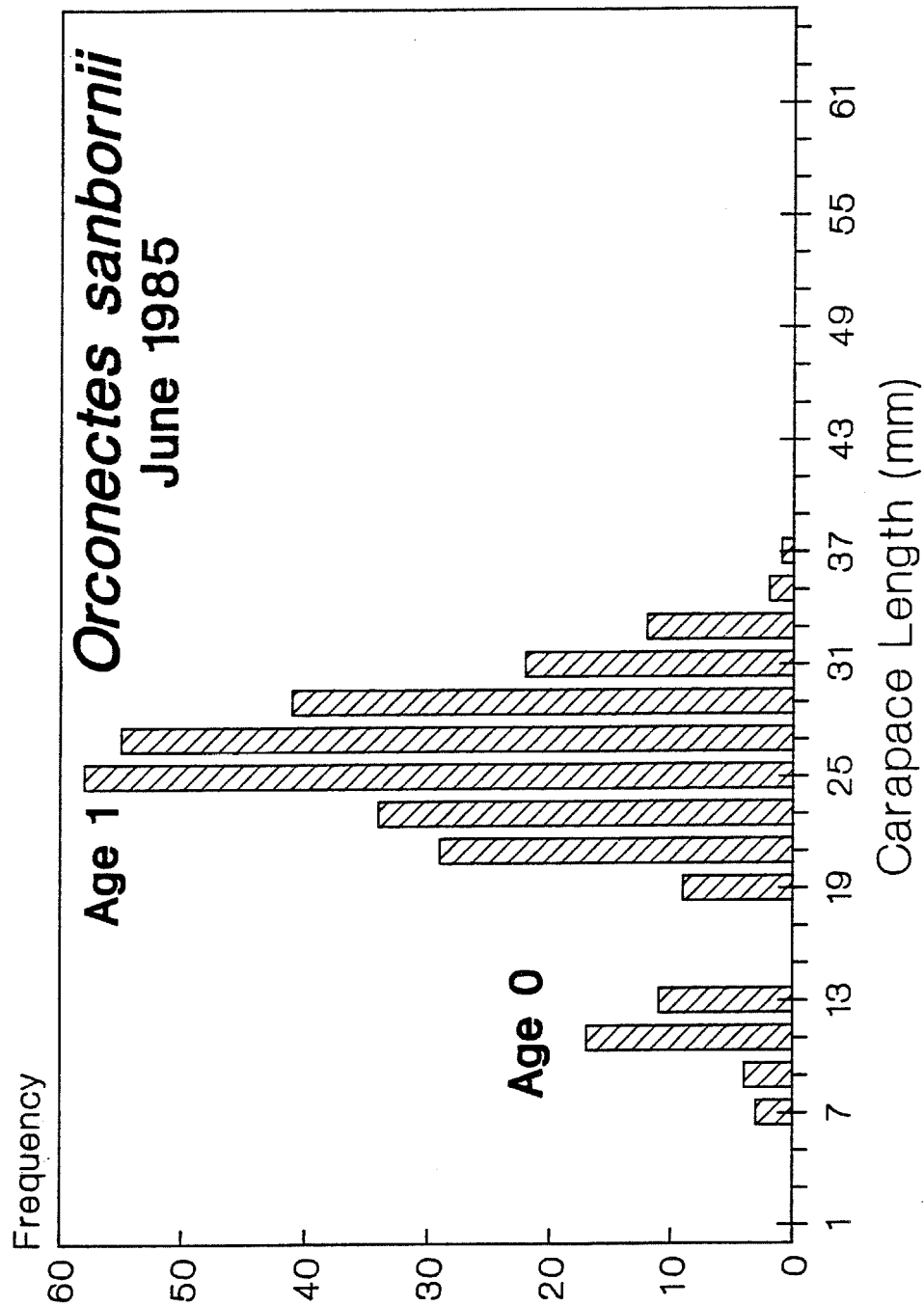


Figure 13. Frequency distribution of carapace lengths of *Orconectes sanbornii* captured from the study reach of the New River, West Virginia, on 13, 14, 22, and 23 June 1985 (data pooled); N = 298.

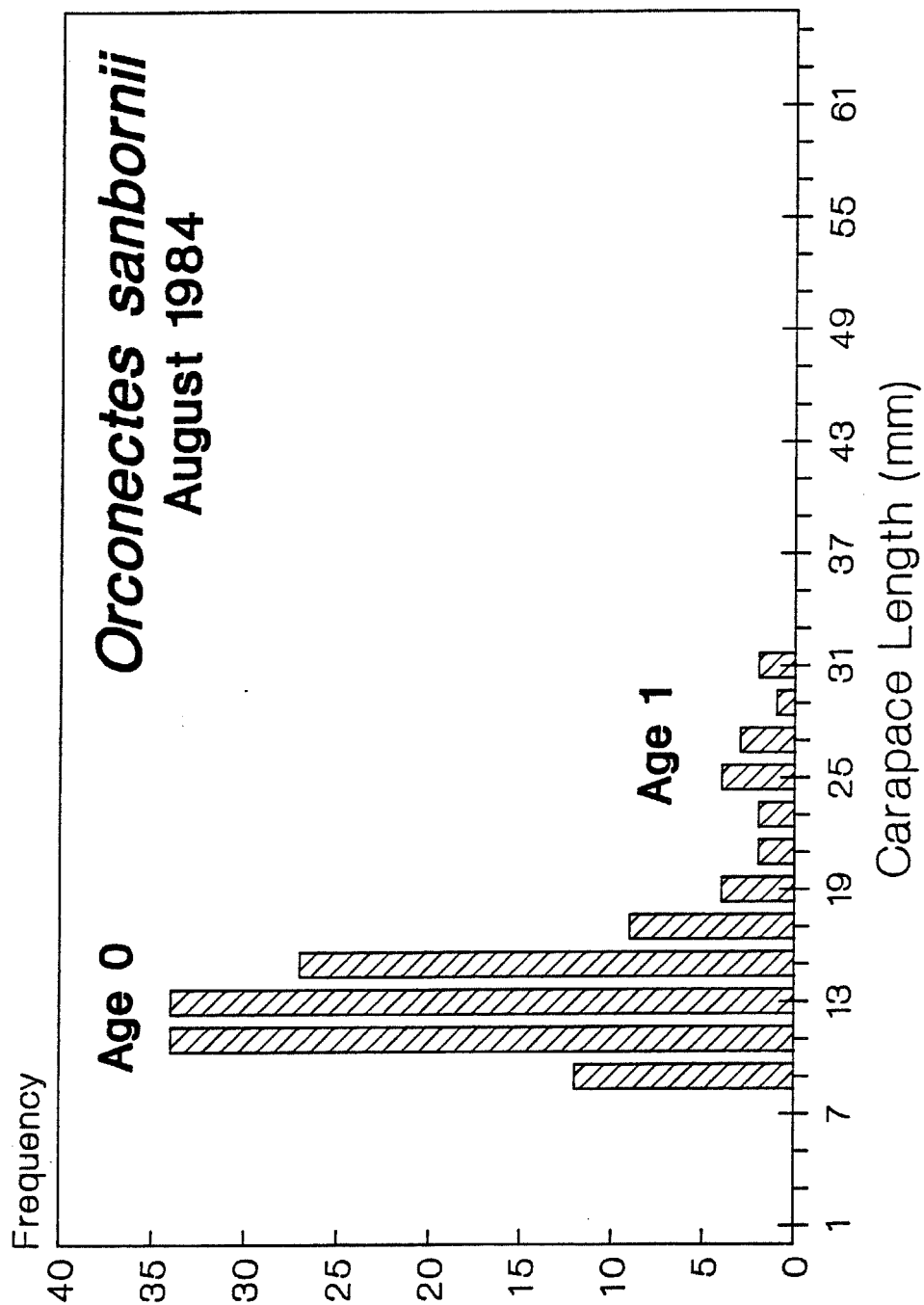


Figure 14. Frequency distribution of carapace lengths of *Orconectes sanbornii* captured from the study reach of the New River, West Virginia, on 7 and 8 August 1984 (data pooled); N = 134.

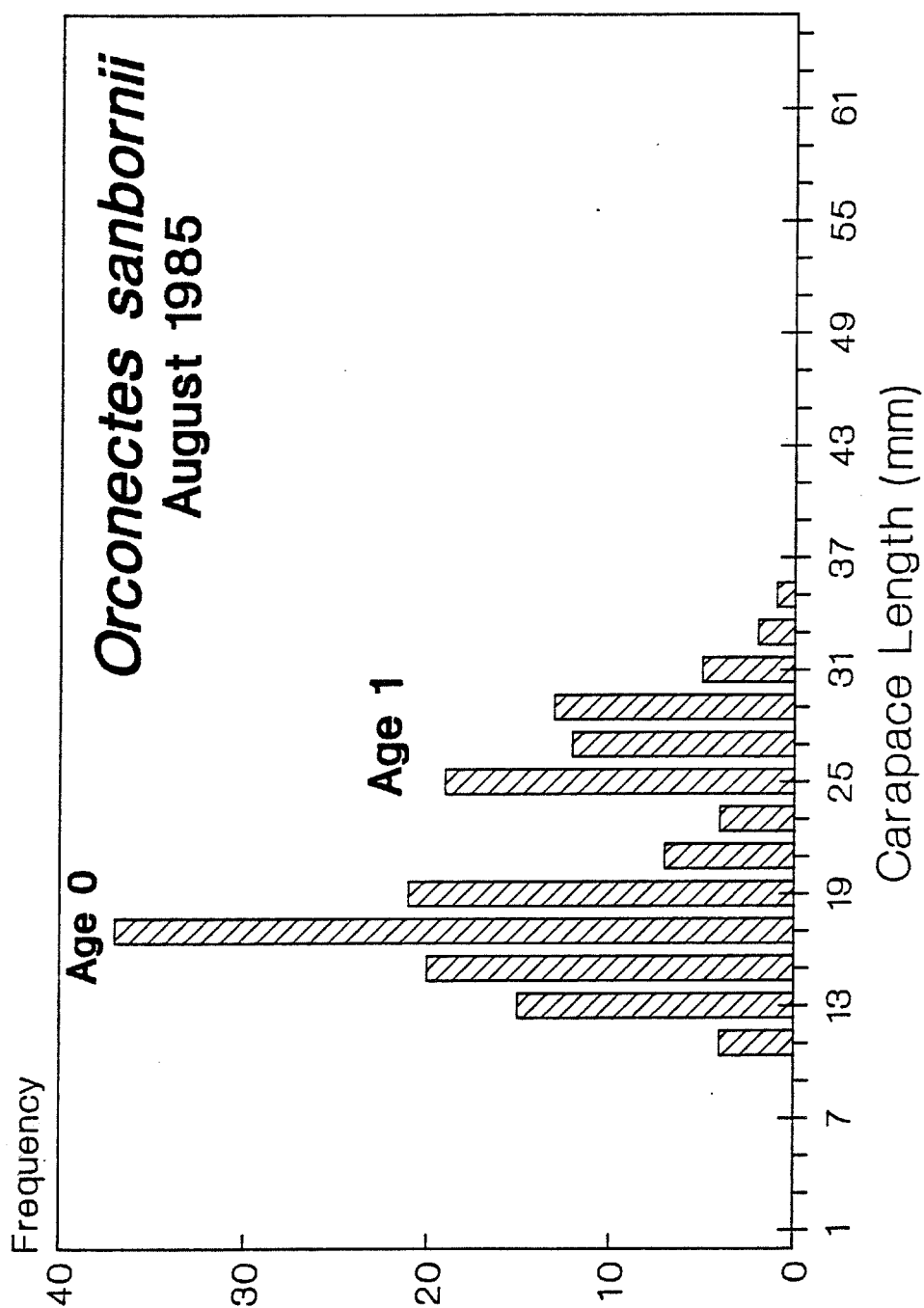


Figure 15. Frequency distribution of carapace lengths of *Orconectes sanbornii sanbornii* captured from the study reach of the New River, West Virginia, on 31 July and 2 August 1985 (data pooled); $N = 160$.

