

Assessing Potential Navigation Impacts
to the Kanawha River Ecosystem:
A Modeling Approach

by

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(ABSTRACT)

An extensive study of the biota of the Kanawha River was integrated to examine the trophic basis of fish production and predict potential impacts of increased tow traffic at two sites in the Winfield Pool. Total standing stock and production of adult fish were estimated as 242 kg/ha and 188 kg/ha/yr, respectively. Sixty-one species were categorized into six trophic groups. Trophic generalists (omnivores and herbivore/detritivores) consumed a variety of foods including considerable detritus. These groups accounted for 73 to 83% of total ichthyomass and 77 to 81% of total adult production. Total fish consumption at the more riverine upper site was partitioned into 35% detritus, 28% invertebrates, 20% plant matter, 12% other fish, and 5% crayfish. At the lower, more lentic site the diet consisted of 34% detritus, 25% plant matter, 21% other fish, 17% invertebrates, and 3% crayfish. The overall basis

of production relies upon imports of allochthonous materials.

A linear, donor-controlled mathematical model was developed to trace inputs, outputs, and exchanges of energy flow through nineteen functional groups of aquatic organisms/organic matter at each site. Temporary increases in turbidity were considered a predominant effect of passing tows relevant to river ecosystem function. This was simulated by periodic lapses in photosynthetic rates. Under the highest projections of traffic, the model predicted slight declines (< 6%) in the abundance of most heterotrophic groups. The consistent pattern observed at each trophic level was the dominance of detritivores and trophic generalists functioning as collector filterers and gatherers. An energy flow analysis revealed that the key trophic groups within the ecosystem ultimately relied more upon allochthonous sources of organic matter than autochthonous sources as the basis of their production. Both in terms of the success of detritivores and the importance of energy pathways that are detritus-based, these results lend support to the prevailing theory of large river ecosystem structure and function.

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There were many persons who made generous contributions of their time, talents, energy, and love, and without whom this thesis could not have been completed. I lack sufficient space to adequately express my gratitude to all these individuals here, and yet there is one Person I cannot leave unrecognized. I thank my Lord Jesus Christ. It took 25+ years to find out Who to put my trust in! To Him I dedicate this work, which would have been completed long ago had I only met Him sooner and kept my eyes more firmly fixed on Him thereafter.

"All things by immortal power
near or far
hiddenly
to each other linked are,
that thou canst not stir a flower
without troubling of a star"

Francis Thompson 1897

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Chapter I

Trophic Basis of Fish Production in a Large Navigable River

INTRODUCTION

Purpose and Objectives

This portion of the study was primarily undertaken to provide basic data for use in an energy flow model. However, fish production in large rivers has received little attention due to the large number of species encountered and the difficulty in making quantitative estimates of abundance from these systems. Large rivers support many fish species, but typically a few species comprise the majority of the biomass. Total fish biomass from large rivers has been reported to range from 143 kg/ha in the Coosa River to as high as 1730 kg/ha in the Tenson River (Swingle 1954). Estimates of total fish biomass from various locations on the Ohio River have ranged from 205 to 470 kg/ha (Pearson and Krumholz 1984). Total fish production has been reported in only two large rivers. In the River Thames, Mann et al. (1972) estimated total production by all species and life stages as 2000 kg/ha/yr. Total fish production estimates from the Kafue River, Africa, have ranged from 630 - 870 kg/ha/yr (Kapetsky 1974).

Fish production in a large river is generally thought to be supported more by imports of detritus from upstream than by primary production in the river reach itself (Hynes 1970). In contrast Adams et al. (1983) suggested that for reservoirs (impounded rivers), the importance of allochthonous organic matter may have been overemphasized, and that autochthonous sources of energy may often be sufficient to support biological productivity. Along the continuum between large river and reservoir, then, the primary source of energy driving the ecosystem would appear to depend at least in part on the degree to which particulate matter remains suspended, contributing to increased turbidity and reduced levels of primary production.

Benke et al. (1985) found fish production in the Satilla River, Georgia, depended to a considerable extent on aquatic insects which inhabit snag habitats, while Mann et al. (1972) concluded that terrestrial insects and detritus were the primary sources of energy supporting production of fish in the River Thames, England. Thus depending on such factors as habitat availability for invertebrates and the quality and quantity of the terrestrial/aquatic interface, large rivers may support fish production by very different

means. The Kanawha River is impounded and demonstrates characteristics of habitat and interface that are intermediate within the range of published accounts of large rivers. These characteristics make the Kanawha River a valuable system to be studied and described. The specific objectives of this portion of the study were to determine: 1) the species composition of fish in the Kanawha River, 2) the standing stock and production of the total fish assemblage, and 3) the trophic basis for this production.

Study Area

The Kanawha River is a tributary of the Ohio River, flowing 156 kilometers in a northwesterly course from Gauley Bridge to Point Pleasant, West Virginia (Figure I.1). The Kanawha is a sixth order stream formed by the confluence of the New and Gauley Rivers. It is a low gradient (0.195 m/km), warmwater river throughout its length, having a drainage area of 26,985 km² and an average discharge of 424.8 m³/s at Charleston, West Virginia. The Winfield Pool extends from Winfield Locks and Dam (located fifty kilometers above the Ohio River, R.M. 31.1) approximately 59 kilometers to Marmet Locks and Dam (R.M. 67.7). The general nature of the Winfield Pool shifts at the confluence of the

Elk River (R.M. 57.2). Above this point the pool is characterized as distinctly lotic (approximately 50 meters wide, with a perceptable current at all but the lowest flows, 3-4 meter depths, and cobble, pebble, and sand substrates). Below the confluence of the Elk, the pool assumes a more lentic nature. The lower reach widens to over 60 meters, current is less perceptable, depths range from 9-10 meters, and substrates are dominated by sands. The channel is relatively uniform in cross section, and banks are steep throughout the length of the pool.

Regional History

The lower Kanawha River has a long history of industrial and municipal water pollution. Johnson (1977) relates the following regarding the early history of water quality in the river:

"In testimony at a public hearing (regarding iron oxides being discharged from mining activities upstream) in Charleston on June 25, 1910, Asst. Engineer Thomas E. Jeffries, in charge of the Charleston Suboffice, recalled that when he first saw the Kanawha in 1855 the stream was clear as crystal. He remembered swimming in the river with open eyes and gigging for fish that were visible fifty feet away in the clear water. But since 1895, Jeffries testified, the Kanawha had been murky. This testimony was confirmed

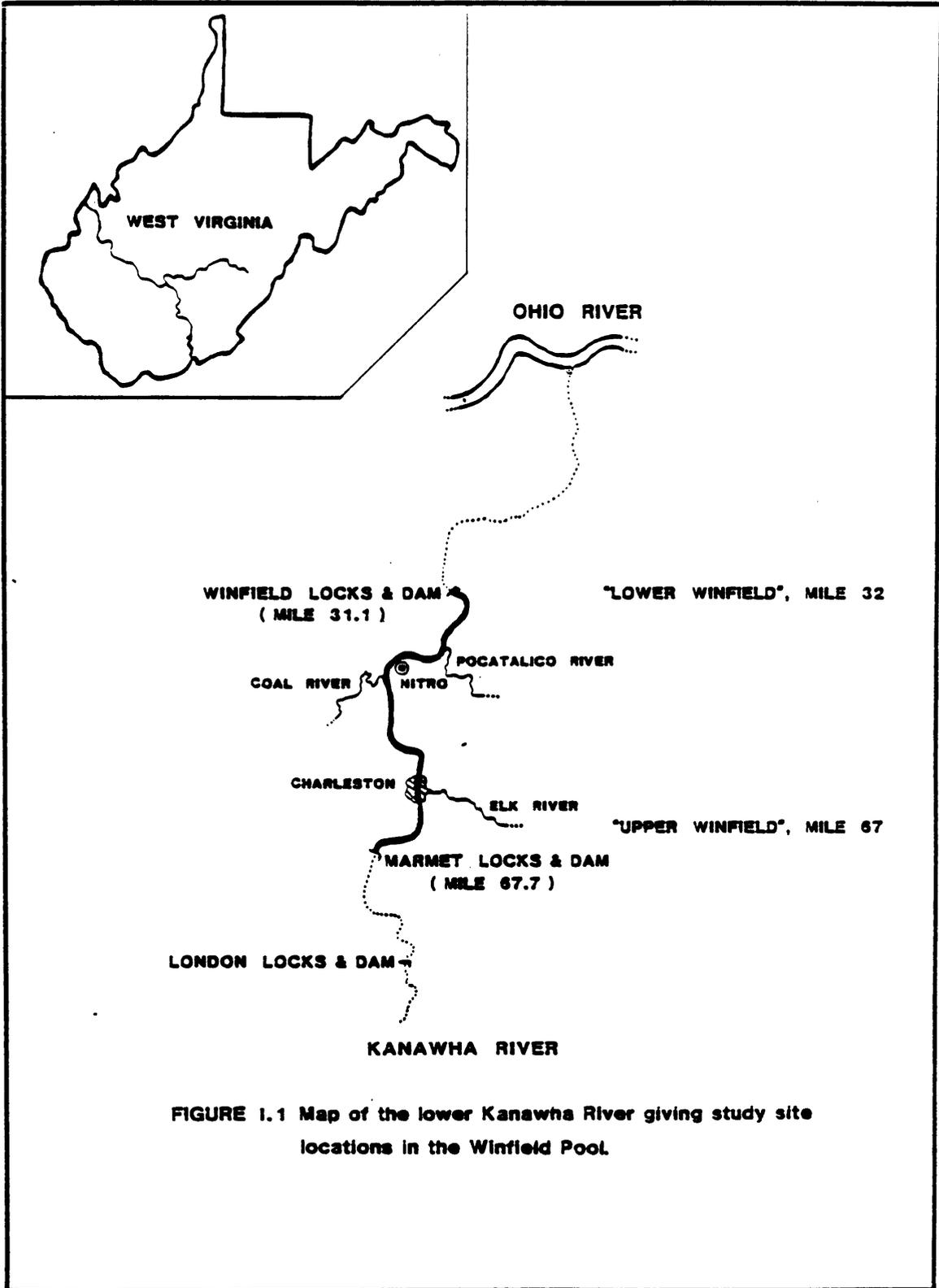


FIGURE 1.1 Map of the lower Kanawha River giving study site locations in the Winfield Pool.

by many other witnesses, one of whom was Gov. W. A. MacCorkle of West Virginia, who declared the Kanawha was a 'foul sewer, abhorrent to the eye, and absolutely destructive of all life within it and useless to the community through which it flows.' "

Prior to 1948 wastewater received little or no treatment. Dissolved oxygen concentrations of zero were prevalent, even during high flow conditions. This and unfavorable pH conditions severely limited aquatic life in the river. With the formation of the Kanawha River Industrial Advisory Committee in 1958 and the U.S. Department of the Interior Federal Water Pollution Control Administration in 1963, enforcement of wastewater treatment requirements was initiated. This gradually led to an improvement in the quality of municipal and industrial discharges into the river (USACOE 1983). These and other clean water measures have allowed marked improvements in river water quality and an associated biological recovery has taken place. The Kanawha currently supports a diversity of aquatic life typical of other large rivers in the region, although it is by no means pristine.

The results of ichthyological studies which have included or focused on the Kanawha River are summarized in Appendix A. The earliest extensive survey of the fishes of

the Kanawha River was conducted by Addair (1944). He found a total of 86 species and subspecies of fish in the Kanawha River system in West Virginia. Of these, 39 occurred in the mainstem below the Kanawha Falls (c.a. river mile 95), and 30 were found in the Winfield Pool. Southern Appalachian regional ichthyological data, compiled from museum records, literature references and field observations, were summarized by Jenkins et al. (1971). They reported 86 native freshwater forms, 4 forms classified as marine, and 8 introduced or possibly introduced forms (Dorosoma petenense, Salmo gairdneri, S. trutta, Salvelinus fontinalis, Esox niger, Carassius auratus, Cyprinus carpio, and Pimephales promelas) in the Kanawha River drainage below Kanawha Falls. No endemic species were reported to occur in the river below the falls. The ichthyofauna of the Kanawha River are similar to other major drainages of the Ohio River Basin; the Kanawha River drainage system below the falls shares 75 species with both the Cumberland River below its falls and the Tennessee River (Jenkins et al. 1971).

Fish have been sampled since 1968 at the London and Winfield Locks in a cooperative effort by several state and federal agencies (Ohio River Sanitation Commission 1981). Sampling protocol involves leaving the downstream gates of one lock chamber open overnight while maintaining some flow

through the chamber to attract fish. The gates are then closed, rotenone is applied to kill the fish, and all fish dying and surfacing the first day are collected. Only 50 to 90% of the fish population are recovered the first day, and the species composition of the sample does not truly reflect relative abundances of all species in the river. However, the 12 samples taken since 1968 do allow some conclusions to be drawn. Lock rotenone samples taken at Winfield and London during the period 1968-1983 document the recent occurrence of at least 58 species as compared to the 39 found by Addair (1944) in the Kanawha mainstem below the falls (Ohio River Sanitation Commission 1981, West Virginia Department of Natural Resources, unpublished data). This is a conservative estimate of species richness in the Kanawha River mainstem because only two locations were sampled. The increase in species richness since Addair's work is primarily attributable to improved water quality.

From the period 1968 through 1983 the number of species collected per sample ranged from 8 to 25 (Table I.1). At both sites there has been an increase in the number of species collected per sample. At London, the number of species collected averaged 11.5 for 1968-73 and 22 for 1976-83. At Winfield, the increase was significant but not as dramatic (10.8 for 1968-73 and 15.6 for 1976-83). Over

the entire period more species were collected at London Locks than Winfield Locks in 9 out of 12 years. Since 1976, an average of 6.4 more species were collected from London Locks than from Winfield Locks. The apparent recovery and reestablishment of fish populations at both sites is evident; for example, sauger and walleye have occurred regularly in lock samples since 1976 (Table I.1). However, it appears that the recovery has occurred more rapidly in the reaches near London and further improvement is still possible near Winfield.

Numbers and weight of fish collected in lock samples were much higher at Winfield Locks than at London Locks (Table I.1). Mean numbers per hectare averaged 4,021 at London and 13,412 at Winfield. Number of fish collected was highly variable and no trends were apparent at either lock. Biomass of fish collected averaged 148.18 kg/ha at London and 230.81 kg/ha at Winfield. Biomass was less variable than numbers through time. Biomass at London has increased from 72.77 kg/ha for 1968-73 to 185.86 kg/ha for 1976-83. No comparable increase in biomass was apparent at Winfield.

Although species richness was greater at London than at Winfield, the dominant fish species were the same at both sites (Table I.2). Numerically, the emerald shiner was the

Table I.1. Summary of rotenone samples of fish at the London and Winfield locks, Kanawha River. Area of lock chambers was 0.187 ha. Data from 1968-1980 extracted from Ohio River Sanitation Commission (1981) and data since 1981 West Virginia Dept. Natural Resources unpublished stream surveys.

Year	London			Winfield		
	No. of Species	Number	Weight(kg)	No. of Species	Number	Weight(kg)
1968	9	219	12.62	10	2055	45.52
1969	13	446	9.66	8	1653	35.67
1970	14	1461	10.16	12	14716	51.72
1973	10	79	21.99	13	1055	25.32
1976	25	827	17.96	16	1278	27.55
1977	25 ²	238	16.89	13 ¹	166	19.57
1978	25 ²	2614	29.44	15 ¹	1208	53.17
1979	18 ¹	470	31.03	13 ¹	252	35.97
1980	21 ³	644	75.13	15 ²	423	47.89
1981	22 ²	757	12.63	20 ²	2532	96.66
1982	17 ¹	203	67.20	17 ²	3708	34.99
1983	23	1060	27.77	16 ²	1043	45.92
mean:		752	27.71		2508	43.16
mean/ha:		4021	148.18		13412	230.81

¹ sauger collected

² sauger and walleye collected

³ walleye collected

dominant species at both sites. At London, six species (emerald shiner, mimic shiner, channel catfish, gizzard shad, flathead catfish, and freshwater drum) made up 91.9 and 86.3% of the total numbers in 1968-73 and 1976-83, respectively. At Winfield, five species (emerald shiner, gizzard shad, channel catfish, mimic shiner, and freshwater drum) made up 96.3 and 95.0% of the total numbers in 1968-73 and 1976-83, respectively. The gizzard shad and carp were the dominant species by weight at both sites. At London, seven species (gizzard shad, carp, channel catfish, flathead catfish, freshwater drum, silver redhorse, and longnose gar) made up 74.7 and 86.0% of the total weight in 1968-73 and 1976-83, respectively. At Winfield, five species (carp, gizzard shad, channel catfish, emerald shiner, and freshwater drum) made up 96.9 and 87.3% of the total weight in 1968-73 and 1976-83, respectively. A notable difference in the species composition between sites was the lower abundance and fewer species of the redhorse (Moxostoma spp.) at Winfield. Redhorses are intolerant of industrial pollutants and siltation (Trautman 1981) and may not yet have reestablished large populations in the vicinity of Winfield.