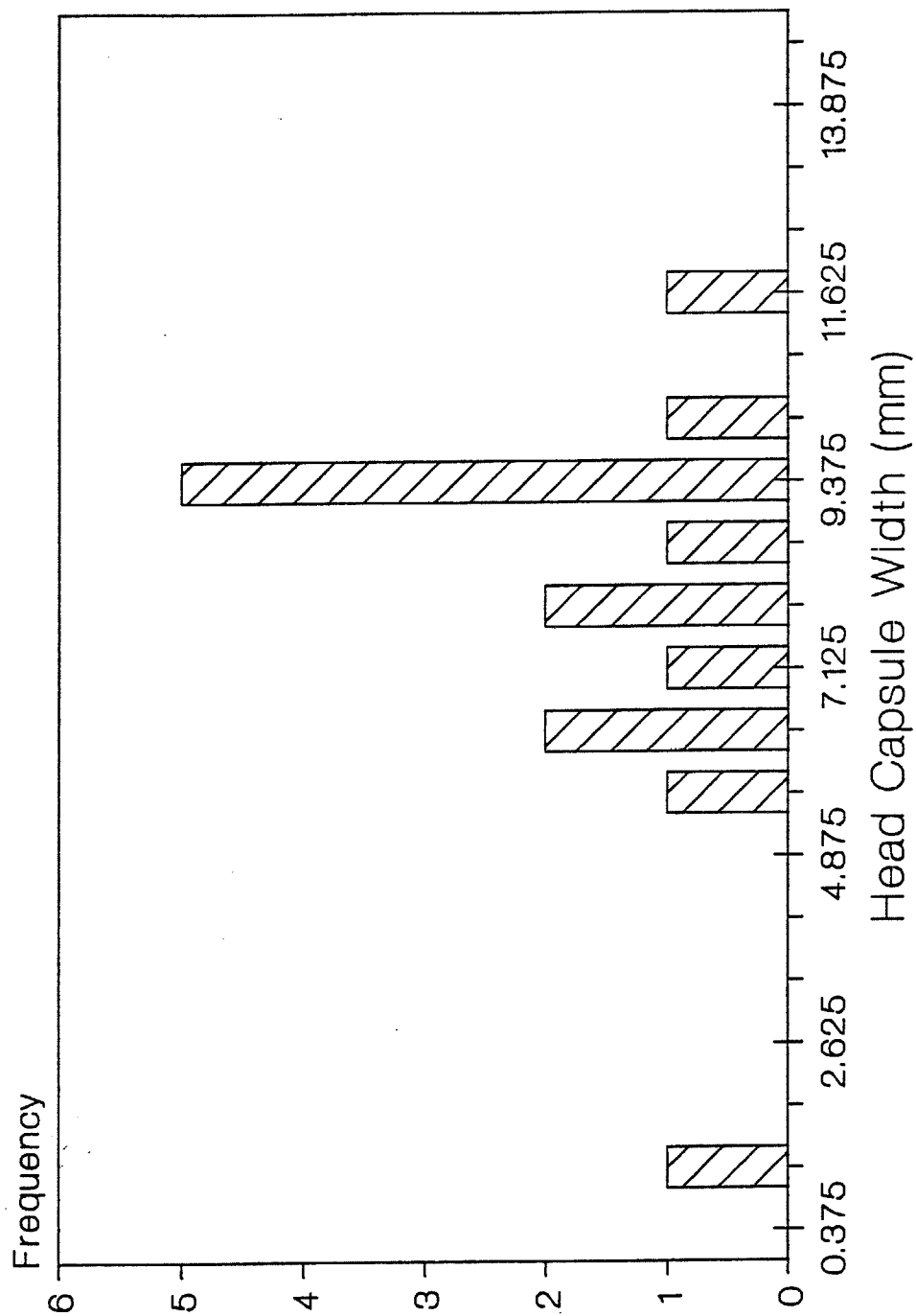
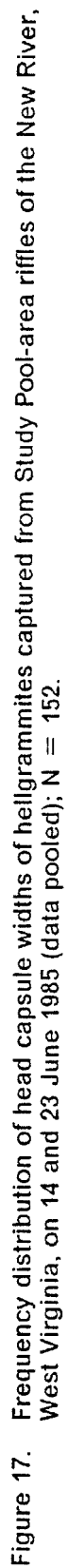


Figure 16. Frequency distribution of head capsule widths of all hellgrammites removed from the stomachs of smallmouth bass, rock bass, and flathead catfish captured from the Study Pool of the New River, West Virginia, in 1984 and 1985 (data pooled); $N = 15$.



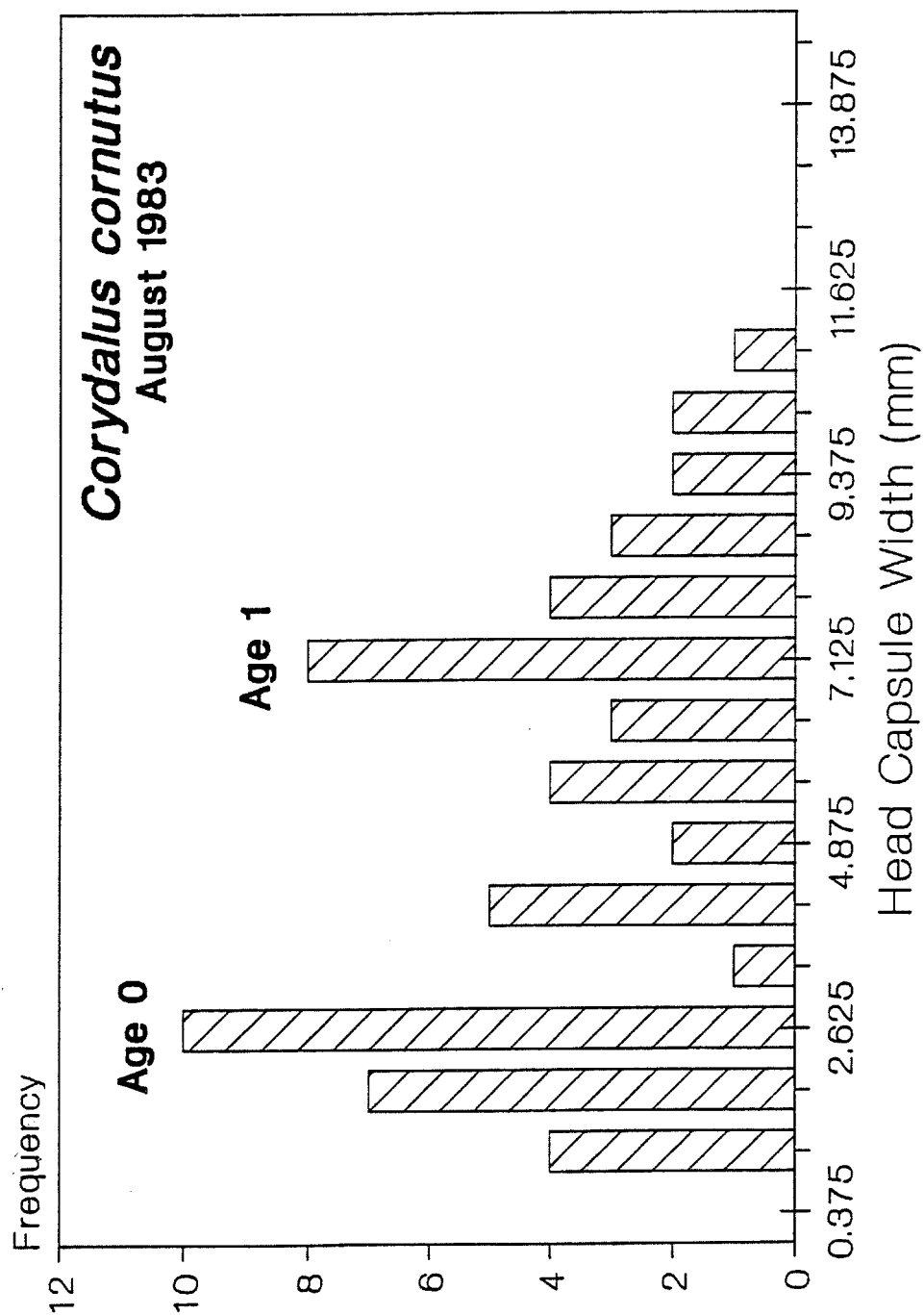


Figure 18. Frequency distribution of head capsule widths of hellgrammites captured from Study Pool-area riffles of the New River, West Virginia, on 29 August 1983 (data pooled); N = 56.