Table I.2. Percent composition of common fishes (70.1% of total weight or number at either site over all years) in lock-rotenone samples taken from London and Winfield Locks, Kanawha River, from years 1968-1973 and 1973-83. Data from 1968-1980 extracted from Ohio River Sanitation Committee (1981) and data since 1981 are from West Virginia Department of Natural Resources stream survey forms. T = < 0.1%.

Species	London				Winfield			
	Numbers		Weight		Numbers		Weight	
	1968-73	1976-83	1968-73	1976-83	1968-73	1976-83	1968-73	1976-83
<u>Lepisosteus osseus</u> (Longnose gar)	0.3	0.5	3.5	4.4	-	-	-	-
<u>Anquilla rostrata</u> (American eel)	0.1	T	0.3	0.1	-	T	-	-
<u>Alosa chrysochloris</u> (Skipjack herring)	-	T	-	0.3	T	1.2	T	1.0
<u>Dorosoma cepedianum</u> (Gizzard shad)	0.4	6.8	3.8	24.3	5.5	24.1	23.6	30.7
<u>Esox masquinongy</u> (Muskellunge)	T	T	11.2	1.0	-	-	-	-
<u>Campostoma anomalum</u> (Stoneroller)	-	T	0.1	T	-	-	-	-
<u>Cyprinus carpio</u> (Carp)	0.4	0.5	4.7	26.6	1.2	0.4	44.2	25.8
<u>Hybopsis aestivalis</u> (Speckled chub)	-	0.2	-	T	-	T	-	T
<u>Hybopsis amblops</u> (Bigeye chub)	-	1.0	-	T	T	-	T	-
<u>Notropis atherinoides</u> (Emerald shiner)	62.3	55.3	4.1	1.5	75.5	50.4	13.1	4.9

Species	London				Winfield			
	Numbers		Weight		Numbers		Weight	
	1968-73	1976-83	1968-73	1976-83	1968-73	1976-83	1968-73	1976-83
<u>Notropis buchanaani</u> (Ghost shiner)	4.4	6.8	0.3	0.1	T	0.6	T	T
<u>Notropis stramineus</u> (Sand shiner)	T	0.4	T	T	1.8	-	0.2	0.1
<u>Notropis volucellus</u> (Mimic shiner)	12.2	16.5	0.3	0.3	2.3	9.2	0.2	0.2
<u>Pimephales notatus</u> (Bluntnose minnow)	0.3	0.2	T	T	T	0.5	T	-
<u>Ictiobus bubalus</u> (Smallmouth buffalo)	T	T	0.1	T	T	T	0.2	0.7
<u>Ictiobus niger</u> (Black buffalo)	-	T	-	2.4	-	T	3.6	1.6
<u>Moxostoma anisurum</u> (Silver redhorse)	0.2	0.7	4.4	6.7	-	-	-	-
<u>Moxostoma carinatum</u> (River redhorse)	-	0.1	-	0.7	-	-	-	-
<u>Moxostoma erythrurum</u> (Golden redhorse)	-	T	-	0.3	-	-	-	-
<u>Moxostoma macrolepidotum</u> (Shorthead redhorse)	-	0.2	-	0.7	-	T	-	0.1
<u>Ictalurus melas</u> (Black bullhead)	-	-	-	-	0.1	-	0.7	-
<u>Ictalurus nebulosus</u> (Brown bullhead)	-	-	-	-	0.2	-	1.3	-
<u>Ictalurus punctatus</u> (Channel catfish)	10.8	5.1	30.7	10.1	13.0	7.2	15.9	25.4

Species	London				Winfield			
	Numbers		Weight		Numbers		Weight	
	1968- 73	1976- 83	1968- 73	1976- 83	1968- 73	1976- 83	1968- 73	1976- 83
<u>Pylodictis olivaris</u> (Flathead catfish)	4.9	0.4	19.5	7.8	-	0.1	-	1.3
<u>Morone chrysops</u> (White bass)	0.4	0.3	1.0	0.9	-	0.8	-	2.3
<u>Ambloplites rupestris</u> (Rock bass)	-	0.1	-	0.2	-	T	-	T
<u>Lepomis macrochirus</u> (Bluegill)	0.2	0.3	T	0.3	T	0.2	0.1	0.1
<u>Lepomis megalotis</u> (Longear sunfish)	0.2	0.1	0.1	0.1	-	0.1	-	T
<u>Micropterus dolomieu</u> (Smallmouth bass)	T	0.2	0.3	0.4	-	-	-	-
<u>Micropterus punctulatus</u> (Spotted bass)	0.8	0.6	6.0	1.2	T	0.1	0.2	0.2
<u>Micropterus salmoides</u> (Largemouth bass)	-	0.1	-	0.2	-	T	-	0.1
<u>Pomoxis annularis</u> (White crappie)	0.7	T	1.2	0.2	T	T	0.1	0.1
<u>Stizostedion canadense</u> (Sauger)	-	0.2	-	1.2	-	0.5	-	2.2
<u>Stizostedion vitreum</u> (Walleye)	-	0.1	-	1.9	-	0.1	-	0.4
<u>Aplodinotus grunniens</u> (Freshwater drum)	1.3	2.2	8.1	6.1	T	4.1	0.1	10.5

METHODS

Field Collections

The ichthyofauna of the Kanawha River were sampled monthly (excluding January) from October 1982 through September 1983 at two sites representing the upper (UW) and lower (LW) reaches of the Winfield Pool. Upper and lower sites were located in the vicinity of river miles 66-67 and 33-34, respectively (Figure I.1). Four sampling areas were chosen at each study site to encompass the various habitats that were evident. A secondary consideration in site selection was suitability for the use of a particular sampling gear type. The collection methods employed were identical in each sampling area, and the resultant four data sets were combined to represent the study site.

Electrofishing was done by boat during daylight hours. A 3500-watt, 220-volt generator and Coffelt VVP-15 variable voltage pulsator was used to produce pulsed, direct current. The electrode system consisted of two Wisconsin hoop anode arrays and 10 flexible conduit droppers for cathodes. Generated amperages ranged from 6 to 8. The outboard motor used on the electrofishing boat was equipped with a jet unit (Specialty Manufacturing, Inc., San Leandro, Calif.) instead

of the conventional propeller-drive lower unit. This feature provided a high degree of maneuverability around structures where fish appeared to be concentrated, such as brush piles and over-hanging vegetation, and permitted electro-fishing in very shallow water. Two people captured stunned fish from the front of the boat using 4.8 mm bar-mesh dip nets at four electrofishing locations at each site.

It became apparent during the October 1982 sampling period that shore-line seining for smaller fish was not feasible due to a scarcity of areas compatible with the use of this sampling gear type. Most banks dropped off sharply into water too deep to seine effectively, and in areas shallow enough to permit seining frequent snags were encountered. Subsequently, young-of-the-year and smaller species (principally cyprinids) were sampled during separate electrofishing runs at the four electrofishing locations at each site using 1.6 mm bar-mesh dip nets. The use of the smaller mesh dip nets reduced the loss of smaller cyprinids. All electrofishing was conducted by proceeding upstream and weaving in and out of the shoreline for a duration of fifteen minutes. The distance covered at each location (150-200m) varied slightly over the course of the study due to differences in the velocity of river flow and its effects on boat-handling.

Nylon experimental gill nets (38.1 m long by 1.8 m deep) were used to sample species that frequented deeper water. Each net was composed of five 7.6 m panels, each panel of a different mesh size (1.9, 2.5, 3.2, 3.8, or 5.1 cm bar-mesh). Gill nets were fished overnight with the smallest mesh inshore and increasing mesh sizes extending out into the channel. The nets were set at an approximate 45 degree angle to the downstream shoreline. The lead lines of the gill nets, for the most part, rested on the river bottom along their entire lengths.

Larger fish collected by electrofishing or gill-netting were identified, weighed, and measured in the field. Scales (or spines from ictalurids) were collected. Stomachs were removed and preserved in 10% formalin for future analyses. Smaller fish were preserved in their entirety using 10% formalin and returned to the lab for identification and other analyses.

Species Composition

All fish were identified in accordance with descriptions given by Eddy (1969), Pflieger (1975), or Trautman (1981) and subsequently enumerated by species. Weights of all individuals collected were recorded with the

following exceptions: when gizzard shad or small cyprinids appeared in abundance, weights were recorded for individuals from subsamples. Each month at each site, at least forty randomly selected members of each species were weighed. The remaining fish of each species were weighed en masse for the relative species abundance estimates. Length-weight relationships for gizzard shad and smaller cyprinids were developed from the subsample data. Fish from which lengths, but not weights, were taken could then be included in the growth analyses. Relative species abundance was estimated both by numbers and by weight.

Age Determinations

Most species were aged by counting scale annuli. Scale impressions were made in acetate slides and subsequently projected at 40X to facilitate reading. Catfish were aged from pectoral spine sections. Pectoral spines were decalcified, sectioned, stained and mounted on glass slides using methods of Ashley and Garling (1980). Each fish was aged independently by two people. A third person resolved any disagreements. Scale impressions that lacked clarity were discarded. Subsamples of 40 randomly selected gizzard shad per site were aged in May and June. The Petersen method

(inspection of the length frequency distribution) was used to age emerald shiners (Jearld 1983), since attempts to age this species using scales were unsuccessful. Longnose gar, members of the family Cyprinidae (other than emerald shiners and common carp), and other species of which only a few specimens were collected were not aged.

Growth

Von Bertalanffy growth models were fitted for the eighteen most common species of fish. Fish were assigned ages in months by adding to the annular age (expressed in months) the number of months elapsed between the month of collection and January of the same year. Thus an Age 0 fish taken in October was assigned an age of 10 months ($0 \times 12 + 10$); an Age I, 22 months, etc. Ages were then converted back to years for input to the von Bertalanffy growth models. Age/length and age/weight relationships were established using:

$$W_t = W_\infty (1 - e^{-k_w(t-t_0)})^3$$

$$L_t = L_\infty (1 - e^{-k_l(t-t_0)})$$

where:

W_t = predicted weight of fish at time t

L_t = predicted length of fish at time t

W_∞ = asymptotic maximum weight

L_{∞} = asymptotic maximum length

t_0 = time intercept for $W = 0$ or $L = 0$

K_w = coefficient for growth in weight

K_l = coefficient for growth in length The parameters of

these relationships were obtained by least-squares estimation using a nonlinear regression (SAS User's Guide, 1979 Edition). Fitted growth models were used as predictors of fish size (length or weight) at age.

Instantaneous growth rates (G) for each species and age group (t) were calculated as follows:

$$G_{t,t+1} = \ln(W_{t+1}) - \ln(W_t)$$

where:

W_t = weight (g) at time t predicted from the fitted von Bertalanffy equation

Mortality

In the absence of suitable data for application of catch-curve analysis, mortality rates (Z) were estimated from median lengths for 18 fish species. Hoenig et al. (1983) concluded that methods of estimating Z from mean length possessed undesirable statistical properties and proposed an estimator requiring an exponential transformation of fish lengths:

$$y_i = - \ln(1 - (\frac{l_i}{L_\infty}))$$

where:

L_i = length of the i^{th} fish in the sample

L_∞ = asymptotic maximum length

The median of the transformed lengths, along with a transformation of the length at which the fish is first vulnerable to the gear, is used to estimate mortality as follows:

$$Z = K(\frac{\ln(2)}{(y_m - y_c)})$$

where:

K = von Bertalanffy growth coefficient

y_m = median of transformed lengths

Other estimators based on mean length (Beverton and Holt 1956, Ssentongo and Larkin 1973) and age-composition (Robson and Chapman 1961) were also used for comparison. Hoenig's estimator, which is relatively insensitive to variability in year class strength, was used in cases where the estimates of mortality obtained by the four methods had a standard deviation greater than 0.1. When in closer agreement (standard deviation of the estimates less than 0.1), the average of the four mortality estimates was used.

Production:Biomass Ratios

The approach taken in estimating production follows Ricker's (1975) derivation of yield from an arbitrary recruitment. Ricker's method is a tabular computation which divides a fish population of arbitrary initial weight into age intervals. One-thousand kilograms of recruits were assumed at the beginning of the first age interval. Each age interval is characterized by an instantaneous growth rate (G) and an instantaneous mortality rate (Z). These rates define a weight change factor (e^{G-Z}) used to predict the weight of recruits remaining at the end of the interval. Weights at the beginning and end of an interval were averaged and the result multiplied by the growth rate to estimate production during the interval. Production over all intervals was summed to give total production per kilogram of recruits. Similarly, biomass was summed over all intervals to give total biomass per kilogram of recruit. The sum of production was then divided by the sum of biomass to yield the P:B ratios. Young of the year and juveniles of most species were not vulnerable to the collection gear, and hence this period of growth is not reflected in the above method.

Production estimates reflect only production by adults and as such underestimate total production for each species. However, since the diet of the young-of-year fish often differs considerably from older fish of the same species, they may not belong to the same functional groups as adults.

Production

Estimates of actual production per unit area were calculated as the product of the production:biomass ratios and biomass density factor for each of the eighteen most common species. Annual lock rotenone sampling by the West Virginia Department of Natural Resources at Winfield Locks and Dam provided estimates of total fish biomass per unit area. Estimates made during the 1977 - 1982 timespan were selected as representative of conditions following improvements in the water quality of the river. Over this timespan the biomass of all species (combined) was more consistent than the biomass estimates for individual species, therefore total biomass estimates were averaged for the five-year period and partitioned according to the relative weights of fish species collected during 1982-83 field collections at UW and at LW. This approach is less sensitive to temporal and behavioral biases inherent in the annual lock rotenone surveys.

Wet weights were converted to dry weights using a factor of 25 percent. Caloric density conversions of 4.677, 5.761, and 6.360 (kcal/g dry weight) were applied for the Centrarchidae, Cyprinidae, and Clupeidae, respectively (Cummins and Wuycheck 1971). Caloric density conversions of 4.677 kcal/g dry weight were assumed for members of the Percidae family, while all other species were assumed to have a conversion factor of 5.761.

Production:biomass ratios were then multiplied by the biomass estimate for each species to estimate its production per unit area. Production by each trophic group was calculated by summing the available production estimates of species in the group and then multiplying this by a correction factor to account for the contribution of species for which production estimates were not available.

Food Habits

The food habits of the fishes of the Kanawha River were investigated by examining gut contents. A number of different techniques were required to gain this information, due to anatomical and dietary differences among species.

The stomach contents of species exhibiting a distinct stomach (centrarchids, ictalurids, etc.) were examined. Stomachs were emptied, food items blotted dry, and the volume of the stomach contents was measured by displacement. Individual food items were identified, often microscopically, and counted. Descriptions in Pennak (1978) and in Merritt and Cummins (1978) were used to identify invertebrates to the lowest feasible taxon. The volume of each food type was measured by displacement whenever possible. Individual food items too small to be measured by displacement were combined together and the relative contribution of each estimated. Absolute volume estimates for these smaller food items were then calculated by partitioning the difference in volume between measurable food items and the total volume of all stomach contents.

Catostomids and common carp food habits were also examined using these methods. However, only the contents of the first loop of the intestine was considered, since these species lack true stomachs.