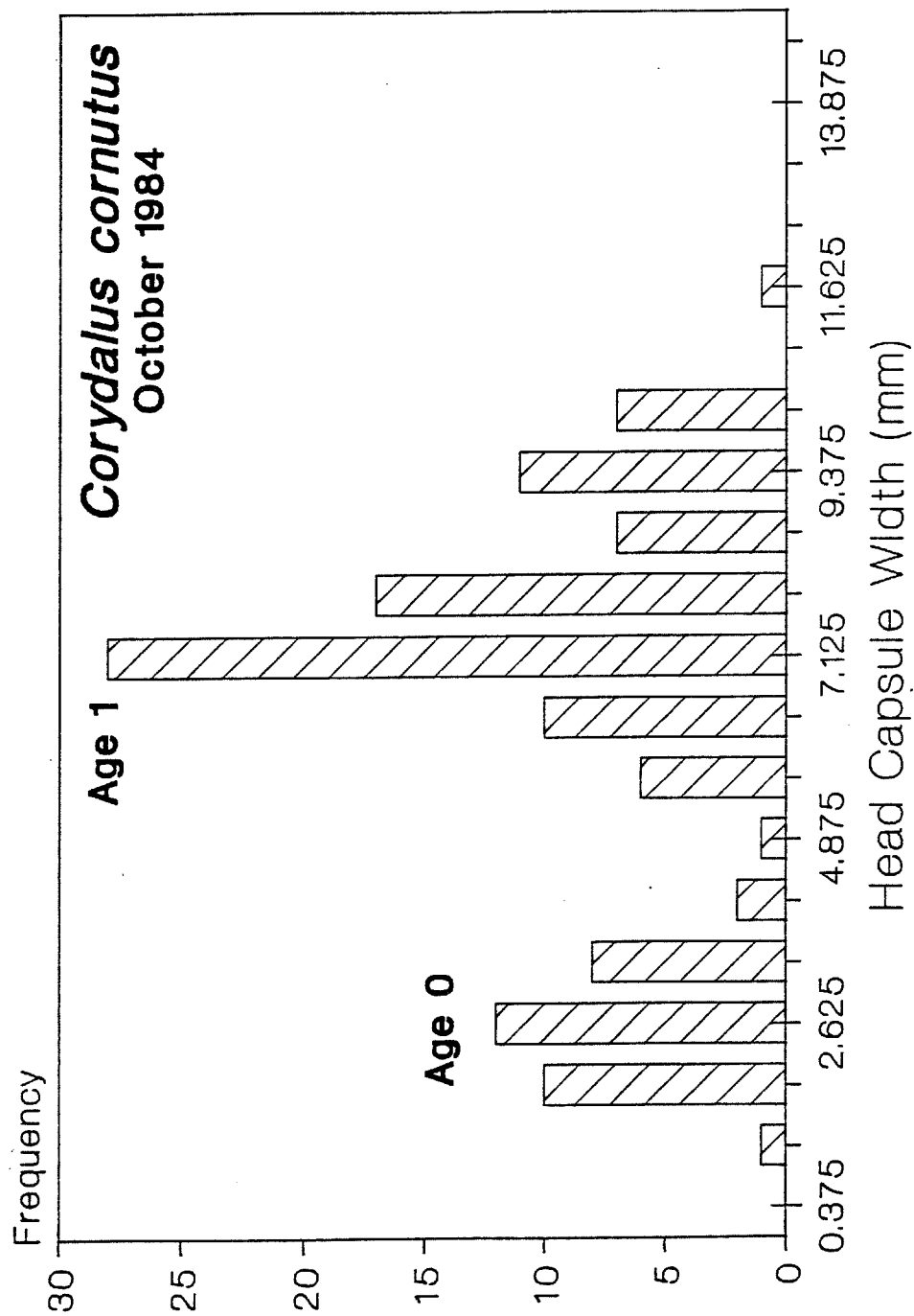


Figure 19. Frequency distribution of head capsule widths of hellgrammites captured from Study Pool-area riffles of the New River, West Virginia, on 14 October 1984 (data pooled); N = 121.

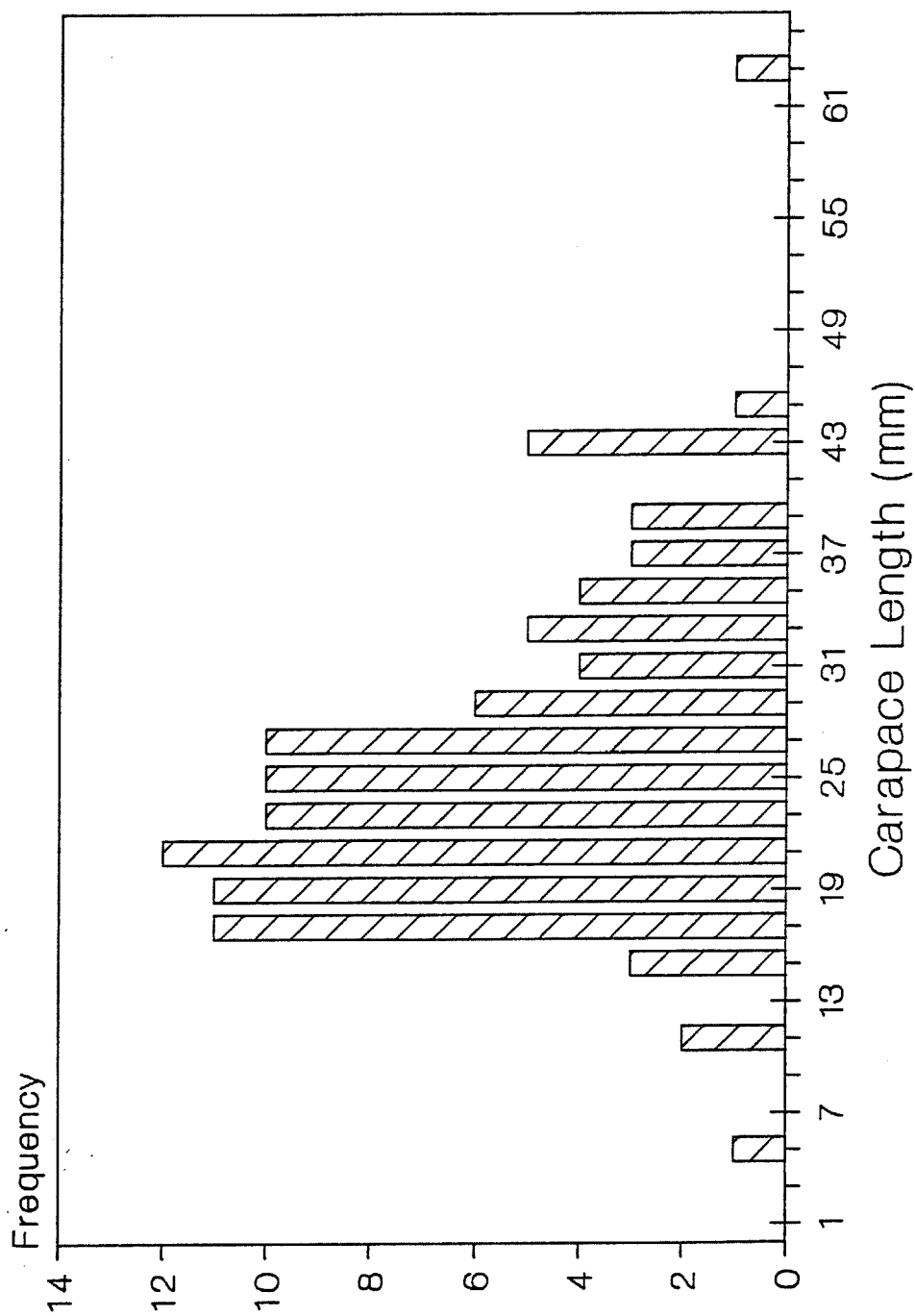


Figure 20. Frequency distribution of carapace lengths of all crayfish removed from the stomachs of smallmouth bass captured from the Study Pool of the New River, West Virginia, in 1984 and 1985 (data pooled); $N = 102$.

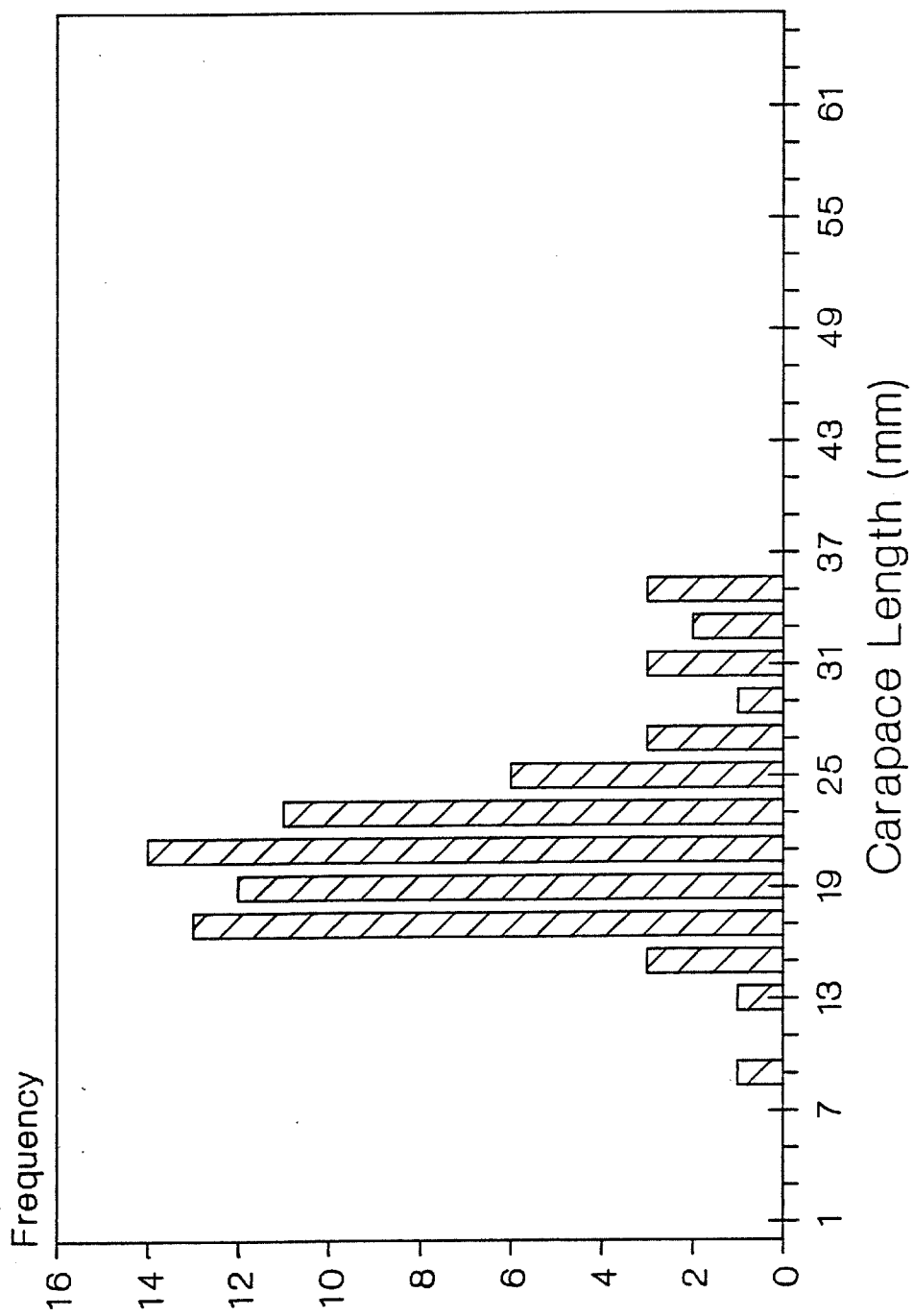


Figure 21. Frequency distribution of carapace lengths of all crayfish removed from the stomachs of rock bass captured from the Study Pool of the New River, West Virginia, in 1984 and 1985 (data pooled); N = 73.

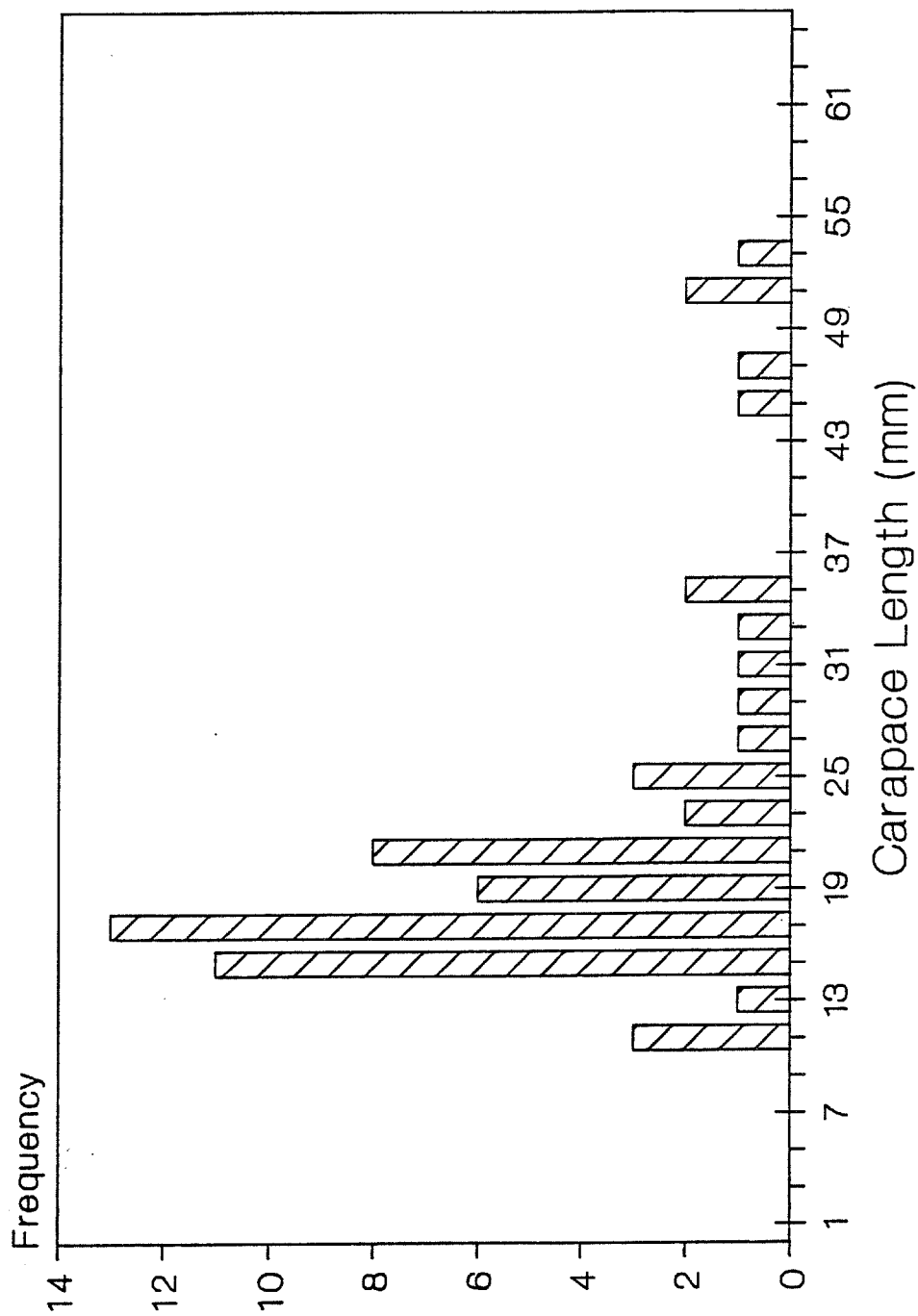


Figure 22. Frequency distribution of carapace lengths of all crayfish removed from the stomachs of flathead catfish captured from the Study Pool of the New River, West Virginia, in 1984 and 1985 (data pooled); $N = 58$.

Job II: Impacts of commercial harvest of invertebrate baits on the predator-prey interactions in the New River.

Job Number: II - d

Job Title: Model of interactions among invertebrate bait species, sport fishes, and commercial bait harvest.

Objective: Incorporate the estimates of abundance, mortality, growth, production, and consumption, and information from a bait harvest survey into a conceptual model to predict the effect of present and future bait harvest on sport fishes in the New River, West Virginia.

Period Covered: June 14, 1983 - July 21, 1986

Status: Completed

Abstract:

A conceptual energy flow model, representing four prey types (crayfish, hellgrammites, insects, and fish), three fish predators (smallmouth bass, rock bass, and flathead catfish), and two bait harvest groups (bait retailers and anglers), was developed from previous knowledge of the prey-predator-human interactions in the New River, West Virginia, between Bluestone Dam and Sandstone Falls. Total annual mean biomass of the three fish predators (43,491 kcal/ha) was about 7% of that of the four prey groups (628,330 kcal/ha); smallmouth bass contributed the most to predator biomass (24,307 kcal/ha), and aquatic insects were the dominant prey group (460,355 kcal/ha). Energy flow was the greatest between aquatic insects and the three predator species (181,388 kcal/ha/yr); flow was also substantial between crayfish and the three predators (47,763 kcal/ha/yr). Flows associated with bait harvest of crayfish (3,555 kcal/ha/yr) and hellgrammites (4,019 kcal/ha/yr) were insignificant relative to other flows within the system. However, expected increases in harvest of at least crayfish may adversely affect fish predators, because current total use of the annual production of age 1 and 2 crayfish by predators and humans is relatively great. Specific management recommendations were 1) to assess the magnitude of the annual harvest of crayfish and hellgrammites on a regular basis, 2) to monitor the growth and diet composition of important sport fishes for indications of changes in the quantity and quality of the forage base, and 3) to establish individual harvest quotas for commercially-licensed bait retailers, if bait harvest becomes excessive. The New River prey-predator system is very productive, and, with proper management, can provide substantial benefits to West Virginia residents and out-of-state visitors.

Introduction

People harvest aquatic organisms in the New River, West Virginia, at essentially two levels, macroinvertebrates (crayfish and hellgrammites) and fish predators (numerous species). The value of the bait fishery for crayfish and hellgrammites in 1983 was substantial, totaling an estimated \$132,000 (Job I-a and -b report). Although the value of the sport fishery is not known, the New River harbors the most valuable warmwater fishery in the state of West Virginia. Use by anglers can be expected to increase, following a nation-wide trend (United States Fish and Wildlife Service 1987), and, therefore, bait harvest will increase to satisfy the angler demand for live crayfish and hellgrammites. Other major human influences appear imminent, for example, the control of blackflies by poisoning larvae and temperature and flow alterations due to changes in Bluestone Dam operations. The impacts of harvest, pest control, and environmental alterations on the New River ecosystem were not predictable prior to this research due to a limited knowledge base. Few quantitative studies of the trophic links in this ecosystem have been conducted; exceptions are Voshell (1985) and Voshell et al. (1987), who investigated trophic relations among benthic macroinvertebrates. This research provided baseline information about the trophic interactions among the principal fish predators (smallmouth bass, rock bass, and flathead catfish) and their prey (crayfish, hellgrammites, insects, and fish), and may prove useful in the development of future management strategies which involve aquatic biota downstream from Bluestone Dam.

Most studies of predator-prey interactions have been theoretical in nature (Larkin 1966; Dickie 1976; Brauer and Soudack 1979; May et al. 1979; Beddington and May 1980; Beddington and Cooke 1982), and provide only generalizations, not specific recommendations for management. An implicit theme in most predator-prey studies is that detailed, site-specific investigation is required. May et al. (1979) discussed five points important to the management of multispecies fisheries. First, top predators experiencing nominal natural mortality can likely be harvested on a ("optimum" or "maximum") sustained yield basis; theoretically, harvest of top predators affects only prey, which will probably respond favorably (that is, increase). Second, populations in lower trophic levels should not be harvested to a point at which other dependent predator populations are significantly reduced. Third, multispecies management must consider the time scales of the various population's processes; the longest time

scales (slowest processes) determine the extent of harvest at each trophic level. Turnover rates (production/mean biomass ratios) are typically slower at higher trophic levels, therefore harvested biomass is replaced through growth and recruitment more slowly than at lower trophic levels. Fourth, the true values of population parameters (rarely known) should be expected to fluctuate, and parameter estimates will probably be in error, thus harvest levels should be conservative. Lastly, economic, social, and political factors influence the above four points, and thus directly affect management strategies and their outcome. Regarding the New River, the first three points can be immediately addressed. First, smallmouth bass, rock bass, and flathead catfish are the dominant predator fishes, and are heavily fished; further increases in the abundances of crayfish and hellgrammites as an indirect result of angler harvest of these predators are probably not forthcoming. Second, harvest of crayfish and hellgrammites would have to be controlled, if harvest adversely affected, for example, smallmouth bass, which supports an important sport fishery. Third, hellgrammites have a greater turnover rate than crayfish (Job II-a report), and can probably be harvested at a greater rate.

Detailed investigation of invertebrate bait harvest (Job I-a and -b report), prey and predator population dynamics (Job II-a and -b report), and trophic linkage between prey and predators (Job II-c report) provided the basis for development of a preliminary concept of how exploited populations in the New River interact, and may be useful in evaluating alternative fishery management strategies and other human influences. Specific objectives were 1) to integrate information on bait and fish harvest and dynamics of principal fish predators and their prey into a conceptual energy flow model, and 2) to speculate on the effects of different fishery management and resource use strategies on the prey-predator-human interactions in the New River, West Virginia, between Bluestone Dam and Sandstone Falls.

Methods

System Definition

The system in this research was defined as the principal fish predators (smallmouth bass, rock bass, and flathead catfish), their prey (crayfish, hellgrammites, insects, and fish), and bait and fish harvesters (bait retailers and anglers) occurring between Bluestone Dam and Sandstone Falls. The system was considered to be comprised of two subsystems, the prey-predator subsystem representing selected biota in the river, and the harvest subsystem representing selected human influences on the prey-predator subsystem. Energy flow was modeled only for the prey-predator subsystem. Energy inputs to this subsystem were assumed to be that entering via seston from Bluestone Lake and that captured within the system by primary producers. Energy outputs from the prey-predator subsystem were assumed to be only through bait and fish harvest, and natural mortality of prey and predators.

System Model

Each component of the New River system was represented by a compartment in the system model (Figure 23). Therefore, seven compartments, representing four prey types and three predator species, comprised the prey-predator subsystem, and two compartments, representing bait retailers and anglers, formed the harvest subsystem. The annual flow of energy (kcal/m²/yr) between any two compartments was represented in absolute terms. Energy flows from each of the four prey types to each of the three predator populations were estimated using bioenergetics simulations (Job II-c report). Energy flows from smallmouth bass, rock bass, and flathead catfish (young-of-year) to the smallmouth bass and flathead catfish compartments were distinguished from the total flow 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 not identifiable. Unidentified fishes in the diet were assumed to be other than young predators, resulting in a more conservative estimate of predation on young predators.