Foreguts were collected from 20 gizzard shad per site per month, when available. The contents of the esophagus and gizzard were extracted. Pooled samples from all 20 gizzard shad were examined. These were stained with rose

bengal to help distinguish between inorganic and organic matter. A subsample of the pooled sample was placed in the Sedgewick-Rafter counting chamber and viewed microscopically at a magnification of 200X. Ten fields of view per subsample were observed. Mean values for each pooled sample were derived from three subsamples. The area covered by each food type in the Sedgewick-Rafter chamber was estimated by using an ocular micrometer grid. Area was considered to be proportional to volume. Estimating the volume of stomach contents from area has been used for threadfin shad (Gerdes and McConnell 1963) and gizzard shad (Baker and Schmitz 1971). Gerdes and McConnell (1963) developed "relative thickness factors" for various taxa found in the diet and calculated relative volume by multiplying area by relative thickness. The abundance of amorphous matter found in the gut contents of gizzard shad in this study prevented the development of relative thickness factors. The volume of a particular food item in the gut contents of gizzard shad was based on area covered and a visual estimate of relative thickness.

The food habits of the emerald shiner were considered to be representative of all the cyprinid species with the exception of common carp. Methods used to examine the gut contents of emerald shiners were similar to those used for

gizzard shad. However, the entire contents of the first intestinal loop were scrutinized, rather than subsamples taken from pooled samples of the foregut. Depending on availability, between 50 and 100 emerald shiners from each month's collection were used in the analysis (exception: June, where only 42 were collected).

Longnose gar lack a distinct stomach. The contents of the complete digestive tract were examined. Techniques for quantification of the gut contents were the same as those for species with true stomachs.

Food habits for several species were not analyzed because only very few individuals were collected. Gut contents of Ohio lamprey, brook silversides, Etheostoma spp., and Percina spp. were not examined for the above reason. The exclusion of these data does not present any serious difficulty since these species represent only a small proportion of the fish biomass in the trophic groups to which they belong. The food habits of the American brook lamprey were not studied, since this species does not feed during the adult stage of its life.

Proportional annual consumption (PAC), the contribution of a given food item to the total annual consumption of a given species of fish (or trophic group of

fishes), was calculated from gut contents observations. These observations were corrected for estimated changes in rates of food intake and for the proportion of fish of a given species that had non-empty guts when collected each month from the Winfield Pool. Thus, the PAC for each food item type was obtained for each species of fish through a series of calculations.

The average percent of total volume ($V_{a,i,m}$) in the gut contents of a species of fish (a), comprised of an individual type of food item (i), was computed from each of the monthly field samples. Monthly ($V_{a,i,m}$) values were then weighted to take into account two factors. First, each monthly ($V_{a,i,m}$) was weighted according to the proportion of fish examined with non-empty guts relative to that proportion for the entire sampling season. Second, monthly ($V_{a,i,m}$) values were weighted according to estimated digestive tract evacuation rates derived from water temperatures measured each month in the Winfield Pool and from egestion times for sauger in the Gallipolis Pool of the Ohio River as reported by Wahl (1982). This weighting factor was applied under the assumption that evacuation time is inversely proportional to the rate of food intake. Hence, diet during periods of faster evacuation contributed more to the annual ration of a species than did diet during slower periods of evacuation. The two

weighting factors, therefore, were used to compute adjusted diet composition volumes for each food item type ($V_{a,i,m}$) according to the formula:

$$AV_{a,i,m} = V_{a,i,m} \left(\frac{N_{a,m}}{N_{a,t}} \right) E_m$$

where:

$AV_{a,i,m}$ = adjusted diet composition volume for diet item i
in species a during month m

$V_{a,i,m}$ = average percent of total volume for diet item i
in the gut contents of species a during month m

$N_{a,m}$ = number of fish of species a captured in
month m with non-empty guts

$N_{a,t}$ = total number of fish of species a with
non-empty guts captured throughout the study

E_m = the weighting factor for evacuation time
from Table I.3

The proportional annual consumption of a particular type of food item for a given species of fish ($PAC_{a,i}$) was then calculated by summing the adjusted diet composition volumes ($AV_{a,i,m}$) and dividing by the total of such sums for all diet items:

Table I.3. Weighting factors used to adjust fish consumption data for variable digestion rates.

Sampling Month	Kanawha River water temp. (C)	Evacuation time (hours) ¹	Weighting factor ²
October	20.0	16.0	0.41
November	14.0	16.5	0.40
December	6.2	38.5	0.17
February	3.0	186.5	0.04
March	4.7	112.5	0.06
April	9.0	39.8	0.16
May	15.0	16.5	0.40
June	22.6	8.2	0.80
July	26.0	7.1	0.93
August	26.6	6.6	1.00
September	25.6	7.6	0.87

¹ based on Wahl and Nielsen (1985)

² calculated as (6.6 hrs/evacuation time in hrs)

$$PAC_{a,i} = \frac{\sum_{m=1}^{11} VI_{a,i,m}}{\sum_{i=1}^n \sum_{m=1}^{11} VI_{a,i,m}}$$

where:

$PAC_{a,i}$ = proportional annual consumption of diet
item i by species a

m = index for months

n = number of diet items

Proportional annual consumption was calculated for the 17 most common species of fish in the Winfield Pool. The PACs were then used to assign each of these species to one of five trophic groups, namely, piscivores, crayfish/piscivores, invertivores, omnivores, or herbivore/detritivores. PAC data for the various member species in each trophic group were then weighted according to the relative abundance within the group and averaged. Accordingly, the proportional annual consumption of a given diet item by each trophic group was computed for UW and LW as follows:

$$PAC_{t,i} = \sum_{a=1}^x PAC_{a,i} \left(\frac{B_a}{\sum_{a=1}^x B_a} \right)$$

where:

$PAC_{t,i}$ = proportional annual consumption of diet
item i by trophic group t

$PAC_{a,i}$ = proportional annual consumption of diet
item i by species a

B_a = total biomass of species a captured at a given
site (UW or LW) during the study

x = number of species in the trophic group

Consumption

Because food consumption estimates are rare and difficult to obtain, energetics models typically predict consumption from observed growth (e.g. Kitchell and Breck 1980, Stewart et al. 1981, Kerr 1982). Annual consumption by each trophic group was derived from total annual production by applying a series of general bioenergetics relationships involving consumption (C), assimilation (A), production (P), respiration

(R), and wastes (W). Consumption is first partitioned into its various fates:

$$C = (P + R + W)$$

Assimilation, defined as consumption less wastes, was assumed to occur at approximately 80% efficiency for pure carnivores and 50% efficiency for pure herbivores (Webb 1978). Intermediate efficiencies were assumed for species demonstrating diet habits between these two extremes (Table I.4). Net production efficiencies in the range of 30% have been estimated for fish (Kozlovsky 1968), implying that respiration requires approximately 70% of assimilated energy. Using these relationships it was possible to back-calculate the consumption necessary to support observed production. The overall relation between consumption and production was obtained as follows:

Let

E_a = assimilation efficiency (A/C)

E_r = respiration efficiency (R/A)

E_p = production efficiency (P/A)

$$R = P \left(\frac{E_r}{E_p} \right)$$

$$C = \frac{(P + R)}{E_a}$$

Table I.4. Assumed conversion efficiencies used to estimate consumption (C).

Species	Efficiencies		
	Respiration (R/A)	Production (P/A)	Assimilation (A/C)
Gizzard shad	0.8	0.2	0.5
Common carp	0.7	0.3	0.5
Channel catfish	0.6	0.4	0.7
Smallmouth buffalo	0.7	0.3	0.5
Sauger	0.8	0.2	0.8
Silver redhorse	0.7	0.3	0.7
Golden redhorse	0.7	0.3	0.7
Shorthead redhorse	0.7	0.3	0.5
Freshwater drum	0.7	0.3	0.8
Smallmouth bass	0.7	0.3	0.8
Emerald shiner	0.8	0.2	0.7
Spotted bass	0.7	0.3	0.8
Largemouth bass	0.7	0.3	0.8
White bass	0.8	0.2	0.8
Bluegill sunfish	0.7	0.3	0.7
Spotted sucker	0.7	0.3	0.6
Longear sunfish	0.7	0.3	0.7
White crappie	0.7	0.3	0.8

Consumption by trophic groups was determined in the same manner as was production, by summing available estimates for species within a group and then proportionally increasing this to account for species for which estimates were not available.

RESULTS

The total number of fish collected over the course of the study was 12,377. Of this total 47.6% (5892) came from the UW site and 52.4% (6485) from the LW site. The weights of fish collected at UW and LW were 400.295 kg (53%) and 354.430 kg (47%), respectively for a total of 754.725 kg. Sixty-one species in all were found during the study (Appendix A).

Abundance and Composition

Total fish biomass for the Winfield pool of the Kanawha River was estimated as 242 kg/ha. Gizzard shad was the most abundant species at both UW (71.2 kg/ha) and LW (68.0 kg/ha) and accounted for 28-29% of the total fish biomass in the samples. The next three most abundant species at UW were the common carp (45.5 kg/ha), smallmouth buffalo (27.8 kg/ha), and channel catfish (14.0 kg/ha). At LW these same species were again the next three most abundant but were ranked in a different order: channel catfish (41.6 kg/ha) followed by common carp (37.3 kg/ha), and smallmouth buffalo (36.8 kg/ha). Thus these four species together comprised 65.5 and 75.9% of the total fish biomass at UW and LW, respectively. Silver redhorse, shorthead redhorse, smallmouth bass, and sauger were the secondarily abundant

species at UW, while sauger and freshwater drum were the other quite common species at LW (Table I.5).

Relative abundance of major fish species varied somewhat between the two sites. Several species made up larger percentages of the total fish biomass at UW than at LW, for example silver, golden, and shorthead redhorse, white bass, and smallmouth bass. The complimentary trend (a larger percentage at LW than UW) was exemplified by channel catfish, freshwater drum, bluegill sunfish, white crappie, spotted sucker, and largemouth bass (Table I.5).

Species encountered consistently throughout all parts of the year included the common carp, smallmouth buffalo, spotted sucker, sauger, and silver redhorse. Many species occurred most frequently during only parts of the year. Species captured most commonly during the summer included white bass, white crappie, and black crappie. Other species occurred primarily in the summer and fall (catfishes from July-Nov., sunfishes from July-Aug.) or occurred commonly from spring through fall (gizzard shad, spotted bass, largemouth bass, drum, and gar). Smallmouth bass and emerald shiners were most prevalent in samples made during the colder months. The redhorses appeared consistently except for declines during spring samples, when they may have ascended tributaries to spawn.

Table I.5. Abundance of some common adult fish species from the Kanawha River, West Virginia.

Species	UW			LW		
	kg/ha	kcal/m ²	%	kg/ha	kcal/m ²	%
Gizzard shad	71.2	11.32	29.4	68.0	10.81	28.1
Common carp	45.5	6.55	18.8	37.3	5.37	15.4
Channel catfish	14.0	2.02	5.8	41.6	6.00	17.2
Smallmouth buffalo	27.8	4.00	11.5	36.8	5.30	15.2
Sauger	8.2	0.96	3.4	13.1	1.53	5.4
Silver redhorse	13.1	1.88	5.4	0.5	0.07	0.2
Golden redhorse	9.2	1.33	3.8	0.5	0.07	0.2
Shorthead redhorse	12.3	1.77	5.1	-	-	-
Freshwater drum	3.6	0.42	1.5	9.9	1.16	4.1
Smallmouth bass	9.2	1.08	3.8	0.2	0.02	tr
Emerald shiner	3.9	0.56	1.6	2.9	0.42	1.2
Spotted bass	2.9	0.34	1.2	1.7	0.20	0.7
Largemouth bass	0.5	0.06	0.2	2.9	0.34	1.2
White bass	1.9	0.23	0.8	1.0	0.11	0.4
Bluegill sunfish	0.2	0.03	0.1	4.6	0.54	1.9
Spotted sucker	-	-	-	4.1	0.59	1.7
Longear sunfish	0.7	0.09	0.3	1.5	0.17	0.6
White crappie	0.4	0.05	0.4	1.2	0.14	0.5
Others	17.4	2.42	6.9	14.2	2.10	6.0
Total:	242.0	35.19	100.0	242.0	35.78	100.0

The number of different taxa observed per sampling period declined slightly during mid-winter. Total weight of fish captured in a sampling period varied throughout the year without any apparent seasonal trends.

Diet Analysis

Proportional annual consumption values were derived for the 17 most common fish species (Table I.6). Based on these data species considered to be piscivores included sauger, longnose gar, flathead catfish, and white bass. The omnivores included shorthead redhorse, common carp, and channel catfish. Gizzard shad and smallmouth buffalo were categorized as herbivore/detritivores. The bluegill sunfish, freshwater drum, golden, and silver redhorses were categorized as benthic invertivores. Smallmouth, largemouth, and spotted bass were grouped together as crayfish/piscivores. The emerald shiner was categorized as a midwater invertivore. Each of the remaining 43 species was assigned to one of the six trophic groups using all available gut contents data (VPI&SU 1985 Appendix Tables A9.4.1-35). These species occurred too infrequently in the collections to reliably determine PAC values and comprised only a small percentage of the biomass in their respective trophic groups (Tables I.7-12).

Table I.6 PAC values and trophic group classifications for common¹ fish species. Numbers of non-empty stomachs examined are in parentheses.

Trophic Group Classifications	Percent of Diet				
	Fish	Cray.	Invert.	Plant	Detrit.
Herbivore/Detritivores:					
Gizzard shad (440)	-	-	-	4.3	95.7
Smallmouth buffalo (25)	-	-	5.0	62.9	32.1
Midwater Invertivores:					
Emerald shiner (800)	-	-	83.0	17.0	-
Omnivores:					
Shorthead redhorse (30)	-	-	28.8	67.5	3.7
Common carp (46)	-	0.2	65.9	23.9	10.0
Channel catfish (141)	43.5	5.2	5.2	44.5	1.5
Benthic Invertivores:					
Golden redhorse (20)	-	-	93.0	2.4	4.6
Silver redhorse (17)	-	-	98.6	-	1.4
Freshwater drum (49)	15.3	38.8	44.4	0.3	1.7
Bluegill sunfish (117)	2.4	-	75.9	21.7	-
Crayfish/Piscivores:					
Largemouth bass (18)	60.0	34.7	-	5.3	-
Smallmouth bass (30)	29.9	59.9	10.2	-	-
Spotted bass (34)	35.1	64.1	0.8	-	-
Piscivores:					
White bass (12)	81.1	17.6	1.3	-	-
Longnose gar (16)	99.6	-	0.4	-	-
Flathead catfish (10)	98.4	1.6	-	-	-
Sauger (32)	100.0	-	-	-	-

¹ see Tables I.7-12 for all species listed in each trophic group

Table I.7. Relative abundance of fish species considered considered midwater invertivores.

Species	Biomass Collected (g)			
	UW	%	LW	%
Emerald shiner ¹	6370	86	4209	84
Mimic shiner	441	6	46	1
Spotfin shiner	103	1	222	4
Silver chub	60	1	38	1
River shiner	110	1	119	2
Bluntnose minnow	14		313	6
Sand shiner	7		18	
Steelcolor shiner	3		30	
Unident. Cyprinidae	8		5	
Mooneye	246	3	0	
Creek chub	51	1	0	
Striped shiner	20		0	
Bullhead minnow	4		0	
Streamline chub	3		0	
Rosyface shiner	2		0	
Brook silversides	1		0	
Silver shiner	1		0	
Ghost shiner	0		0	
Total:	7,444		5,022	

¹ This species was analyzed for diet composition and represents 86 and 84% of this trophic group at UW and LW, respectively.

Table I.8. Relative abundance of fish species considered omnivores.

Species	Biomass collected (g)			
	UW	%	LW	%
Common carp ¹	75145	58	54399	39
Channel catfish ¹	23372	18	60983	44
Shorthead redhorse ¹	20499	16	0	1
Quillback	2706	2	1177	1
River carpsucker	1912	1	786	
Goldfish	198		0	
Yellow bullhead	0		1087	1
Spotted sucker	0		5998	
Brown bullhead	0		715	
Black bullhead	0		178	
Total:	123,782		125,323	

¹ These species were analyzed for diet composition and represent 92 and 84% of this trophic group at UW and LW, respectively.