Energy flows from the crayfish and hellgrammite compartments to each bait harvest group were estimated from harvest data (Job I-a and -b report) and weight-energy relationships for these invertebrates (Job II-a report). Annual energy flows from smallmouth bass, rock bass, and flathead catfish to anglers (that is, harvest) were estimated from harvest information in Pierce et al. (1981), who conducted an angler survey on the New River, West Virginia, from April through November 1980. The river reach surveyed by Pierce et al. (1981) was comprised of three sections, the first two of which were the reach between Bluestone Dam and Sandstone Falls. The estimated total harvest for this reach for each of the three species was assumed to be the total annual harvest by anglers from the system. The caloric equivalent of the annual harvest of each species was calculated as the product of age-specific harvest (numbers of fish), mean individual fish weight, and caloric density (1000 cal/g live weight), summed over all recruited age groups. Age 2 and older smallmouth and rock bass, and age 4 and older flathead catfish were assumed to be fully recruited to the sport fishery. The age composition of the harvest (numbers of fish) was assumed to be directly proportional to the abundances of the fully-recruited age groups; 1 June abundances of ages 2 - 6 smallmouth bass (Table 34; Job II-c report) and ages 2 - 5 rock bass (Table 35; Job II-c report), and 15 June abundances of ages 4 - 8 flathead catfish (Table 36; Job II-c report) were used. The mean of individual fish weights on 1 June and 22 November for smallmouth and rock bass, and on 15 June and 22 November for flathead catfish was used as an estimate of mean weight of individual fish in each age group in the harvest.

Annual mean biomass of each of the three fish predator populations was estimated with a mark-recapture technique and mortality estimates (Job II-b report). Crayfish and hellgrammite annual mean biomass was estimated from quadrat samples collected over a period of three years (Job II-a report); estimates were calculated only for marketable-sized age 1 and 2 animals, because reasonable estimates of young-of-year abundance were not possible. Annual mean biomass of aquatic insects was approximated from total biomass estimates reported by Voshell et al. (1987) for benthic macroinvertebrates in riffle areas; aquatic insect biomass was considered negligible in pools, based on qualitative observations in this research and by J. Reese Voshell (Associate Professor, Department of Entomology, VPI & SU; personal communication). Prey fish annual mean biomass was estimated from abundances reported by Lobb (1986) for several species-life stage groups counted along underwater transects within the pool in which predator dynamics were assessed. Two size groups of prey fish were distinguished. The first group was comprised of smaller fishes (bluntnose minnow, *Pimephales notatus*; logperch, *Percina caprodes*; central stoneroller, *Camptostoma anomalum*; *Notropis* spp.; greenside darter, *Etheostoma blennioides*; rainbow darter, *E. caeruleum*; sharpnose darter, *P. oxyrhyncha*; unidentified darters; and young-of-year bigmouth chub, *Nocomis platyrhynchus*); a mean weight of 1 g was assumed for this group, and was chosen based on length-weight data provided by Paul L. Angermeier (Research Scientist,

Department of Fisheries and Wildlife Sciences, VPI & SU) for the same or similar fish species caught in the New River, Virginia. The second group included larger fishes (young-of-year and juvenile northern hogsucker, *Hypentelium nigricans*; young-of-year spotted bass, *Micropterus punctulatus*; and young-of-year and juvenile sunfishes, *Lepomis* spp.) for which a mean weight of 3 g was chosen based on data from this research. A caloric density of 1000 cal/g live weight was assumed for all prey fishes. Young-of-year smallmouth bass, rock bass, and flathead catfish were not included with prey fish, because they already comprised part of corresponding predator components.

Results

The prey base, or energy resources, of the smallmouth bass, rock bass, and flathead catfish populations was substantial, averaging about 628,330 kcal/ha (sum of the annual mean biomass estimates for the four prey types) during the year (Figure 23). Young-of-year predators (annual mean biomass of 12,839 kcal/ha) represented an additional source of energy to older predators. The estimated annual mean biomass of aquatic insects (460,355 kcal/ha) was much greater than that of crayfish (61,339 kcal/ha), hellgrammites (23,166 kcal/ha), and prey fish (83,470 kcal/ha) combined.

The total of annual mean biomass estimates of the three predator populations, an indicator of potential predation pressure, was about 7% (43,491 kcal/ha; Figure 23) of that of the prey. Smallmouth bass annual mean biomass (24,307 kcal/ha) was nearly twice as great as that for rock bass (13,765 kcal/ha) and more than four times greater than flathead catfish mean biomass (5,419 kcal/ha).

The estimated total annual energy flow within the prey-predator subsystem was 244,495 kcal/ha/yr, and that from the prey-predator subsystem to the harvest subsystem was 18,540 kcal/ha/yr. The greatest flows of energy from the hellgrammite component were to rock bass (6,042 kcal/ha/yr) and bait retailers (3,534 kcal/ha/yr; Figure 24); much lower flows went to flathead catfish, anglers, and smallmouth bass (509, 485, and 116 kcal/ha/yr, respectively). Crayfish supplied the most energy to smallmouth and rock bass (21,812 and 19,470 kcal/ha/yr, respectively; Figure 25); a moderate flow went to flathead catfish (6,481 kcal/ha/yr) and lesser flows went to bait retailers and anglers (2,576 and 979 kcal/ha/yr, respectively). Aquatic insects provided more energy than any other prey type to smallmouth bass (93,845 kcal/ha/yr), rock bass (78,181 kcal/ha/yr), and flathead catfish (9,362 kcal/ha/yr; Figure 26). Prey fish (other than young predators) supplied more energy to smallmouth bass (5,118 kcal/ha/yr) and flathead catfish (614 kcal/ha/yr), and virtually none (8 kcal/ha/yr) to rock bass (Figure 27). In addition, young-of-year smallmouth bass supplied relatively substantial amounts of energy to adult smallmouth bass (1,542 kcal/ha/yr) and flathead catfish (498 kcal/ha/yr), as did young-of-year rock bass (149 kcal/ha/yr) and flathead catfish (398 kcal/ha/yr) to adult flathead catfish. Young-of-year rock bass (140 kcal/ha/yr) and flathead catfish (210 kcal/ha/yr) were relatively unimportant energy

sources to adult smallmouth bass. Young-of-year smallmouth bass and flathead catfish were apparently not preyed upon by rock bass.

Anglers annually harvested about 10,966 kcal/ha/yr of the three predator fishes. More energy as smallmouth bass (7,774 kcal/ha/yr) was harvested than was rock bass (704 kcal/ha/yr) or flathead catfish (2,488 kcal/ha/yr; Figure 28).

Discussion

System Energy Sources

Three sources of energy, one allochthonous and two autochthonous, appear to energetically support the New River system between Bluestone Dam and Sandstone Falls. The organic fraction of the high-quality seston (suspended organic and inorganic particulate matter) from Bluestone Lake is probably the greatest single source of energy input to the system. Aquatic insects, primarily members of the collector-filterer functional guild, flourish below Bluestone Dam as a result of seston input from Bluestone Lake (Voshell 1985; Voshell et al. 1987). Every component of the system is directly or indirectly supported to some extent by aquatic insects (Figures 24 - 28). Aquatic insects are utilized as an energy source by hellgrammites (Stewart et al. 1973; Michael and Culver 1987), most prey fishes, and, to a limited extent, by crayfish (Tack 1941; Bovbjerg 1952; Vannote and Ball 1972).

Autochthonous inputs of energy from aquatic macrophytes (as decomposing plant tissues) and periphyton (primarily epilithic algae) in the New River are probably substantial (Hill 1981; Hill and Webster 1982). Voshell et al. (1987) concluded that aquatic macrophytes were not an important food source to aquatic insects in the New River, because live macrophytes are rarely consumed by them and the estimated contribution to seston and sedimentary detritus by the two predominant plant taxa (water willow, *Justicia americana*, and river weed, *Podostemum ceratophyllum*) was four orders of magnitude lower than input of seston from Bluestone Lake; in addition, detrital input from aquatic macrophytes occurs as an autumnal pulse further limiting its utility as an energy source. However, crayfish probably benefit substantially from live and detrital aquatic macrophyte tissues. The diet of two species of crayfish, *Orconectes luteus* and *O. punctimanus*, in a Missouri stream was approximately 70% plant detritus (from aquatic macrophytes and leaves of riparian vegetation), 15% animal materials (invertebrates), and 15% algae (presented by Charles F. Rabeni at the 117th Annual American Fisheries Society meeting). The diet of *O. propinquus* in an enriched, warmwater stream was about 80% vegetation, 10% detritus, and 10% animal materials (Vannote and Ball 1972); Tack (1941) reported nearly identical percentages for *O. immunis*. Bovbjerg (1952) found that *O. propinquus* fed primarily on algal and higher plant tissues, and to a limited extent on aquatic insects.

Periphyton appears to be used to a limited extent by aquatic insects below Bluestone Dam (Voshell 1985), but is probably more important to crayfish and grazing prey fishes, such as central stoneroller, than to insects. Estimated periphyton production was greater than production by aquatic macrophytes in the New River, Virginia (Hill and Webster 1982).

Allochthonous input of leaf litter from riparian vegetation is apparently not a significant source of energy to the New River system. Although input of leaf litter was considered significant in the New River, Virginia (Hill 1981), and the Greenbrier River, which enters the New River 1 km below Bluestone Dam, may supply large quantities of leaf litter, Voshell et al. (1987) considered leaf litter inputs to be unsubstantial between Bluestone Dam and Sandstone Falls for three reasons. First, the dam limits transport of leaf litter from upstream reaches, second, a high ratio of river surface area to shoreline length results in relatively low leaf litter input, and, lastly, aquatic insects which feed on leaves (shredder functional feeding guild) were few in number.

Recent and/or proposed actions concerning nuisance organisms and water use in the New River may have important effects on energy source and flow for aquatic biota below Bluestone Dam. In 1986, a bacterial insecticide, *Bacillus thuringiensis israelensis* (BTI), was systematically applied to the New River below Bluestone Dam and selected tributaries with the intent of consistently reducing the density of black fly larvae (Simuliidae), thereby controlling the abundance of nuisance adult black flies in adjacent uplands. Voshell (1985) estimated that the elimination of black fly larvae immediately below Bluestone Dam could reduce the annual production of the six dominant macroinvertebrate taxa by about 11%. Further, production by invertebrate predators (such as hellgrammites), which prey on black fly larvae, could also be substantially reduced, although the potential for prey switching by predators tempers that conclusion. Recent evidence suggests 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); chironomids contributed the most production of the six dominant taxa residing on rock outcrops in the New River (Voshell et al. 1987). The impact of BTI application in the New River was not fully assessed, and re-application in 1987 did not occur, presumably due to the high cost.