Table I.9. Relative abundance of fish species considered benthic invertivores.

Species	Biomass collected (g)			
	UW	%	LW	%
Silver redhorse ¹	21420	45	541	4
Golden redhorse ¹	15204	32	521	4
River redhorse	3487	7	0	
Black redhorse	3423	7	0	
Freshwater drum ¹	5908	5	14635	10
White crappie	1388	3	1926	14
Longear sunfish	1213	3	2200	16
Bluegill sunfish ¹	538	1	6614	49
Northern hogsucker	533	1	0	
Logperch	77		13	
Redear sunfish	40		185	1
Dusky darter	13		0	
Banded darter	3		0	
Bluebreast darter	2		0	
Black crappie	0		1039	8
Pumpkinseed	0		371	3
White sucker	0		0	
Total:	53,250		28,065	

¹ These species were analyzed for diet composition and represent 83 and 67% of this trophic group at UW and LW, respectively.

Table I.10. Relative abundance of fish species considered piscivores.

Species	<u>Biomass collected (g)</u>			
	UW	%	LW	%
Sauger ¹	13617	47	19159	55
Longnose gar ¹	4463	15	2550	7
White bass ¹	3334	12	1321	4
Flathead catfish ¹	3024	10	10816	31
Walleye	2277	8	0	
Skipjack herring	1745	6	786	2
Muskellunge	189		0	
American eel	142		0	
Ohio lamprey	81		0	
Total:	28,872		34,632	

¹ These species were analyzed for diet composition and represent 84 and 97% of this trophic group at UW and LW, respectively.

Table I.11. Relative abundance of fish species considered herbivore/detritivores.

Species	<u>Biomass collected (g)</u>			
	UW	%	LW	%
Gizzard shad ¹	117808	71	99659	65
Smallmouth buffalo ¹	46117	28	53779	34
Black buffalo	1200	1	700	1
Total:	165,125		154,138	

¹ These species were analyzed for diet composition and represent 99 and 99% of this trophic group at UW and LW, respectively.

Table I.12. Relative abundance of fish species considered crayfish/piscivores.

Species	<u>Biomass collected (g)</u>			
	UW	%	LW	%
Smallmouth bass ¹	15388	71	226	3
Spotted bass ¹	4609	21	2486	34
Rock bass	1206	5	178	2
Largemouth bass ¹	619	3	4360	61
Total:	21,822		7,250	

¹ These species were analyzed for diet composition and represent 95 and 97% of this trophic group at UW and LW, respectively.

When grouped by feeding guilds, herbivore/detritivores and omnivores taken together comprised over two-thirds of total fish biomass in the Kanawha River. Crayfish/piscivores, benthic invertivores, and midwater invertivores were more abundant at UW than LW, while the remaining three groups (omnivores, piscivores, and herbivore/detritivores) exhibited the reverse trend (Table I.13). The benthic and midwater invertivore classifications included the greatest number of taxa per trophic group (17). The fewest number of taxa per trophic group (4) were observed for herbivore/detritivores and crayfish/piscivores. Thus the greatest number of species feed on invertebrates, although the proportion of total fish biomass represented by invertivores (14% at UW, 5% at LW) is small.

In what follows, the food habits results are presented in two levels for each trophic group. The first level is the contribution of general food types to the diet of each group (Table I.14). At the second level the general food types are partitioned further into specific diet items (except for crayfish and detritus). Only the most important components of the diet are highlighted here. For a complete breakdown of the specific diet items consumed, the reader is referred to Tables I.15-20. Where two percentages appear

Table I.13. Abundance of Kanawha river fishes by trophic group.

Trophic Group (number of taxa)	UW			LW		
	kg/ha	kcal/m ²	%	kg/ha	kcal/m ²	%
Herb/Detritivores (4)	99.94	15.48	41	105.27	16.28	43
Omnivores (10)	78.41	11.24	32	95.59	13.43	40
Benthic Invertivores (17)	28.56	4.26	12	9.20	2.21	4
Piscivores (9)	17.42	2.02	7	23.72	2.79	10
Cray/Piscivores (4)	13.31	1.55	6	4.84	0.57	2
Midwater Invertivores (17)	4.36	0.65	2	3.39	0.50	1
(61 taxa)	<u>242.00</u>	<u>35.20</u>	<u>100</u>	<u>242.00</u>	<u>35.78</u>	<u>100</u>

together in the text, the first applies to UW and the second to LW.

Omnivores fed primarily on invertebrates (47.4, 33.7%) and plants (35.5, 34.8%) but also made use of other fish (8.7, 23.1%), especially at LW (Table I.14). Terrestrial insects, pelecypoda, and diptera were the principal invertebrates consumed. Filamentous algae and allochthonous materials were the plants in the diet (Table I.15).

Benthic invertivores at UW fed primarily on invertebrates (83%), while those at LW utilized crayfish (24.5%), other fish (10.5%), and plant matter (6.8%) in addition to invertebrates (56.9%) (Table I.14). Pelecypoda, diptera, terrestrial insects, and Odonata were the principal invertebrates consumed. Pelecypoda were more important at UW, while Odonata and terrestrials were more important components of the diet at LW (Table I.16). Cyprinids were the primary fish and allochthonous material the major plant in the diet at LW (Table I.16).

Crayfish/piscivores consumed crayfish (60.0, 47.2%), other fish (32.4, 52.5%) and at UW utilized invertebrates to a lesser degree (Table I.14). Cyprinids and catfish were the principal fish consumed (Table I.17). Hemiptera were the major invertebrate eaten at UW (Table I.17).

Table I.14. Diet composition by food type for each trophic group.

Trophic Group	Percent of Diet				
	Fish	Cray.	Invert.	Plant	Detrit.
UW					
Omnivore	8.7	1.2	47.4	35.5	7.2
Piscivore	97.3	2.4	0.3	-	-
Cray/Piscivore	32.4	60.0	7.6	-	-
Herb/Detritivore	-	-	1.4	20.7	77.9
Benthic Invertivore	2.2	5.4	88.7	1.1	2.6
Midwater Invertivore	-	-	83.0	17.0	-
Weighted averages ¹ :	11.8	4.8	28.5	20.3	34.6
LW					
Omnivore	23.1	2.9	33.7	34.8	5.5
Piscivore	98.7	1.2	0.1	-	-
Cray/Piscivore	52.5	47.2	0.3	-	-
Herb/Detritivore	-	-	1.8	24.8	73.4
Benthic Invertivore	10.5	24.5	56.9	6.8	1.3
Midwater Invertivore	-	-	83.0	17.0	-
Weighted averages ¹ :	20.6	3.2	17.4	25.0	33.8

¹ based on percentage of total fish biomass

Table I.15. Major food types by diet item for omnivores.

Food type	Diet items	<u>Percent of Food Type</u>	
		UW	LW
Fish	Cyprinidae	21.0	21.0
	Gizzard shad	79.0	79.0
Invertebrates	Oligochaeta	0.7	0.0
	Amphipoda	0.4	0.3
	Ephemeroptera	1.9	5.0
	Odonata	0.5	1.2
	Hemiptera	0.5	1.2
	Trichoptera	2.7	0.0
	Coleoptera	0.5	1.2
	Diptera	21.3	12.0
	Pelecypoda	43.2	27.8
Terrestrial	28.3	51.3	
Plants	Filamentous algae	61.0	68.1
	Allochthonous	39.0	31.9

Table I.16. Major food types by diet item for benthic invertivores.

Food type	Diet items	<u>Percent of Food Type</u>	
		UW	LW
Fish	Cyprinidae	94.5	94.5
	Catfish	5.5	5.5
Invertebrates	Oligochaeta	6.4	0.4
	Amphipoda	0.5	2.7
	Ephemeroptera	1.9	8.7
	Odonata	4.0	18.6
	Trichoptera	0.1	0.8
	Diptera	18.4	14.0
	Gastropoda	0.2	1.0
	Pelecypoda	66.0	25.9
Terrestrial	2.5	27.9	
Plants	Allochthonous	100.0	100.0

Table I.17. Major food types by diet item for crayfish/piscivores.

Food type	Diet items	<u>Percent of Food Type</u>	
		UW	LW
Fish	Cyprinidae	78.1	42.3
	Catfish	21.5	50.8
	Gizzard shad	0.4	6.9
Invertebrates	Ephemerae	12.0	50.0
	Odonata	13.3	50.0
	Hemiptera	74.7	0.0

Detrital (77.9, 73.4%) and plant (20.7, 24.8%) matter were the main components in the diet of the herbivore/detritivores (Table I.14). Diatoms and filamentous algae comprised the most important plant-type foods (Table I.18).

Invertebrates (83%) and plant matter (17%) were the general food types eaten by midwater invertivores (Table I.14). Diptera , Pelecypoda , and Trichoptera were the principal invertebrates consumed and filamentous algae was the only plant in the diet (Table I.19).

Piscivores demonstrated the most uniform food habits of any group by consuming almost entirely other fish (97.3, 98.7%). The principal fish prey were various Cyprinidae while Centrarchidae and freshwater drum comprised most of the remainder (Table I.20).

Table I.18. Major food types by diet item for herbivore/detritivores.

Food type	Diet items	<u>Percent of Food Type</u>	
		UW	LW
Invertebrates	Zooplankton	69.3	69.3
	Amphipoda	11.5	11.5
	Diptera	11.5	11.5
	Pelecypoda	7.7	7.7
Plants	Filamentous algae	33.2	39.5
	Allochthonous	6.0	5.6
	Diatoms	60.8	54.9

Table I.19. Major food types by diet item for midwater invertivores.

Food type	Diet items	<u>Percent of Food Type</u>	
		UW	LW
Invertebrates	Oligochaeta	4.2	4.2
	Trichoptera	15.7	15.7
	Diptera	44.9	44.9
	Pelecypoda	35.2	35.2
Plants	Filamentous algae	100.0	100.0

Table I.20. Major food types by diet item for piscivores.

Food type	Diet items	<u>Percent of Food Type</u>	
		UW	LW
Fish	Lamprey	2.5	2.6
	Gizzard shad	2.0	0.8
	Cyprinidae	80.9	74.7
	Catfish	1.0	1.0
	Centrarchidae	4.9	12.1
	Freshwater drum	8.7	8.8

Growth and Mortality

Fitted parameters for the von Bertalanffy growth equations for length and weight are given in Table I.21. These equations describe growth patterns of the fish populations in the Kanawha River over the range of ages sampled (Table I.22). Instantaneous annual mortality rates (Z) varied among fish species, ranging from 0.3002 for spotted sucker to 1.2959 for emerald shiner over the range of ages sampled (Table I.22).

Production and Consumption

Production:biomass ratios ranged from 0.367 for spotted sucker to 1.578 for emerald shiner (Table I.23). At UW the highest single species production estimates (kcal/m²/yr, kg/ha/yr) were observed for gizzard shad (11.76, 74.0) followed by common carp (2.97, 20.6), smallmouth buffalo (2.11, 14.7), shorthead redhorse (1.26, 8.8), channel catfish (1.10, 7.7), and smallmouth bass (1.03, 8.8). The highest production estimates at LW were for gizzard shad (11.23, 70.26), channel catfish (3.28, 22.8), smallmouth buffalo (2.80, 19.4), common carp (2.43, 16.9), sauger (1.19, 10.14), and freshwater drum (0.97, 8.3). Arranging the production estimates by trophic group, we find that

Table I.21. Growth parameters for weight (g) and length (mm) of common adult fish species. K = coefficient for growth; W_{∞}, L_{∞} = asymptotic maximum weight, length; t_0 = time intercept for $W = 0$. (years)

Species	Weight			Length		
	K	W_{∞}	t_0	K	L_{∞}	t_0
Gizzard shad	0.18	2243	-0.34	0.24	550	0.07
Common carp	0.13	12735	0.22	0.08	1239	-1.05
Channel catfish	0.12	7340	-0.11	0.14	784	-0.38
Smallmouth buffalo	0.23	4327	-0.09	0.25	664	0.12
Sauger	0.12	8954	-0.92	0.14	837	-0.92
Silver redhorse	0.17	3080	-1.27	0.16	647	-1.80
Golden redhorse	0.23	1571	-0.49	0.10	674	-2.72
Shorthead redhorse	0.38	950	0.12	0.28	525	-0.02
Freshwater drum	0.35	1067	0.56	0.19	573	-0.14
Smallmouth bass	0.39	1858	1.00	0.11	872	-0.12
Emerald shiner	0.31	31	0.05	0.20	192	-0.16
Spotted bass	0.16	2263	-0.40	0.12	662	-0.46
Largemouth bass	0.41	1351	0.63	0.30	449	0.29
White bass	0.58	620	-0.28	0.57	370	-0.09
Bluegill sunfish	0.56	110	0.29	0.22	237	-0.82
Spotted sucker	0.88	900	1.50	0.29	528	0.31
Longear sunfish	0.30	162	-0.15	0.20	233	-0.64
White crappie	0.42	502	0.26	0.34	364	0.05

Table I.22. Estimated instantaneous mortality rates for common adult fish species. Z = mortality rate; l_c = length (mm) when species is considered first fully vulnerable to the gears.

Species	Z	age range	l_c
Gizzard shad	1.10	2 - 4	200.
Common carp	0.86	3 - 5	520.
Channel catfish	0.44	1.5- 5.5	260.
Smallmouth buffalo	0.59	4 - 6	410.
Sauger	1.16	2 - 6.5	350.
Silver redhorse	0.55	2 - 3	365.
Golden redhorse	0.97	2 - 3.5	340.
Shorthead redhorse	1.01	2 - 4	300.
Freshwater drum	1.02	2 - 5.5	200.
Smallmouth bass	1.26	1.5- 4.5	160.
Emerald shiner	1.30	1 - 2.5	55.
Spotted bass	0.84	2 - 4	170.
Largemouth bass	0.46	1.5- 4.5	140.
White bass	0.85	2 - 4	250.
Bluegill sunfish	0.57	1.5- 5	105.
Spotted sucker	0.30	1.5- 5	115.
Longear sunfish	0.68	2 - 4	95.
White crappie	1.00	2 - 5	190.

production by herbivore/detritivores represented over half of total fish community production, omnivores comprised nearly one quarter, and benthic invertivores, midwater invertivores, and piscivores comprised the remainder at each site (Table I.24). Total adult production was estimated as 25.82 kcal/m²/yr at UW and 25.84 kcal/m²/yr at LW (c.a. 188 kg/ha/yr overall). The P:B ratio for the entire adult fish assemblage was approximately 0.78 at UW and LW.

Annual consumption was estimated indirectly as the consumption required to support measured production. Thus the consumption results reflect the same trends noted above for production (Tables I.23 and I.24). Production and consumption data for the trophic groups are extrapolations of data obtained for single species. The species for which production and consumption estimates were estimated directly represented at a minimum 59% of the biomass of the trophic group. In 10 out of the 12 cases where single species data were extrapolated, 84-99% of the biomass was directly represented (Table I.24).

Table I.23. Production-biomass ratios (P/B), production (kcal/m²/yr), and consumption (kcal/m²/yr) of common adult fish species of the Kanawha River, West Virginia.

Species	P/B	Production		Consumption	
		UW	LW	UW	LW
Gizzard shad	1.04	11.76	11.23	117.62	112.34
Common carp	0.45	2.97	2.43	19.79	16.23
Channel catfish	0.55	1.10	3.28	3.94	11.70
Smallmouth buffalo	0.53	2.11	2.80	14.09	18.65
Sauger	0.78	0.75	1.19	4.67	7.43
Silver redhorse	0.40	0.76	0.03	3.61	0.13
Golden redhorse	0.44	0.58	0.03	2.74	0.14
Shorthead redhorse	0.71	1.26	-	8.40	-
Freshwater drum	0.83	0.35	0.97	1.47	4.03
Smallmouth bass	0.95	1.03	0.02	4.27	0.07
Emerald shiner	1.58	0.88	0.66	6.28	4.71
Spotted bass	0.81	0.28	0.16	1.15	0.67
Largemouth bass	0.66	0.04	0.22	0.15	0.93
White bass	0.74	0.17	0.08	1.05	0.52
Bluegill sunfish	0.62	0.02	0.33	0.08	1.59
Spotted sucker	0.37	-	0.22	-	1.21
Longear sunfish	0.66	0.06	0.11	0.27	0.53
White crappie	0.89	0.04	0.13	0.17	0.52

Table I.24. Production and consumption (kcal/m²/yr) for adult fish species arranged by trophic group. % = proportion of biomass in each group analyzed for production and consumption.