A second potential impact on energy source and flow is from the planned retrofitting of Bluestone Dam for hydroelectric operations. Water is currently released from Bluestone Lake from a depth of about 3.4 - 6.4 m below the surface, allowing the release of high-quality seston from the metalimnion and lower epilimnion (Voshell et al. 1987). Aside from other effects of dam operation for hydroelectric purposes, a change in the depth of release from the lake could severely affect the release of seston to downstream reaches, especially if release was hypolimnetic. In addition, proposed fluctuating flows from hydroelectric operations, if significant dur-

ing the growing season, may inhibit establishment of aquatic macrophytes, and thus affect a major energy pathway to crayfish.

Fish predators would likely be negatively affected by the above two activities through changes in their principal sources of energy, aquatic insects and crayfish. Such activities will require careful evaluation before they are implemented.

Exploitation of Invertebrates

The complexity and difficulty of managing multispecies fisheries involving more than one trophic level has been aptly demonstrated (Larkin 1966; Walters 1971; Dickie 1976; Brauer and Soudack 1979; May et al. 1979; Beddington and May 1980; Beddington and Cooke 1982). However, the complexity of aquatic food webs has precluded definitive methods of accurately estimating sustainable yields in multispecies fisheries. The New River system, although simplified conceptually here, is no less complex due to prey-predator interactions, exploitation of some prey and predators, and often-conflicting management and resource use strategies, and emphasizes the need to address the management of all exploited populations simultaneously, not in a single-species context.

Crayfish

The total estimated use of the annual production of age 1 and 2 crayfish was substantial (55%; Job II-c report); the majority of use was attributed to predation by smallmouth bass (23%), rock bass (21%), and flathead catfish (7%), and a much lesser amount was associated with bait harvest (4%). Consideration of use by other less numerous predators, even if only the equivalent of 10% of estimated use, suggested that harvest was or could become excessive and thus affect predator populations. However, at least three factors temper that conclusion. First, for each crayfish species, estimates of the annual production of age 1 and 2 animals were considered underestimates, primarily due to the difficulty of capturing smaller age 1 individuals, but also due to the inherent underestimation of crayfish abundance using quadrat sampling. Second, young-of-year crayfish of the two orconectid species became vulnerable to predation in the last half of the growing season, but because reliable production estimates were not possible for young-of-year, the proportion of crayfish production used by predators was based on the estimated annual production of age 1 and 2 crayfish, and was overestimated in this regard. Lastly, the majority of crayfish harvest was very localized, occurring in the riffle area immediately above and adjacent to Sandstone Falls (Job I-a and -b report); although impacts of crayfish

harvest on fish predators in this area may be severe, effects on predators throughout the study reach are probably less than total crayfish use suggests. Therefore, minor increases in future crayfish harvest should not be detrimental to fish predator populations throughout the reach between Bluestone Dam and Sandstone Falls, because harvest is very localized (primarily Sandstone Falls) and estimated total use of crayfish was overestimated at least to a small extent.

Major increases in crayfish harvest, however, may adversely affect fish predator populations. The number of anglers on the New River is expected to increase as is their demand for live bait. Future crayfish harvest can be expected to eventually reach and, if unrestricted, exceed the level at which fish predators are adversely affected. The point at which crayfish density becomes detrimental to fish predators is very difficult to ascertain, because many factors operate in predator-prey interactions. Theoretically, a predator's energetic cost of searching for prey operates on a gradient of prey densities; maximum energetic dividends are realized by predators in an environment of maximum (or optimum) prey density. Increased mortality of prey increases a predator's energetic cost of searching for prey (increased search time between prey encounters), and the predator's energetic benefit/cost ratio decreases, resulting in decreases in growth, production, and/or recruitment. Difficulty arises in discerning the prey density at which energetic benefit/cost to a predator begins to decrease, and at which point the decrease results in a predator growth rate which is no longer acceptable to fishery managers. Potential competitors within a system, such as smallmouth bass and rock bass, may determine a less-than-acceptable benefit/cost outcome through competition for food. Abundance, growth, and production of smallmouth and rock bass in the New River were above average (Job II-b report), which suggests that the prey base (primarily crayfish for age 2 and older fish) was adequate.

Another scenario, restrictions on angler harvest to reduce high mortality of smallmouth bass, could have the effect of increasing total predator abundance and, therefore, predation pressure on crayfish stocks. Theoretically, increased predation pressure would lower the energetic benefit/cost ratio of individual smallmouth bass, thereby affecting growth and production. Thus, a reasonable level of crayfish harvest before implementation of angling restrictions could be excessive following implementation.

The effects of crayfish harvest and angling restrictions on predator food resources in the New River may be detected through concurrent monitoring of predator growth and diet composition. Although predators may switch to prey fishes (including young-of-year predators) during periods of low crayfish abundance, the relatively low abundance of prey fishes (Job II-c report) should translate to poorer predator growth rates. In the diet of predator fishes, substantially lower proportions (by wet

weight) of crayfish relative to the other three prey types should also be indicative of over-utilized crayfish stocks.

The crayfish stocks appear to be efficiently utilized by fish predators and bait harvesters; fish predator use is relatively high (51% of the annual production of age 1 and 2 crayfish), supporting above average growth in older smallmouth and rock bass. The additional use of crayfish for bait (4% of annual crayfish production) represents an economically significant portion of a thriving bait industry. Additional unknown uses of crayfish by amphibians, reptiles, mammals, birds, and other fishes, and the expected increase in the future demand for bait certainly warrants periodic monitoring of crayfish harvest and, if necessary, control of future harvest levels.

Hellgrammites

The total estimated use of the annual production of age 1 and 2 hellgrammites by fish predators and bait harvesters was lower (22%; Job II-c report) than use of crayfish production. Rock bass consumed about 13% of this production, while smallmouth bass and flathead catfish together consumed less than 2%; bait retailers and anglers harvested about 8%. Hellgrammites supplied 17% of the annual energy needs to ages 2 - 5 rock bass, and, if crayfish became limited, would represent an important alternative prey. Increases in hellgrammite harvest in the near future would probably not be detrimental to rock bass. At least three factors support this conclusion. First, as stated for crayfish, the quadrat method inherently underestimates abundance, hence production was probably underestimated. Second, hellgrammites experience relatively high turnover rates, and are thus more able to sustain heavier use by predators and bait harvesters. Lastly, few if any other animals include hellgrammites in their diets. The difficulty of determining the level of prey harvest which would adversely affect a predator population was discussed above. Because rock bass depend on both crayfish and hellgrammites to a significant extent, effects on the rock bass population from increased crayfish and hellgrammite harvest are more difficult to address. Although the hellgrammite population appears to be presently underutilized, the expected increase in recreational use of the New River promises to increase future demands for live bait. Assuming that the harvest of crayfish would be regulated first due to its present high use, bait retailers may accelerate harvest of hellgrammites to meet angler demands. Thus, as for crayfish, periodic monitoring of hellgrammite harvest, control of harvest levels (when necessary), and concurrent inspection of predator growth and diet composition would be justified.

Management Recommendations

The findings of this research suggest that the future increase in crayfish harvest below Bluestone Dam by bait retailers and anglers may result in adverse effects on fish predator populations. Further, if harvest restrictions were implemented for crayfish, bait harvesters may accelerate the harvest of hellgrammites to meet the demand by anglers for bait. The following recommendations are suggested:

- 1) Periodic surveys of commercially-licensed bait retailers and anglers should be conducted to assess the magnitude of the annual harvest of crayfish and hellgrammites, and characterize further the location and extent of harvest in the New River and its tributaries. Commercially-licensed bait retailers could be required to report their annual catch at the end of the harvest season as an alternative to periodic surveys, and the survey of anglers could be coupled with a creel survey to make information acquisition more efficient. Knowledge of total harvest effort (man-hours) could be applied to the optimization of harvest per unit effort.
- 2) The growth and diet composition of the important sport fishes should be periodically monitored to indirectly ascertain major changes in the quantity and quality of the forage base; poorer growth and/or a lower proportion (by wet weight) of crayfish relative to other prey in the diet of older predators may indicate overharvest of crayfish and/or hellgrammite stocks.
- 3) If bait harvest increases significantly or catch per unit effort declines sharply, the number of commercially-licensed bait retailers should be limited to those individuals currently registered, and harvest quotas should be assigned to each individual based on past harvest records, if available. Harvest quotas, if required, should be set conservatively in light of recognized errors in parameter estimates of both predator and prey dynamics, and lag times in the response of predator populations to the harvest of prey should be expected (May et al. 1979).