Species	<u>Production</u>		<u>Consumption</u>		<u>%</u>	
	UW	LW	UW	LW	UW	LW
Herb/Detritivores	14.02	14.17	133.04	132.32	99	99
Omnivores	5.80	6.66	34.93	32.74	92	89
Piscivores	1.55	2.16	9.69	13.49	59	59
Benthic Invertivores	2.02	1.64	9.37	7.16	89	97
Midwtr. Invertivores	1.02	0.79	7.30	5.61	86	84
Cray/Piscivores	1.41	0.41	5.87	1.73	95	97
Total:	25.82	25.83	200.20	193.05		

DISCUSSION

Species Richness and Composition

Sixty-one species of fish were collected (using three gear types) in the present study, which is higher than the number reported in studies of other large rivers (Hesse et al. 1982, Pennington et al. 1983, Sylvester and Broughton 1983). Pearson and Krumholz (1984) reported 100, 94, and 91 species from the upper, middle, and lower third of the Ohio River, respectively. This level of richness exceeds the 61 species found in the present study but represents the integrated findings of numerous and/or periodic impact assessment studies and several long term monitoring programs over the period 1970-83 and over large areas. Overall the Kanawha River appears to support a relatively high number of fish species, and this number may still increase slightly more. Species richness has improved since Addair's (1944) study, in which 39 species were found. Periodic lock rotenone collections at Winfield and Marmet (Tables I.1-2) indicate at least 58 species of fish were present over the period 1968-83. Improved water quality is the most likely reason for the increase in species richness over the last fifty years.

Gizzard shad, common carp, channel catfish, and smallmouth buffalo together account for approximately 70% of total fish biomass from the Kanawha River. These or similar species have been reported as the most abundant in other studies of large rivers as well (Preston and White 1976, Hesse et al. 1982, Pennington et al. 1983, Sylvester and Broughton 1983). Although there are differences in the exact species composition between these studies, the most abundant fish species are consistently trophic generalists with benthic feeding habits. Fish species, which normally occupy the higher trophic levels, are a reflection of the integrated characteristics of the entire aquatic environment (APHA 1981). That a consistent functional role is displayed by the primary fish species in all of these studies suggests that these systems offer similar ecological opportunities to organisms.

Silver, golden, and shorthead redhorse, smallmouth bass, walleye, and white bass made up larger percentages of the total fish biomass at UW than at LW. It is common knowledge that lotic systems, with current and/or rocky substrates present, constitute their preferred habitats, thus their higher relative abundance at UW is in accord with expectations. Similarly, species known to inhabit more lentic habitats, such as bluegill sunfish, black crappie,

and largemouth bass, demonstrated higher relative abundance at LW than UW. Channel catfish, a species most abundant in sluggish rivers, also made up a greater proportion of total fish biomass at LW than UW. This observation is suggestive of the generally lotic nature of even the lower Winfield Pool.

Abundance

Fish abundance is seldom estimated in large river systems due to sampling problems, in particular the difficulty in reliably delineating a known sample area. This difficulty was overcome in the present study since lock chamber rotenone surveys are periodically made at London and Winfield locks and dams. Total fish standing stock in the Winfield Pool of the Kanawha River was estimated for this study as 242 kg/ha. It is important to realize that large habitat differences frequently exist in lotic systems which segregate fish populations (Hynes 1970). Of particular concern in the present case is the possibility that the tailwaters below the navigation dams (from which the lock samples were made) may support a higher biomass than other, more typical areas of a river located further up or downstream. For this reason an estimated lock rotenone

collection efficiency of 75% was not applied in our estimate of abundance.

Estimated Kanawha River fish abundance is less than the grand average of all samples collected between 1957 and 1980 from all locations on the Ohio River (381 kg/ha). The collection methods used in these studies are very similar to those used in the present study. Ohio River average standing stocks are highest (485 kg/ha) in the lower third of the river, dropping to 258 and 251 kg/ha in the middle and upper thirds, respectively (Table I.25). The Kanawha River estimate is nearly equal to the average standing stock in the upper third of the Ohio River over the period noted. However, over this time there has been a greater than two-fold increase in fish biomass from all locations of the Ohio (Table I.26), with estimates ranging from 205 kg/ha in 1957-60 to 470 kg/ha in 1974-77. In particular there has been a steady increase in biomass estimates from Ohio River miles 200-300, the reach which receives the Kanawha. The 1978-80 average standing stock estimate in this portion of the Ohio River was approximately 344 kg/ha (Pearson and Krumholz 1984). This increase is probably attributable to improved water quality over time. It is interesting to note that there have been no directional trends in biomass estimates from Winfield Locks from 1968-1983 (Table I.1).

Table I.25. Average fish biomass 1957 - 1980 from the Ohio River by location (Pearson and Krumholz 1984).

(kg/ha)	Standard Error	Ohio River Mile ¹
251	28	0 - 300
258	28	301 - 700
485	85	701 - 981

¹ River Mile 0 is confluence of Allegheny and Monongahela Rivers at Pittsburgh.

Table I.26. Total fish biomass from the Ohio River over time (Pearson and Krumholz 1984).

(kg/ha)	Standard Error	Period
205	33	1957 - 1960
391	218	1967 - 1970
470	76	1974 - 1977
458	82	1978 - 1980

Thus while the Kanawha River estimate approaches the 23-year average for the upper Ohio, it remains less than that presently observed there.

Total fish abundance in the Kanawha River falls within the range reported for other large rivers and for lotic systems in general. Mann (1965) estimated that the abundance of all fish in River Thames, England, was 659 kg/ha. This was viewed as an exceptionally high fish biomass estimate and one of the unique characteristics of the Thames. Standing stock estimates from Belgian rivers range from 130 to 300 kg/ha (Timmermans 1961, Huet and Timmermans 1963; cited in Mann 1965).

A number of studies on tropical, floodplain rivers demonstrate quite high variability in standing stock, even for the same river at different times. Welcomme (1979) suggests that standing stock is closely linked to both the current flood stage as well as recent flood history in tropical rivers. Ichthyomass from main river channels of tropical rivers ranged from approximately 100 to 600 kg/ha, which is well within the range (130-1100 kg/ha) reported for temperate systems (Table I.27). Standing stocks of between 149 and 5,616 kg/ha have been estimated for tropical river backwater habitats (Table I.27). Thus in both temperate and

Table I.27. Estimates of fish standing stock from various lotic habitats.

(kg/ha)	River	Source
<u>Main channel</u>		
130- 300	Belgian streams	Timmermans (1961), Huet & Timmermans (1963) ¹
143	Coosa R. (deep)	Swingle (1954)
154	Coosa R. (shallow)	Swingle (1954)
200-1100	Vistula R.	Backiel (1971) ¹
311	Horokiwi Stream	Allen (1951)
457	Tombigbee R. (deep)	Swingle (1954)
471	N. American trout streams	McFadden & Cooper (1962) ¹
570	Tombigbee R. (shallow)	Swingle (1954)
659	R. Thames	Mann (1965)
1730	Tenson R.	Swingle (1954)
<u>Backwaters</u>		
149-350	Bandama R.	Daget et al. (1973)
219.8	Mekong R.	Sidthimunka (1970)
300-500	Danube R.	Chitradivelu (1974)
369-5616	Chari R.	Loubens (1969)
2084	Tombigbee R.	Swingle (1954)

¹ Studies cited by Welcomme (1979)

tropical systems backwater habitats support a higher standing stock than main channels. The scarcity of backwaters on the Kanawha River may constrain the overall biomass which is supported there.

Since the Kanawha River had been modified with locks and dams it has characteristics that are intermediate between freeflowing rivers and reservoirs. Therefore, it is appropriate to compare our findings with reservoir investigations. Long term studies (Rainwater and Houser 1982) of Beaver Lake, Arkansas, fish populations have provided a time series of standing stock estimates by treating coves of known area with rotenone. The mean for the years 1969-1980 was 325 kg/ha. However, the data demonstrate considerable variability through time. The highest estimate of standing stock, 498 kg/ha, was made the year following achievement of full pool (1968). Since that time estimates have varied from a low of 209.8 kg/ha to a more recent high of 485.9 kg/ha. Carlander (1955) reported fish abundance as high as 440 kg/ha in reservoirs. For 173 reservoirs throughout the U.S., total standing stocks averaged 200 kg/ha (Jenkins 1975) based on cove rotenone samples. Thus our total abundance estimate for the Kanawha River does not appear to deviate substantially from that observed in reservoirs. It is difficult, however, to

reliably compare the biomass collected in a large river lock chamber (where current is maintained to attract fish into the area) with the biomass of fish present in lentic cove habitats.

Production

Studies of fish production by entire fish communities are scarce for lotic systems and especially large rivers in which numerous species are present. The average adult turnover ratio (P:B) in the present study was 0.78, as compared to the assumed value of 0.7 used by Adams et al. (1983) for adult fish in southeastern and midwest U.S. reservoirs, and the value of 0.64 reported for adult fish from the River Thames (Mann 1965). The turnover ratio for the complete population would undoubtedly be higher still. Annual production by the adult fish taxocene of the Kanawha (c.a. 188 kg/ha/yr) is an underestimate of total fish production since young of the year production is not included. Several investigators cited by Neves (1981) gave estimates of the contribution of young-of-the-year fishes to total species production. These estimates range from 22 to 84%. Burgis and Dunn (1975) concluded that 70% of the

overall production of roach Rutilus rutilus was elaborated by young-of-year. Assuming that these single species ratios can be applied to an entire fish assemblage, the revised estimate of total fish production from the Kanawha River falls between 241 and 1175 kg/ha/yr. Further assuming that the true contribution of fish not fully vulnerable to the collecting gears used includes some yearlings as well as young-of-year fish, we hypothesize total fish production from the Kanawha River to be about 1200 kg/ha/yr.

In the only other studies on large rivers, Mann (1965) reported total adult fish production for the River Thames, England as 426 kg/ha/yr. This of course was also an underestimate of total production, since Mann et al. (1972) later included fish "not yet vulnerable to the net". and revised the original estimate to include production by young-of-the-year fish. Total fish production in the Thames was then estimated as 2000 kg/ha/yr, a nearly 5-fold increase over the production of "adult" fish alone and approximately 67% greater than our production estimate in the Kanawha. Mann's (1965) estimate for adult fish is over two times as great as the Kanawha River adult fish production estimate.

There are two factors which may explain the difference in fish productivity between the two rivers. First, the Thames is noted as an exceptionally productive system having an unusual abundance of fish (Burgis and Dunn 1978, Chapman 1978). It receives "considerable" sewage enrichment (Mann et al. 1972) whereas the Kanawha River is characterized as being "mildly enriched" with organics (VPI&SU 1985). Higher nutrient availability associated with the addition of sewage would result in elevated productivity, and this could account for part of the difference. Secondly, the characteristic fish fauna of the two rivers may demonstrate somewhat different life history strategies. Small, relatively short-lived species (roach, Rutilus rutilus, and bleak, Alburnus alburnus) by numbers account for approximately 80% of the Thames river fish assemblage. In comparison the fish of the Kanawha River tend more towards larger sizes and longer lifespans. P:B ratios for total populations of fish species in the Thames were between 1.75 and 1.95 (Mathews 1971), while adult turnover ratios in the Kanawha River averaged 0.78. The more 'r-selected' characteristics of the populations of the Thames may be another contributing factor towards higher productivity.

The total fish production of the Kafue River, Africa, has been determined several times with estimates between 630

and 870 kg/ha/yr (Kapetsky 1974). These estimates fall somewhat below the extrapolated range calculated for the Kanawha River. Since the Thames case is considered extreme, production in the Kanawha may be reasonable for large rivers in general.

Total fish production in smaller warmwater streams and rivers has been estimated more frequently than for large rivers, but there are relatively few studies (Neves 1981) available for comparison (Table I.28). Mahon and Balon (1985) found fish production and biomass significantly and negatively associated with stream size for Polish streams. Production estimates from smaller rivers and streams range from 77 to 807 kg/ha/yr. This range appears to be somewhat lower than our hypothesized production estimate for the Kanawha River. More studies would be required to reliably compare production in small and large lotic systems.

Table I.28. Estimates of total fish production from lotic systems.

(kg/ha/yr)	P/B ratio	System	Source
Streams and small rivers:			
77	1.4	Baram R. tribs. Malaysia	Watson and Balon (1984)
121	0.7	Nida R., Poland	Watson and Balon (1984)
279	1.2	Grand R., Canada	Watson and Balon (1984)
119-501	0.99-2.46	Ontario streams	Mahon and Balon (1985)
533	1.7	Horokiwi stream New Zealand	Allen (1951)
31-807	0.53-5.29	Polish streams	Mahon and Balon (1985)
Large rivers:			
426	0.64	R. Thames, England	Mann (1965) ¹
630-870	0.75-1.63	Kafue R., Africa	Kapetsky (1974)
2000	1.12-1.92	R. Thames, England	Mann et al.(1972)

¹ note revision by Mann et al. (1972)

Trophic Basis of Production

The proportional annual consumption indices confirmed literature expectations regarding food habits of most common fish species, yet there were several notable exceptions. Only two contrasts between reported and observed food habits are discussed in detail below.

Gizzard Shad

It was anticipated that gizzard shad might rely, at least in part, on plankton as a food source. Gizzard shad are reported to feed extensively on phytoplankton in some systems (Cramer and Marzolf 1970). Hendricks and Noble (1979) studied the food habits of the gizzard shad in Trinidad Lake, Texas, and found that while detritus was the predominant diet item, various planktonic algae species occurred frequently as well. Baker and Schmitz (1971) also found adult gizzard shad from Ozark reservoirs utilizing mainly benthic detritus, along with plankton, molluscs, and insect larvae. At least in some systems, then, gizzard shad are known to feed on plankton. This feeding behavior was not observed in Kanawha River gizzard shad. This may suggest that plankton, while available in the Kanawha, are for other reasons (discussed in Chapter 2) not effectively

utilized. Gizzard shad were frequently observed grazing along lock walls and other solid substrates which supported periphyton growth. Direct observations of benthic feeding were not made due to poor visibility in the Kanawha, but benthic feeding has been either observed or inferred in other studies (Minkley 1963, Pierce et al. 1981, Jude 1973).

Sauger

Sauger are commonly found in large, often turbid rivers, lakes, and impoundments. Sauger are a popular game fish and are generally described as piscivorous. McBride and Tarter (1983) detailed the feeding habits of sauger from the vicinity of Gallipolis Locks and Dam on the Ohio River and found other fish as the main food type. Fish made up nearly 100% of the volume of all foods observed and were present in all stomachs containing food. Emerald shiners and gizzard shad were reported as the most important forage species. Wahl and Nielsen (1985), in a study of sauger feeding ecology conducted in the same area of the Ohio River, also found fish dominating the sauger diet. Gizzard shad made up 42% of all food items, followed by emerald shiners (28%), freshwater drum (16%), and channel catfish (12%). In the present study sauger consumed entirely other fish, 78% of which were Cyprinidae. Surprisingly, no gizzard shad were

observed in the diet. This may be due to rapid growth of gizzard shad in combination with monthly sampling for determination of food habits. This sampling interval could easily have missed a period during which shad of small size were quite vulnerable to predation and were heavily fed upon.

As inferred earlier, the most abundant species in the Kanawha River (common carp, channel catfish, smallmouth buffalo, emerald shiner, freshwater drum, various redhorse species, etc.) appear to be opportunistic benthic feeders. One would expect that their diets would reflect the availability of foods on the bottom, a conclusion drawn for these same species in studies from other systems. Species normally considered trophic generalists or invertivores demonstrated feeding habits in the Kanawha River that consistently varied from those reported in other food habits studies (Fuchs 1965, Minkley 1963, McComish 1967, Hackney et al. 1968, Bowman 1970, Minckley et al. 1970, Summerfelt et al. 1972, Yant et al. 1978, Edwards and Twomey 1982a,b, Zurlein 1982) in that aquatic insects were not as important a component of the diet. This would suggest that the aquatic insects may not be as available to fish in the Kanawha River as in other systems.

For the purposes of this study specific diet items were arranged into 5 food types; fish, crayfish, invertebrates, plants, and detritus. Only a one of the 17 fish species intensively studied for diet composition (sauger) fed exclusively on a single food type. Five out of the 17 species studied included two food types in their diet. In contrast, 11 out of 17 studied consumed three or more food types. Among this group are some of the most abundant species. Common carp included 4 of the 5 food types in their diet, while channel catfish and freshwater drum foraged on all 5 food types. The other very common species, gizzard shad and smallmouth buffalo, included 2 (detritus and plants) and 3 (plants, detritus, and invertebrates) food types, respectively, in their diet. Thus the majority of species, and in general the most abundant species in the Kanawha River, appear to be opportunistic feeders that utilize alternative sources of energy. At the same time, however, it should be noted that for 14 of 17 species studied a single food type constitutes at least 60% of the diet. While this study did not attempt to investigate the degree of selectivity which may be operative, the above fact suggests that there is a principal source of food used by most species. Declining availability of a principal food type would in all probability decrease productivity and/or

abundance of a species and not be completely offset by a shift to other foods.

Study Site Contrasts

The trophic group composite diet summary in Table I.14 revealed some differences between study sites. Forage fish made up a consistently larger percentage of the composite diet at LW than at UW. This shift took place despite the lower abundance of species considered midwater invertivores (an important forage supply) at LW (Table I.7). A second difference between sites was the lower utilization of invertebrates across trophic groups at LW compared to UW. This observation suggests that invertebrates suitable for fish forage are more abundant at UW than LW, a conclusion also supported by the lower relative abundance of benthic invertivores at LW as well (Table I.13).

Specific diet consumption, that is the relative importance of specific food items of each food type in the "diet" of a trophic group, also exhibited some differences between LW and UW. Small cyprinids were the main fish-type forage (80.9%) of piscivores at both sites, but centrarchids became increasingly important at LW. This probably reflects an increased availability of sunfish and the decreased

availability of shiners in this portion of the pool as indicated in Table I.5. The specific components of fish-type forage in the diet of crayfish/piscivores also shifted between the two sites. Cyprinids were the main diet item at UW but were replaced by juvenile catfish at LW. Gizzard shad did not appear to be an important food source for the crayfish/piscivores, however the sampling schedule may have been too infrequent to observe such feeding. Benthic invertivorous fishes consumed a significantly higher proportion of pelecypods at UW than LW, where Odonata and terrestrial insects were the more important forms of invertebrate forage. The same kind of shift was reflected by omnivorous fishes; decreasing utilization of pelecypods and increasing use of terrestrial invertebrates from UW to LW. Differential availability of these foods between sites is implicated by the consistent response of different trophic groups.

If composite food habits of the trophic groups are weighted by biomass and averaged for each site, we obtain a general breakdown of food sources consumed by the entire fish assemblage (Table I.14). Direct consumption of detritus exceeds that of any other single food type at both sites. As will be shown in the second chapter, even where detritus is not consumed directly by a functional group of

fish, the principal food organisms consumed by these fish utilize primarily detritus as their food source. The clearest examples of this are the fairly large roles which filter feeding molluscs and collector gathering and filtering invertebrates play in the feeding habits of all but the piscivore and crayfish/piscivore fish groups. Thus directly and/or indirectly, detritus is the primary food source supporting the Kanawha River fish community. Since nearly all of the detritus, some of the plant material, and even a large proportion of the invertebrates consumed are imported from upstream reaches and not produced locally (see Chapter 2), it is clear that fish production in the Kanawha River is based largely on allochthonous imports as predicted by Cummins (1977) for large rivers in general. This same conclusion was drawn for the River Thames by Mann et al. (1972).

The fish trophic structure of the Kanawha River fish assemblage is dominated by bottom feeders as is typical of reservoir fish communities (Jenkins 1975, Adams et al. 1983). Gizzard shad, common carp, channel catfish, and smallmouth buffalo together account for about 70% of total fish biomass. However, the trophic basis of fish production in the Kanawha River appears to be based much more on detritus and allochthonous sources of energy than on

autochthonous sources as calculated for reservoirs by Adams et al. (1983).

The fish community of the Kanawha River appears typical of a large river, both in terms of total biomass per unit area and its distribution among species. Herbivore/detritivores and omnivores are the main trophic groups in the Kanawha. The trophic basis of production, as expected, is the detritus transported from upstream and other allochthonous imports.

Chapter II

Development and Application of an Energy Flow Model
to Analyze Navigation Impacts to the Kanawha River

INTRODUCTION

In this portion of the study, an energy flow model is developed and used to quantitatively predict the potential effects of future increases in tow traffic on the biota of the Kanawha River. The concept of energy flow as a unifying concept in ecology is now well established as evidenced by many ecology text books. However, it was not until biologists began to recognize that the same functional roles in separate ecosystems could be filled by different taxa that generalizations about ecosystem structure and function were possible. Lindeman (1942) categorized biota in aquatic ecosystems based on nutritional habits or trophic levels, leading to the quantification of energy flow through ecosystems. Odum (1957) constructed an energy flow model of all trophic levels within a lotic ecosystem, allowing quantifiable estimates of the consequences of environmental changes. Since that time models have been widely used in both conceptual and applied ecological studies of aquatic systems. The methodology has been used in lakes (Park et al. 1974, Canale 1976, Scavia and Park 1976, Park et al. 1978), reservoirs (Patten 1975, Ploskey and Jenkins 1982), streams (Warren et al. 1964, Warren 1971, McIntire 1973, Fisher and Likens 1973, Boling et al. 1975, Ruttledge et al.

1976, McIntire and Colby 1978, James 1984), and rivers (Chen and Orlob 1975, Chen and Wells 1976, Webster et al. 1979). The energy budget has become practically a standard approach for lotic ecosystem studies (Minshall et al. 1985). Thus the assessment of navigation impacts through energy flow modeling is not so much a new approach as a new application of an established technology.

The physical consequences of tow passage for the river environment are understood on an individual-tow basis. The motion of a tow through the water affects the physical surroundings of the vessel in a complex, but predictable fashion. The physical forces experienced in the environment of the tow are generated from propeller jet flow velocities, displacement flow velocities, nearshore wave heights, and wave orbital velocities. The forces generated vary with depth and distance from the tow. They are a function of waterway configuration (channel depth, width, blockage ratios, etc.), the characteristics of the tow itself (speed, direction, draft, horsepower and type of power unit, etc.), and other factors. Tow induced forces exist for only a certain length of time at any one river location. However, changes in environmental conditions caused by the passage (e.g. elevated levels of turbidity) may persist for varying lengths of time before returning to ambient, pre-passage

levels. This period is a function of environmental characteristics (ambient current velocities, amounts and sizes of material present and available for resuspension, bank slope ratios, etc.), which are completely independent of the characteristics of the tow having passed. A tow creates forces, these forces effect a change in environmental conditions, and either the environment recovers from the perturbation or stabilizes with new environmental conditions prevailing (Figure II.1). The forces themselves may dissipate quite rapidly, while the alterations they cause may persist for much longer periods. For example Sparks et al. (1980) observed that the complete return to ambient conditions after tow passage on the Illinois River required four hours. Other studies have described shorter recovery times (Sparks 1975, Herricks and Gantzer 1980, Bhowmik et al. 1981, UMRBC Environmental Work Team 1981). Whether or not the environment completely recovers (i.e. ambient pre-passage conditions are re-established) depends on the frequency of disturbance. The only attempts to address the problem have been largely qualitative. No systematic or comprehensive analyses of the environmental effects of tow traffic in large rivers have ever been made (Schnick 1982). Prior work in this area has been summarized by the Academy of Natural Sciences of

Philadelphia (1980) who identified temporary and local resuspension of sediment as one of the major physical effects likely to cause impacts. Increased tow passage frequency, resulting in increased resuspension of sediment and turbidity, diminish the opportunity for primary producers to conduct photosynthesis. As primary production is reduced, the heterotrophic organisms which directly or indirectly rely upon autotrophic organisms will experience some reduction in total energy available for use. The focus of the energy flow model is to simulate these trophic relations and predict the consequences of various levels of traffic to higher trophic levels.

Study Objectives

The fundamental objective of this research was to construct a mathematical model simulating energy flow in a large river ecosystem to assess navigation impacts, but there were other ecological hypotheses which could be explored. The first hypothesis concerned the degree to which our observations qualitatively confirmed theoretical expectations for large rivers. Due to their depth and turbidity, large rivers are thought to depend more upon allochthonous than autochthonous sources of energy. The

Kanawha River is a sixth order stream, and as such should primarily depend on the former.

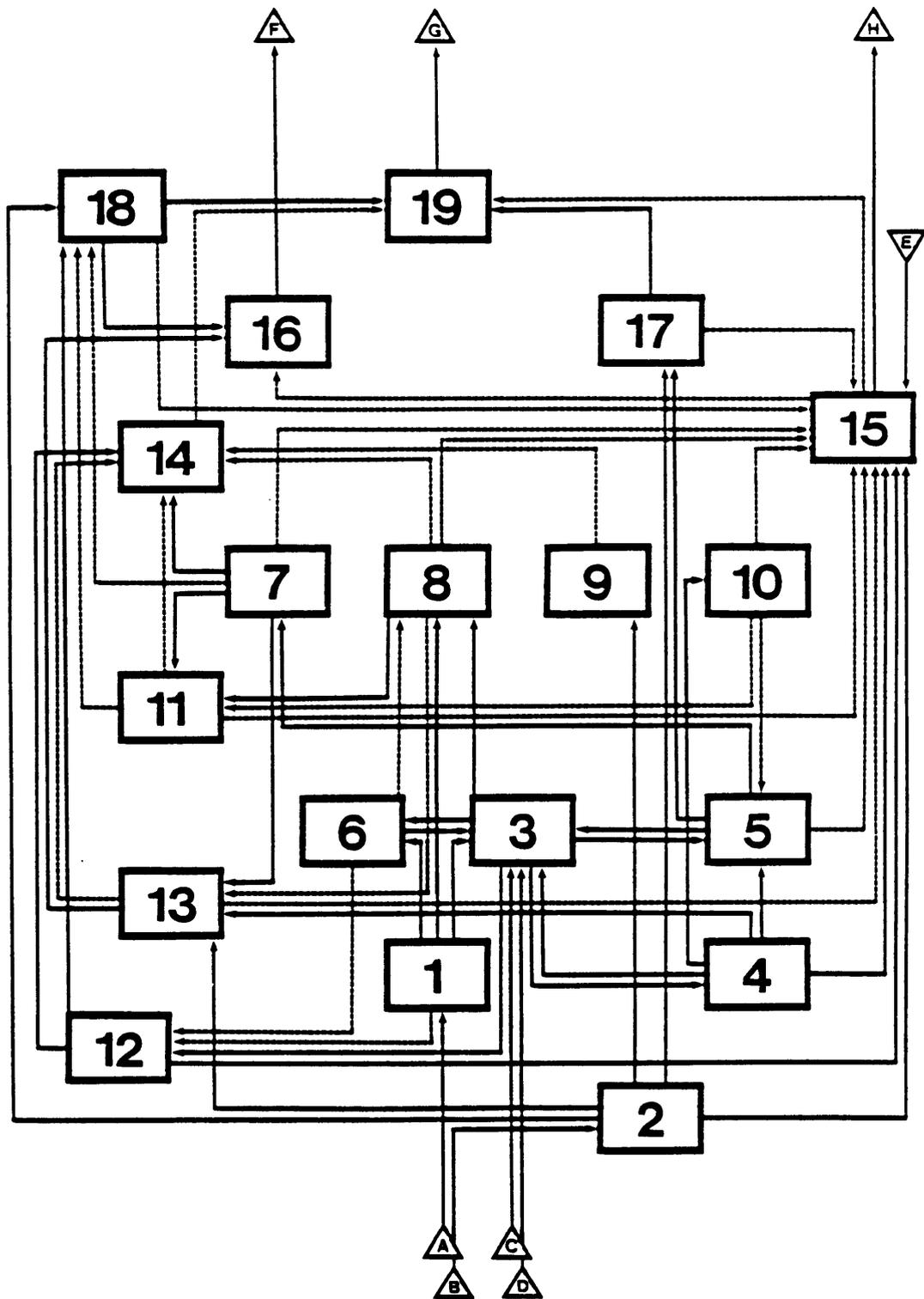
The second hypothesis was that the structure and function of the Kanawha River ecosystem would conform to the main energy source. The river continuum concept (Vannote et al. 1980) predicts that collector gatherers and filterers will predominate in the benthos and that planktivory will be observed within the fish community because of the dependence on FPOM. Two complimentary sub-hypotheses were generated: 2-A) we expected to find that trophic groups in a functional position to utilize allochthonous sources of energy would be most successful, and 2-B) that the most successful trophic groups at any trophic level derived the majority of their energy directly or indirectly from allochthonous sources of energy. These hypotheses were evaluated quantitatively using flow analyses.

METHODS

Model Components and Processes

The first step in model building after defining the abstract system is identifying the system components. One of the basic simplifying assumptions in the model is that organisms or organic matter found in the river can be aggregated into model components. While this is a departure from reality, the effective role of each type of organism in nature is preserved by grouping similar organisms into common functional identities. In a desert stream model Wlosinski and Minshall (1983) represented invertebrates using various levels of aggregation (size groups within taxonomic groups, taxonomic groups, functional groups, and one general group) and compared model predictions with measurements from the stream. The highest agreement between predicted and observed values was observed at the level of resolution using functional groups. Parameters for all model components are weighted based on the relative abundance of those individual species included in the group. The standing stock of each trophic group is expressed as the biomass present throughout the water column or on the bottom under an average square meter of river surface. Averaging simplifies the model by homogenizing the diverse habitats of shoreline, near-shore, and mid-channel areas.

Fig. II.1. Conceptual diagram of energy flow pathways in the Kanawha River.
(See text for definition of symbols)



All interactions and activities of organisms found in the river ecosystem have a common denominator when they are expressed in terms of energy flow. Such diverse processes as the harvest of fish, the fall of leaves into the river, the photosynthetic activity of algae, and decomposition of organic matter on the bottom can be related quantitatively through energy flow. In this form, such diverse processes as consumption, assimilation, respiration, egestion, predation, and non-predatory mortality by are integrated as sources or sinks of energy flow. Conceptually, energy flow might be perceived as a mathematical expression of the "life pulse" of a community. This expression takes the visible form of a web of energy sources and sinks between, to, and from model components (Figure II.1). In the figure, numbered compartments signify the 19 functional groups of the model. Energy flows are given by solid and dashed arrows connecting the compartments. Solid lines represent major flows (defined here as single energy flows greater than 10% of the total energy from all sources leading to a recipient component). Dashed lines represent minor flows, not all of which are shown for the sake of clarity. Also not explicitly depicted in the diagram are the respiration, mortality, waste, or emergence flows. Inputs and outputs of energy to/from the system are denoted by the letters "A"

through "H" (in triangles). Inputs include the capture of light energy by phytoplankton and periphyton (A,B respectively), the capture of suspended particulate organic matter out of transport (C), leaf-fall (D), and utilization of terrestrial insect-fall (E). Harvest of three fish groups is represented by (F), (G), and (H).