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Figures

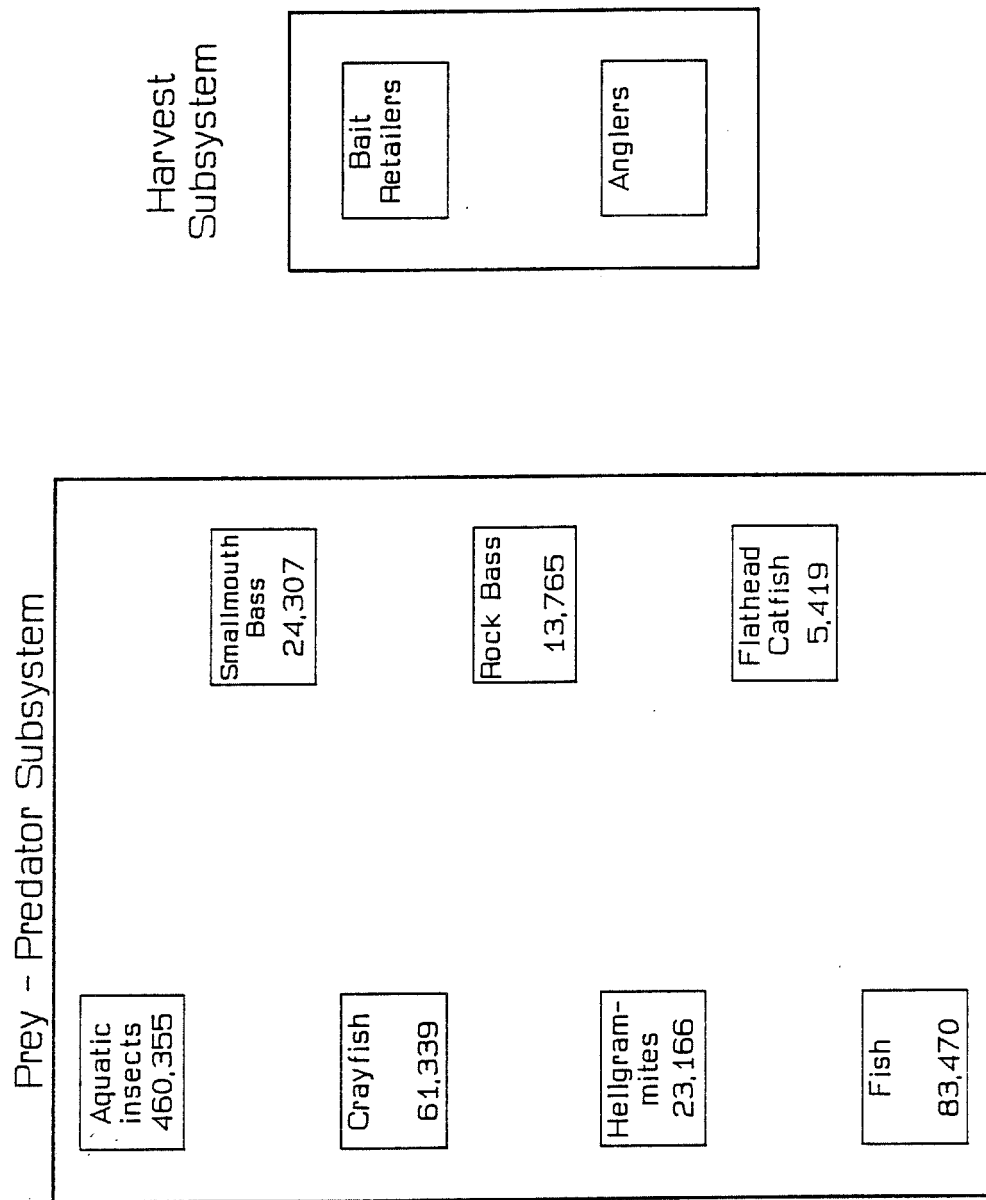


Figure 23. Conceptual model of the New River system showing the prey-predator subsystem, which consists of four prey components (aquatic insects, crayfish, hellgrammites, and fish) and three predator components (smallmouth bass, rock bass, and flathead catfish), and the harvest subsystem, which consists of two exploitation components (bait retailers and anglers); annual mean biomass (kcal/ha) is shown for each component of the prey-predator subsystem.

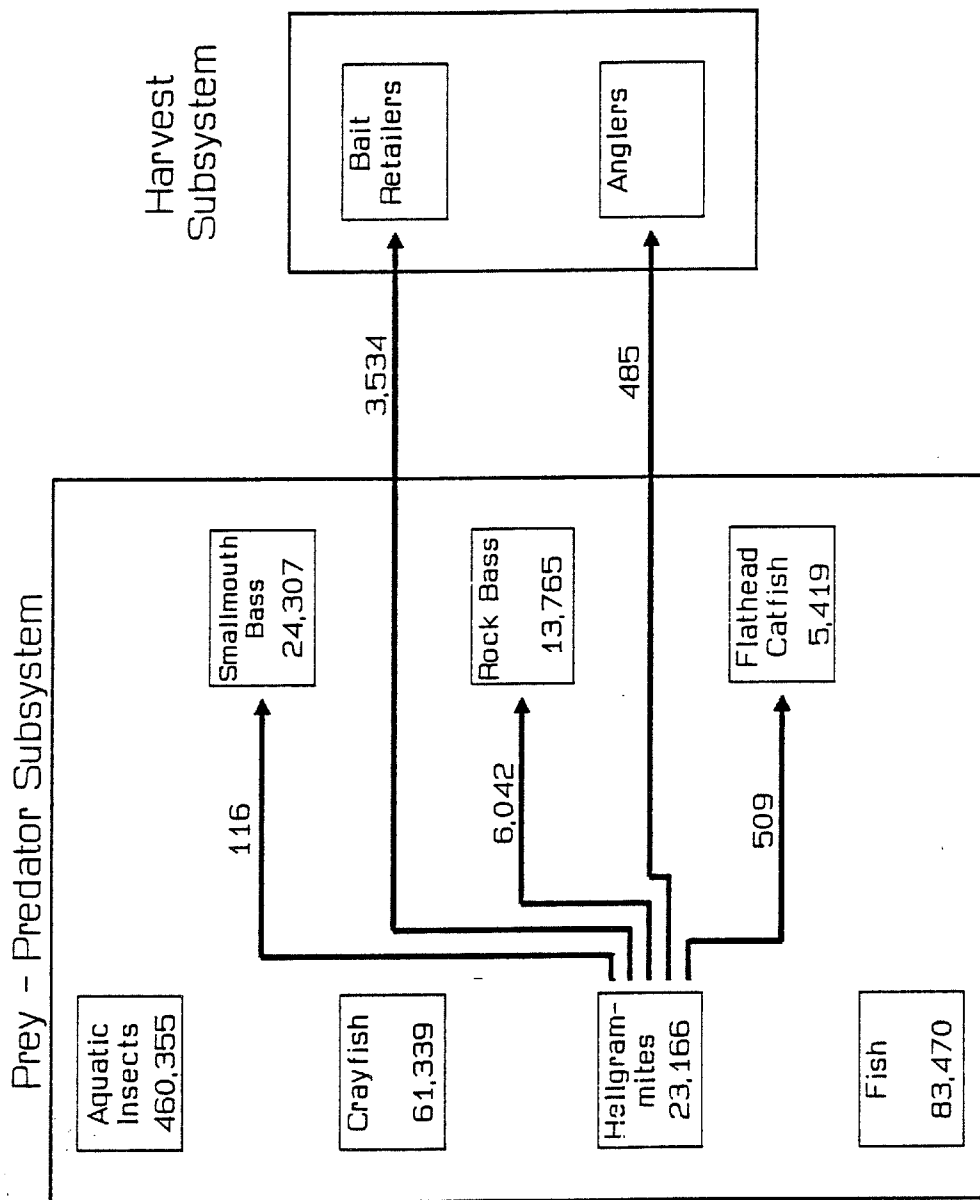


Figure 24. Estimated annual energy flow (kcal/ha/yr) from hellgrammites to each of the three predator fish populations and two harvest groups; annual mean biomass (kcal/ha) is shown for each component of the prey-predator subsystem.

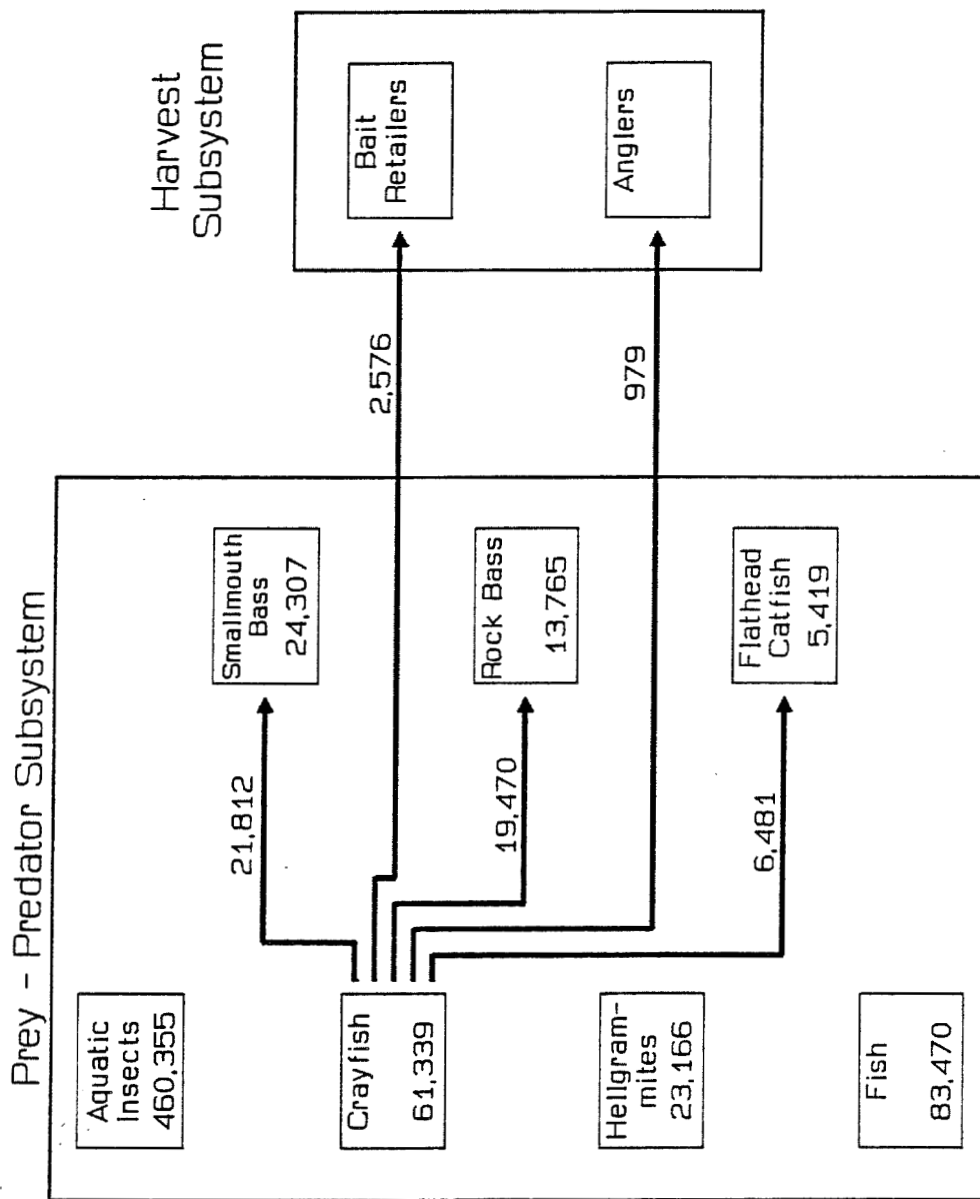


Figure 25. Estimated annual energy flow (kcal/ha/yr) from crayfish to each of the three predator fish populations and two harvest groups; annual mean biomass (kcal/ha) is shown for each component of the prey-predator subsystem.