Definitions and Notation

Each trophic group in the ecosystem is assigned a mathematical counterpart in the model termed a component. Components are referred to by number using the designation $X(i)$, where i ranges from one to nineteen. The complete list of model components with the dominant organisms in each is given in Table II.1. The value of $X(i)$ represents the abundance (kcal/m^2) of trophic group i per average square meter. Changes in the standing stock of the trophic groups are simulated through the use of a set of first order differential rate equations (Tables II.2 and II.3) The rate terms in the equation represent the various transfers of energy to and from model component $X(i)$. Rates of input include consumption or other means by which trophic group (i) obtains energy, while rates of output include predation, mortality, transport out of the system, waste products, and

respiration costs (Figure II.2). Rates are expressed mathematically as simple linear functions of the current standing stock of the donor trophic group using transfer coefficients. Transfer coefficients for linear donor-controlled models are calculated using the following relation:

$$F(i,j) = a_{i,j}X(i)$$

$$a_{i,j} = \frac{F(i,j)}{X(i)}$$

Where:

$a_{i,j}$ = transfer coefficient

$F(i,j)$ = annual rate of energy flow from $X(i)$ to $X(j)$

$X(i)$ = average standing stock of $X(i)$

Thus each transfer coefficient functions as a constant turnover ratio which, when multiplied by the present value of the donor component, yields the present rate of transfer between donor and recipient groups.

The differential equations are of the general form:

$$\frac{dX(i)}{dt} = \sum_{j=1}^n a_{j,i}X(j) - \sum_{j=1}^n a_{i,j}X(i) + U_i - O_i$$

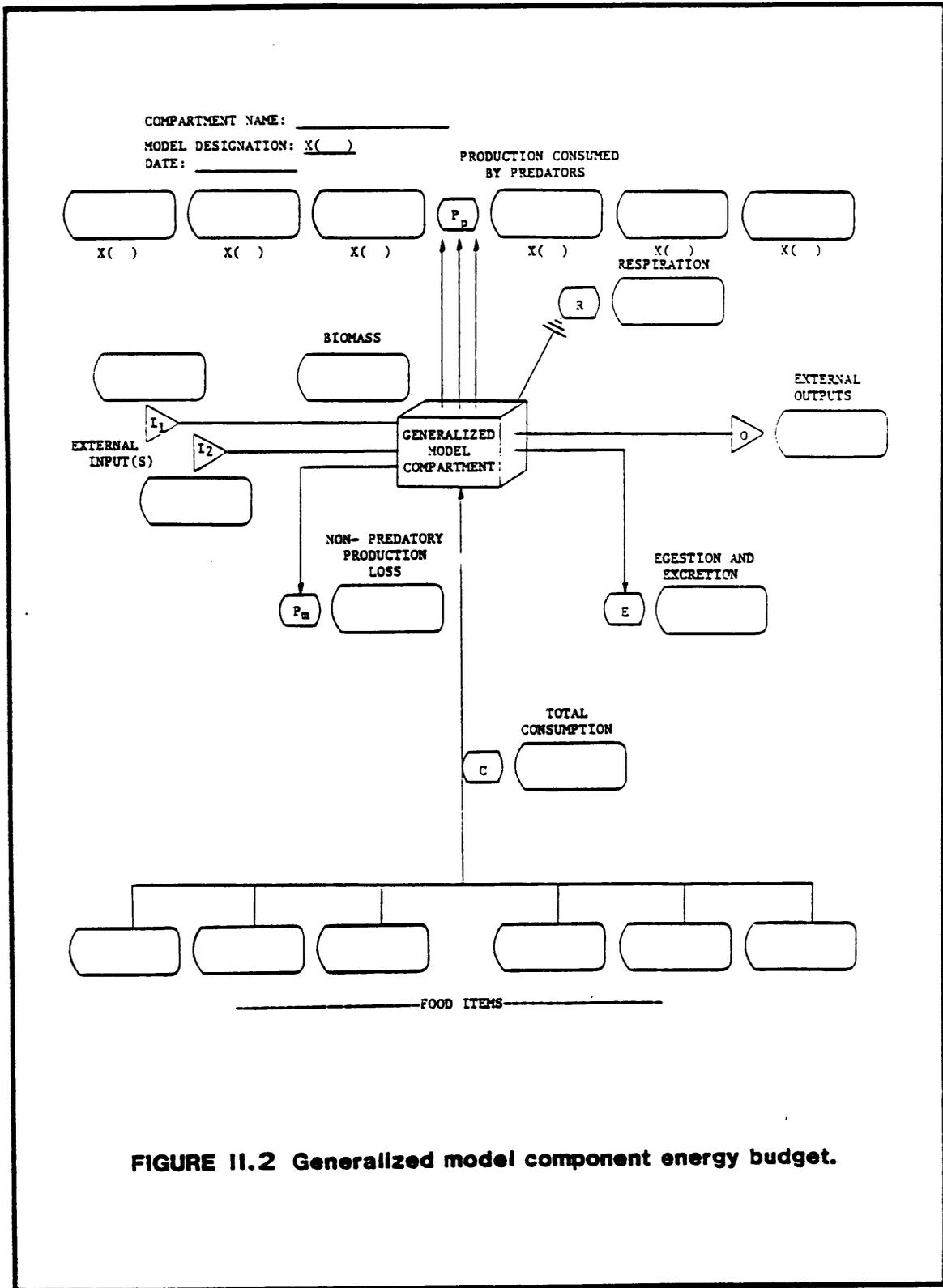


FIGURE 11.2 Generalized model component energy budget.

Table II.1. Representative organisms for model components.

Model Component	Designation	Representative Organisms
(Primary Producers)		
Phytoplankton	X(1)	phytoflagellates, green algae, diatoms
Periphyton	X(2)	diatoms, blue green algae
(Organo-Bacterial Complexes)		
SPOM	X(3)	suspended particulate organic matter
Benthic CPOM	X(4)	coarse particulate organic matter (> 1mm)
Benthic FPOM	X(5)	fine particulate organic matter (< 1mm)
Zooplankton	X(6)	rotifers, protozoans
(Invertebrates)		
Collector Gatherers	X(7)	Orthoclaadiinae, Chironominae
Collector Filterers	X(8)	<u>Hydropsyche</u> , <u>Cheumatopsyche</u>
Scraper Grazers	X(9)	some Trichoptera (rare), snails
Shredders	X(10)	some Plecoptera (rare)
Predators	X(11)	Odonata
Molluscs	X(12)	<u>Corbicula</u>
Crayfish	X(13)	<u>Orconectes</u>
(Fishes)		
Benthic Invertivore	X(14)	redhorse, drum
Omnivore	X(15)	carp, catfish
Crayfish/Piscivore	X(16)	centrarchid basses
Herbi/Detritivore	X(17)	gizzard shad
Midwater Invertivore	X(18)	emerald shiner
Piscivore	X(19)	walleye, sauger, white bass

Table II.3. Definitions of terms used in model equations.

X(i)	term for the biomass (in kcal/m ²) of component (i)
DX(i)	term for the rate of change of component (i). (kcal/m ² /yr)
CFLOW(i,j)	transfer coefficient from X(i) to X(j). (yr -1)
CRESP(i)	transfer coefficient for respiration by component (i). (yr -1)
CSURPL(i)	transfer coefficient for extrasystem energy flow from component (i). (yr -1)
DEFICT(i)	driving function representing extrasystem input of energy to component (i). (kcal/m ² /yr)
NSCTON(i)	utilization of drifting aquatic insects by component (i). (kcal/m ² /yr)
LAVAIL(I)	rate at which light energy is captured by primary producer (i). (kcal/m ² /yr)
LEAVES(i)	leaf-fall to component (i). (kcal/m ² /yr)
SEG	variable designating river segment (1=LW, 2=UW)
TERR(i)	utilization of terrestrial insects by component (i). (kcal/m ² /yr)

net rate
of change = (rates of input) - (rates of output)

where:

$a_{i,j}$ = transfer coefficient from compartment X(i) to X(j)

U_i = inputs to compartment X(i) from outside
the system

O_i = outputs from compartment X(i) to outside
the system

n = the number of compartments in the model

The equations calculate the component's rate of change (per year in this case) as the difference between rates of energy input and rates of energy output. A four step Runge-Kutta method of numerical integration was used to solve the differential equations. Both the equations and the solution technique are imbedded within a time loop in the model program. Two versions of the model were run. The first version simulates individual tows, and execution of the time loop represents a time step of 2.128 minutes (0.000005 years). The time step in the second version, in which individual tows are not explicitly represented, is 8.76 hours (0.001 years). With each iteration, the model computes the solution to a differential equation and multiplies this change-per-year term by the length of the time step (in years) to calculate the change in biomass of a component over one time step. The change (+/-) is added to component's prior biomass value and a new value is assigned

to that component. In the following time step the new biomass value (through multiplication by various transfer coefficients) will cause increases/decreases in the rates of transfer for which that component is a donor. This in turn affects the rates of change calculated for both donor and recipient components when the differential equations are next solved.

Modeling of the Winfield Pool

To accommodate the space and time dimensions in which the disturbance occurs, the model uses a river segmentation approach in which the Winfield pool is subdivided into two segments. Each river segment is simulated independently with uniquely specified model parameters. The more downstream model segment represents Kanawha River miles 31 through 55 (LW) while the remaining portion of the Winfield pool (river miles 56 through 67), are represented in the upstream model segment. The linkage between model segments exists only conceptually, in that during the simulation of a tow passage the perturbation caused by the towboat is first represented in the one river segment, and progressively moves on to the adjacent river segment. Biological processes in one segment, however are modeled independently of those simulated in the other segment.

Modeling of Tow Traffic

Tow passage frequency data at intervals along the pool were projected by the U.S. Army Corps of Engineers (Huntington District Corps of Engineers, unpublished data) for each traffic scenario and are listed in Table II.4. Data pertaining to all intervals upstream or downstream of river mile 58 were averaged to obtain the tow frequencies used by the model in the UW and LW segments. These frequencies are independent of the direction traveled by the tow. It was assumed that over the course of a full year that upbound and downbound towboats were in equilibrium, and with this assumption the tow passage frequencies were halved and the halves assigned a direction of travel either upbound or downbound. In a preliminary version of the model individual tows were explicitly represented in four different scenarios; a baseline simulation and three projected traffic levels. However the rapid rate of return to ambient turbidity conditions after tow-induced disturbance required a very short time step which resulted in an unacceptably long execution time. Therefore a second version of the model was developed which approached the problem differently. Flows from primary producers X(1) and

X(2) were decreased proportionate to the time during which the additional passing tows would be elevating turbidity levels for each traffic scenario. Since recovery periods for individual tow passages were not explicitly simulated in this version, a longer time step could be used. Model runs of 5 years duration were conducted to produce equilibrium conditions for all model components.

Scenario #1: Baseline Conditions

The first scenario represented baseline conditions of tow traffic throughout the Winfield Pool, i.e. the levels of traffic present during the 1982-83 period when biological data were collected. Tow frequencies (bidirectional) ranged from 3,167 tows per year in the upper Winfield pool to 4,167 tows per year near the Winfield Locks. These frequencies, expressed on a per day basis, ranged from slightly under 9 to almost 11.5 tow passages per day. The maximum number of passages per day at Winfield Locks and Dam was 20.8.

As previously discussed, under baseline conditions the increment of tow traffic above and beyond 1982-83 conditions is null and the model does not recognize these tow passages explicitly in the simulation. It is assumed that the biological community of the river is representative of, and

Table II.4. Traffic frequencies for present 1980-1983 and future scenarios.

River mile interval	S1 1) Present tow traffic conditions	S2 2) Future, w/o Project conditions	S3 3) Future, Replace of Winfield	S4 4) Future, Replace W. and Marmet
30.6-39.6	4,167	6,678	7,508	9,250
39.6-49.0	4,167	6,010	6,307	9,250
49.0-55.0	3,959	5,676	5,931	8,788
55.0-58.0	3,584	5,075	5,256	7,955
58.0-64.0	3,167	4,407	4,505	7,030
64.0-67.7	3,334	4,674	4,805	7,400

Traffic frequencies (tows per day)
used by the model

"UW"	9	12.5	13	20
"LW"	11	16	18	24

Traffic increment (tows per day)

"UW"	0	3.5	4	11
"LW"	0	5	7	13

in equilibrium with, this level of traffic. A simulation was performed which demonstrates the model's ability to remain at steady state, i.e. no change in the standing stocks of any trophic group over the course of the simulation. The null simulation was needed only to provide a reference point for the output of other simulations. In the scenarios to follow (#2 - #4), simulations were conducted in which net traffic (in excess of baseline) was considered explicitly by the model.

Scenario #2: Without Project Conditions

The volume of tow traffic using the Winfield Pool is projected to increase beyond 1982-83 levels regardless of whether Winfield or Marmet are replaced (Table II.4). Scenario #2 evaluates the potential impact of this increase in traffic.

Bidirectional frequencies projected to be approximately 4,407 tows per year in the upper pool (between river miles 58. and 64.) and about 6,678 tows per year near the Winfield Locks. These frequencies ranged from slightly over 12 to over 18 tow passages per day, and represent an average traffic increment (modeled over baseline) of 3.5 tows per day in the upper river segment and 5 tows per day in the

lower river segment. The maximum number of passages per day at Winfield Locks and Dam was 33.3, an increment of 12.5 tows per day over baseline conditions.

Scenario #3: Replacement of Winfield

Given the replacement or improvements in Winfield Locks and Dam, there is a projected increase in the volume of tow traffic which can be efficiently passed through the Winfield pool. The potential impact of this increase in traffic is evaluated in Scenario #3.

Tow frequencies projected for this scenario ranged from approximately 4,505 tows per year in the upper pool (between river miles 58. and 64.) to about 7,508 tows per year near the Winfield Locks. There is very little projected increase in tow passage frequencies in the upper pool without improvements to Marmet navigation structures. On a per day basis, tow passage frequencies range from over 12 to over 20.5. The model explicitly recognizes an average traffic increment (over baseline) of 4 tows per day in the upper river reach and 7 tows per day in the lower river. The maximum number of passages per day at Winfield Locks and Dam is projected to be 37.4, an increment of 16.6 tows per day over baseline conditions.

Scenario #4: Replacement of Winfield and Marmet

This scenario represents the highest levels of navigation use in which both Winfield and Marmet lock and dam structures are replaced/improved to more efficiently pass traffic through the Winfield pool. Under this scenario, bidirectional tow passage frequencies range from approximately 7,030 in an upper reach of the pool to 9,250 in the lower reaches of the pool (20 to 24 tows per day). All areas of the Winfield pool would experience a significant increment over baseline traffic conditions (average increments of 11 and 13 tow passages per day modeled for UW and LW, respectively.)

As discussed earlier, one likely form of impact caused by tow traffic is the resuspension of particulate matter with an associated reduction of primary production rates by autotrophs. Although mechanisms exist by which other potential impacts might be simulated, the only influence of tow traffic that was modeled was the reduction in primary production.

Primary production is modeled continuously during the simulation; no seasonal or diurnal fluctuation is assumed.

Primary producers are represented by two trophic groups in the model, phytoplankton and periphyton (X(1) and X(2) respectively). For each of these groups, the potential rate of primary production remains constant throughout the simulated year, although mechanisms are in place to make these seasonal driving functions of the model. The gross primary production rate is considered by the model to be a maximum potential rate which applies under ambient (1982-83) traffic/turbidity conditions.

In the second version of the model in which tows are not represented individually, the reduction in primary production is achieved as follows. For each level of traffic and river segment there is a certain increment of tow passages per day over the present traffic levels. If each tow is assumed to interrupt photosynthesis for the same length of time, we may calculate the portion of any simulated day during which disturbance of photosynthesis by additional tows would occur. The ambient annual rates of primary production were reduced by these proportions throughout the entire simulation. Proportional reductions for traffic scenarios 2, 3, and 4 were 4.86, 5.56, and 15.28% at UW and 6.94, 9.72, and 18.06% at LW, respectively.

In reality, primary production may not be entirely suspended, even in the sailing line, and further it is not reduced to the same extent throughout the river segment occupied by a passing towboat. There is also a gradual return to the pre-passage rate of photosynthesis from the depressed rate. Lacking direct field measurements of photosynthesis during tow passage, the greatest possible reduction was selected. A further conservative feature of the model is that the recent presence of a simulated tow in a segment of river is always assumed to increase turbidity. In reality, this does not occur under high discharge conditions (e.g. seasonal flooding and storms) when "natural" turbidity is already elevated beyond levels which passing tows can induce.