Figures

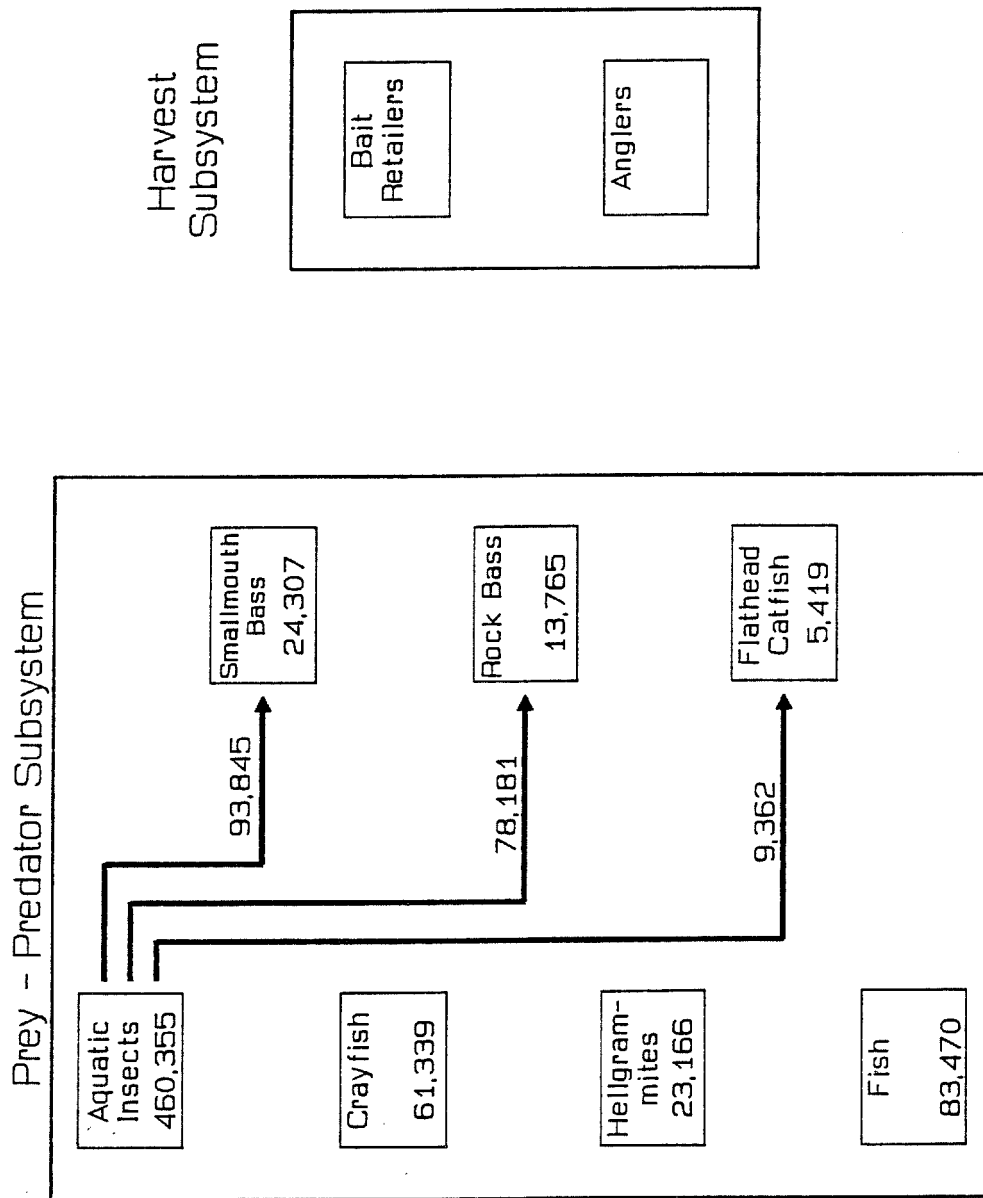


Figure 26. Estimated annual energy flow (kcal/ha/yr) from aquatic insects to each of the three predator fish populations; annual mean biomass (kcal/ha) is shown for each component of the prey-predator subsystem.

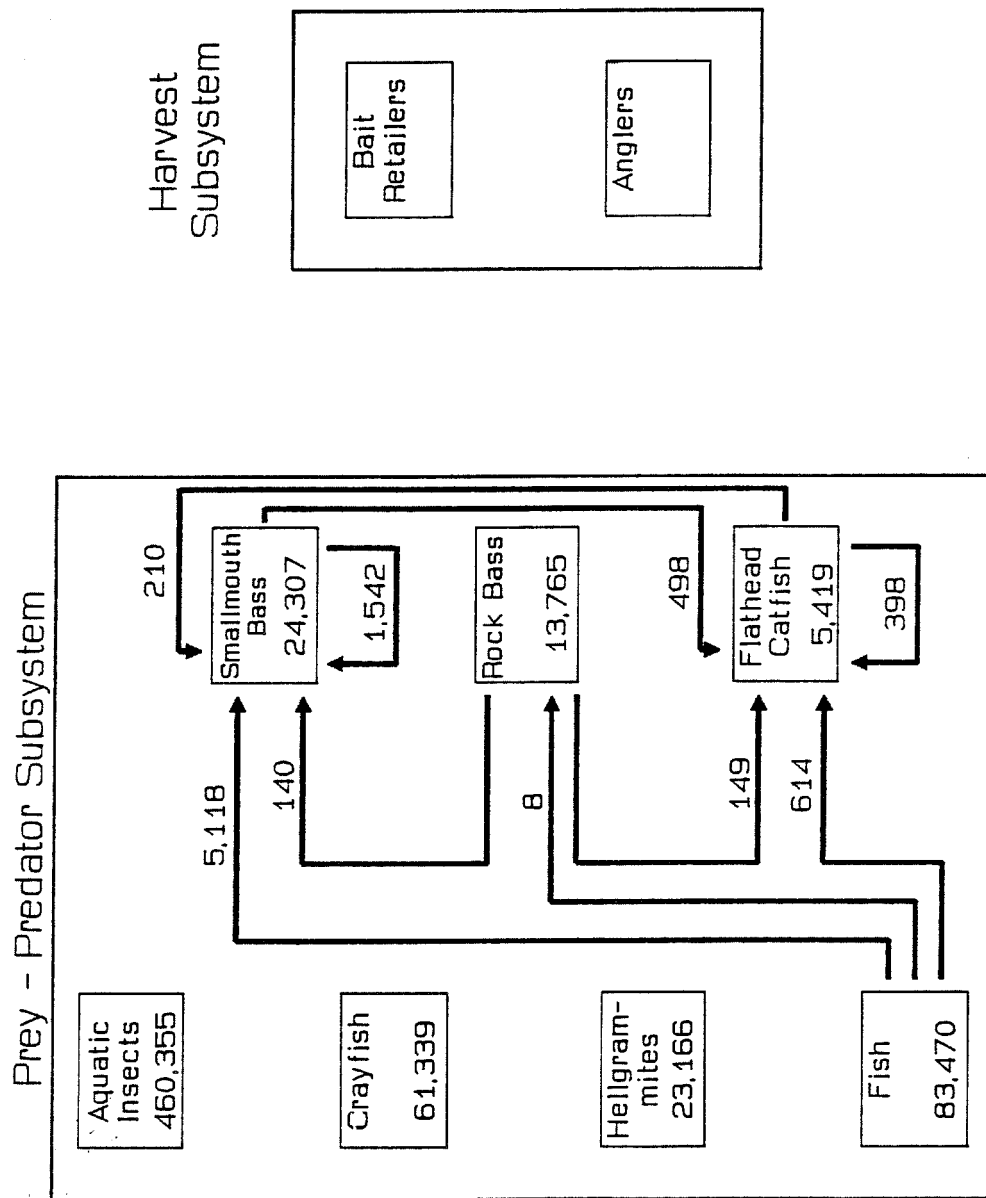


Figure 27. Estimated annual energy flow (kcal/ha/yr) from prey fish and young-of-year predator fishes to each of the three predator fish populations; annual mean biomass (kcal/ha) is shown for each component of the prey-predator subsystem.

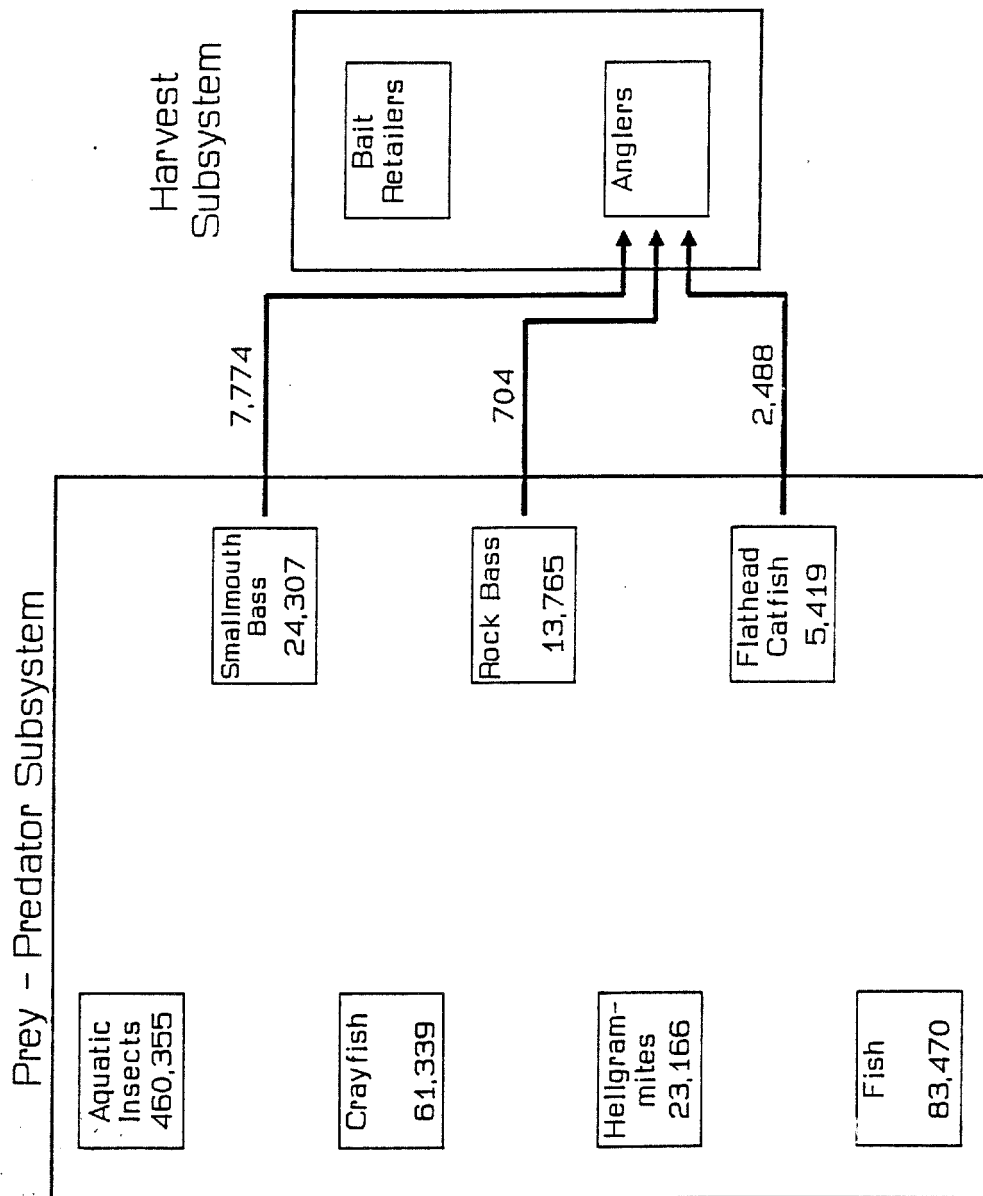


Figure 28. Estimated annual energy flow (kcal/ha/yr) from each of the three predator fish populations to anglers; annual mean biomass (kcal/ha) is shown for each component of the prey-predator subsystem.