Derivation of Model Parameters

This section documents the sources of biological parameters used in the model. In order to minimize repetition of similar information, the nineteen trophic groups of the model are simplified into six classes; primary producers, organic matter, zooplankton, insect invertebrates, other invertebrates, and fish. For each class of trophic groups, general derivations of consumption,

waste, respiration, production, extrasystemic inputs/outputs, and standing stock are presented. Specific exceptions are noted where the treatment of a particular trophic group differs from the norm in its class. Parameter derivations are presented sequentially, that is, the most direct or independent estimates precede other estimates which depend on the former in their own derivation. Average annual standing stock estimates are expressed in kcal/m^2 , while the remaining variables are expressed as annual average energy flows in $\text{kcal/m}^2/\text{yr}$.

Before presenting the methods used to derive parameters, it is important to note that in several instances all flows pertaining to a trophic group have been adjusted by a constant factor. This was done in order to reconcile different trophic levels where apparent production at the lower level was insufficient to meet the estimate of total consumptive demand by trophic groups at higher levels. In such cases greater confidence was placed on the estimate of consumptive demand, and the production of the trophic group at the lower trophic level was increased along with the biomass, consumption, waste, and respiration flows. Adjustment factors are listed in Table II.5. In the sections to follow the application of an adjustment factor will be noted by an asterisk following the names of the affected trophic groups.

Table II.5. Adjustment factors used to reconcile different trophic levels in the model.

Trophic Group	Name	River segment	
		UW	LW
X(1)	Phytoplankton	-	-
X(2)	Periphyton	2	2
X(3)	SPOM	-	-
X(4)	CPOM	-	-
X(5)	FPOM	-	-
X(6)	Zooplankton	-	-
X(7)	Coll/Gatherers	-	2
X(8)	Coll/Filterers	-	70
X(9)	Scraper Grazers	-	-
X(10)	Invt Shredders	-	25
X(11)	Invt Predators	-	2
X(12)	Molluscs	-	-
X(13)	Crayfish	-	-
X(14)	B. Invertivores	-	-
X(15)	Omnivores	-	-
X(16)	Cray/Piscivores	-	-
X(17)	Herb/Detritivores	-	-
X(18)	M. Invertivores	10	10
X(19)	Piscivores	-	-

Class: Primary producers - Phytoplankton X(1),
Periphyton* X(2)

The sole input of energy to phytoplankton and periphyton is modeled specifically as average annual gross primary production. Field measurements by light/dark bottle methods of gross primary production and respiration were obtained from VPI&SU (1985:Tables V.5.6 and V.6.1) for phytoplankton and periphyton, respectively. Note, however, that the respiration estimate by the light/dark bottle methodology does not represent primary producers exclusively, but rather the autotrophs in concert with whatever heterotrophs were present in the bottles. In order to model energy flow through the primary producer trophic groups, production and respiration energy flows must be comparable (pertain only to the autotrophs). As such, the respiration data collected in the field are not appropriate for use in the model, and only the gross primary production estimates were used directly. Energy flows through primary producers were balanced by assuming that respiration (R) required 25% of annual average gross primary production. Extracellular release (ER) of photosynthetic products was assumed to be 10% of gross primary production for both

trophic groups (Fogg 1977). After satisfying various predatory consumptive demands (P_1, P_2 , etc.), the remaining phytoplankton production was partitioned equally between export through downstream transport (T) and non-predatory production loss (NOL) to S.P.O.M.. Transport is not modeled as occurring both into and out of a river segment, but rather as the net of these two processes occurring in a segment over the year. The complete relation is shown below.

$$GPP = R + ER + (P_1 + P_2 +) + T + NOL$$

In the case of periphyton all net production in excess of respiration, extracellular release, and predatory consumptive demands was fated to C.P.O.M..

The methods for determining the abundance of periphyton are given in VPI&SU (1985, Sections IV.5 and IV.6). The original calculation assumed ten square meters of substrate suitable for periphyton per meter of river length but did not include any measure of snag habitat. This estimate was doubled to provide sufficient production to support the estimated demands of other trophic groups which graze on periphyton.

Class: Particulate organic matter - S.P.O.M. X(3), C.P.O.M.
X(4), F.P.O.M. X(5)

Particulate organic matter groups were defined to include dead organic matter with associated microbial decomposers. Energy flows among the particulate organic matter trophic groups are more speculative than those associated with the remaining sixteen groups of the model. This is due to the difficulty in making direct field measurements of detrital processes in a large river. The following section outlines the hypotheses made in order to obtain energy flow estimates for the organic matter groups.

Suspended, benthic-coarse, and benthic-fine particulate matter (hereafter S.P.O.M., C.P.O.M., and F.P.O.M.) are proposed as existing in a dynamic equilibrium within the river environment. Under this hypothesis, assumptions made regarding energy flows for any one of these trophic groups necessarily constrain flows involving the other two groups. Consequently energy flows were estimated for F.P.O.M. first, C.P.O.M. second, and S.P.O.M. last, as then any constraints which might arise from initial hypotheses would be extended "backwards" through the particulate organic matter groups and away from conflicts with more solidly established energy flows for living groups in the rest of the model.

Benthic F.P.O.M.

It is assumed that from year to year F.P.O.M. neither accumulates nor declines; that the combined sources of F.P.O.M. are in equilibrium with all sinks. Sources of F.P.O.M. in the model include the waste products of all non-planktonic biota (W), the breakdown of materials originally present as C.P.O.M. (B), and the settling of materials once present as S.P.O.M. (S1). Sinks of F.P.O.M. include that consumed by other groups (P), that which is resuspended to S.P.O.M. (S2), and that which is decomposed by bacteria with their associated respiratory losses (R). Thus:

$$W + B + S1 = P + S2 + R$$

We further assume that settling (S1) and resuspension (S2) are approximately equal over the year ($S1 = S2 = S$), and that about half of the total combined sources of F.P.O.M. are respired by decomposers per year. Then:

$$(W + B + S) (0.5) = R$$

$$(W + B + S) (0.5) = P + S$$

The above pair of equations were then solved for B and R after hypothesizing a value for S (the amount of settling/resuspension) of ten times the amount of F.P.O.M. consumed by all biota per year.

C.P.O.M.

As with the previous example, we assume that there is no net yearly change in the amount of C.P.O.M., and that the combined sources are in equilibrium with the combined sinks. Sources of C.P.O.M. include that supplied from mortality of nonplanktonic biota (M) and the settling out of leaves and other large organic matter in the water column onto the bottom (L). C.P.O.M. consumed by organisms (P), that resuspended off the bottom (S), that which is broken down into F.P.O.M. (B), and that used in respiration by decomposers (R) are considered as sinks. Thus:

$$M + L = P + S + B + R$$

It is assumed that half of all sources of C.P.O.M. are respired by bacterial decomposers each year. It is also hypothesized that the amount of C.P.O.M. resuspended over the year equals the amount processed to F.P.O.M. ($S = B$). Thus:

$$(M + L) (0.5) = R$$

$$(M + L) (0.5) = P + S + B = P + (2)B$$

The pair of equations are then solved to give estimates of L and R. In the more lentic, LW reach we assumed that the resuspension of C.P.O.M. to S.P.O.M. occurred at half the rate estimated at UW.

S.P.O.M.

The balance of sources and sinks of S.P.O.M. is nearly achieved by the above constraints on energy flows involving S.P.O.M. if given measured estimates of average annual respiration (R) in the water column. Sources include the amount of S.P.O.M. removed or utilized (I) out of that being transported downstream yearly, that contributed through waste and mortality of planktonic biota (WM), leaf inputs onto the river surface (LI), and that resuspended from C.P.O.M. and F.P.O.M. (R1 and R2, respectively). Sinks of S.P.O.M. include that which settles out to C.P.O.M. and F.P.O.M. (S1, S2), that consumed by other trophic groups (P), and that lost to respiration during decomposition (R). Thus:

$$I + WM + LI + S1 + S2 = R1 + R2 + R + P$$

All but the first and last terms above are measured values taken from VPI&SU (1985) or are otherwise constrained

by prior assumptions. Respiration was estimated by and Lizzotte (1984). The equation was then solved to estimate the amount of S.P.O.M. removed from that being transported downstream (I).

The average concentration of S.P.O.M. throughout the year was estimated by subtracting from the average concentration of seston (which includes living and dead organic matter) the combined average concentrations of phytoplankton and zooplankton (data from VPI&SU 1985), yielding 0.0031 g AFDW per liter. Standing stock of S.P.O.M. was estimated by assuming 4.8 kcal per gram AFDW and multiplying by the volume of water over the average square meter of river bottom. Average depths for UW and LW were taken as 5 and 7 meters, respectively.

Direct field measurements of benthic coarse and fine particulate organic matter abundance were not made. Standing stocks are estimated by using the total annual energy flux through each component and assuming turnover ratios of 100 and 50 times per year for C.P.O.M. and F.P.O.M., respectively. Estimates were then rounded to indicate the many approximations used in their derivations.

Class: Zooplankton - Zooplankton X(6)

Estimates for energy flows involving zooplankton came directly from VPI&SU (1985:Section IV.7). Food types consumed by zooplankton included phytoplankton and suspended particulate organic matter. Gross consumption was estimated as that required to support measured production. The production estimate was first divided by an assumed production efficiency of 30%, and the result divided by a composite assimilation efficiency of 61%. Respiration was assumed as 70% of assimilated energy. Net production in excess of consumptive demand was split evenly between S.P.O.M. and downstream transport out of the system. As with phytoplankton, transport is not modeled as occurring both in to and out of a river segment, but rather as the net of these two processes occurring in a segment over the year.

Class: Macroinvertebrates - Collector Gatherers (* LW only)
X(7), Collector Filterers (* LW only) X(8),
Scraper Grazers X(9), Shredders (* LW only) X(10),
Predators (* LW only) X(11)

Four of the five aquatic insect groups were sufficiently abundant to make biomass and production estimates from the field data collected

(collector/gatherers, collector filterers, shredders, and predators). The production estimates were made for suitable substrates only, and do not represent the average habitat simulated by the model (VPI&SU 1985: Section V.8). These data were first converted to kilocalories and then adjusted by the proportions of suitable substrate found at each site (Table II.6). Production estimates for these four benthic invertebrate groups, after the adjustment for the average square meter of substrate at LW, fell short of the combined predatory demands of the fish trophic groups at that site. As greater confidence was placed on fish abundance, production, and consumption estimates, we elected to multiply the biomass, production, consumption, and respiration, and waste flows of the LW insect groups by the following factors: collector/gatherers (x 2), collector filterers (x 70), shredders (x 25), and predators (x 2). The most probable explanation for this deficit is that snags or other debris provide suitable substrates and that this factor was not reflected in the original measurements.

Section V.8 of VPI&SU (1985) details the trophic basis for production for the major insect invertebrate taxa. Food types included the following categories: animal, diatom, other algae, detritus, and vascular plant. Total consumption for the four trophic groups is calculated as

Table II.6. Conversion factors used to derive model biomass and production estimates of UW and LW benthic invertebrate groups. CP = cobble/pebble, SS = silt/sand substrates.

Trophic Group	Name	kcal conversion ¹	% suitable substrate UW	substrate LW
X(7) Collector Gatherers				
	CP <u>Baetidae</u>	5.3	0.28	0.01
	CP <u>Stenacron</u>	5.3	0.28	0.01
	CP <u>Stenonema</u>	5.0	0.28	0.01
	CP <u>Ephemerella</u>	5.0	0.28	0.01
	CP <u>Tricorythodes</u>	5.0	0.28	0.01
	CP <u>Caenis</u>	5.0	0.28	0.01
	CP <u>Cyrnellus</u>	5.0	0.28	0.01
	CP <u>Orthocladiinae/</u> <u>Chironominae</u>	5.5	0.28	0.01
	SS <u>Orthocladiinae/</u> <u>Chironominae</u>	5.5	0.72	0.99
X(8) Collector Filterers				
	CP <u>Cheumatopsyche</u>	5.6	0.28	0.01
	CP <u>Isonychia</u>	5.0	0.28	-
	CP <u>Hydropsyche</u>	5.6	0.28	0.01
	CP <u>Simulium</u>	5.0	0.28	-
X(10) Shredders				
	CP <u>Taeniopteryx</u>	5.0	0.28	0.01
	CP <u>Strophopteryx</u>	5.0	0.28	0.01
X(11) Predators				
	CP <u>Argia</u>	5.1	-	0.01
	CP <u>Tanypodinae</u>	5.5	0.28	0.01
	SS <u>Tanypodinae</u>	5.5	0.72	0.99

¹ taken from Cummins and Wuycheck (1971) for same or similar taxa (kcal/gram dry weight)

² Corps of Engineers unpublished sediment survey data

that required to support measured production, assuming 1) net production efficiency of 50% and 2) a 10, 30, and 70% assimilation efficiencies for detritus/vascular plants, diatoms/other algae, and animal matter in the diets, respectively. Respiration was assumed to be 50% of total assimilated energy. The energy of non-assimilated food was directed to F.P.O.M. X(5) as waste products. Gross consumption was then partitioned into individual feeding flows between trophic groups. Partitioning was based on individual taxa diet percentages (VPI&SU 1985: Table V.8.6) weighted according to the relative proportions of the taxon in each trophic group. Net production in excess of consumptive demand was divided between emergence by adults (20%) and natural mortality losses to C.P.O.M. (80%). Estimates of standing stock come from data (VPI&SU 1985: Tables V.8.4 and V.8.5). Again, these data pertain specifically to suitable substrates, and do not represent the average square meter of river habitat simulated by the model. Abundance estimates are first converted from dry weights to kilocalories, then weighted to represent the average square meter of available substrate. Conversion and weighting factors are given in Table II.6.

One group, the scraper grazers X(9), was not well represented in the field collections and was given only

token representation in the model. Energy flow estimates for this group were generated on the basis of the only data available, that being the total consumption of scraper grazer organisms (primarily snails) by other trophic groups. Scraper/Grazer biomass was estimated indirectly by establishing a total production value which would satisfy consumptive demand for these organisms, and then assuming a production to biomass ratio of 0.5. Consumption and respiration were back calculated from the assumed production value using a net production efficiency of 34% and an assimilation efficiency of 30%. Evidently scraper grazers play an insignificant role in the functioning of the Kanawha River ecosystem, thus the lack of field derived measurements is not expected to influence the results of the modeling effort.

Class: Larger Invertebrates - Molluscs X(12), Crayfish X(13)

No direct measurements of production or abundance were made for molluscs or crayfish. These were estimated using methods similar to Scraper/Grazers above. A production value sufficient to satisfy consumptive demands was adopted, after which a P/B ratio of 4.1 was used to approximate mollusc biomass (Aldridge and McMahon 1978), while crayfish

biomass was estimated using a P/B ratio of 1.25 (Momot and Gowing 1977). Net production efficiencies of 60 and 50%, and assimilation efficiencies of 13 and 15% were used in the back calculation of total consumption by molluscs and crayfish, respectively. The mollusc diet was assumed to consist of 90% S.P.O.M., 7.5% phytoplankton, and 2.5% zooplankton. Crayfish food habits were assumed to include 60% living animal matter (further partitioned between the insect invertebrate groups according to their relative production), 30% plant matter (periphyton), and 10% detritus. The energy of non-assimilated food was directed to F.P.O.M. X(5) as waste products. Net production in excess of consumptive demand for these groups was fated to C.P.O.M. X(4) as natural mortality.

Class: Fish - Benthic Invertivores X(14), Omnivores X(15),
Crayfish/Piscivores X(16), Herbivore/Detritivores
X(17), Midwater Invertivores* X(18),
Piscivores X(19)

The original estimates of biomass, production, and consumption for the most common fish species (Tables I.5, I.23) pertain to the near-shore habitats that were sampled (effective sampling in the main channel was prohibited by

river depths, currents, and the presence of tow traffic), and in some cases were adjusted to represent the average habitat of the river. Since the model represents the river on an average square meter basis, and near-shore and main channel habitats are not utilized equally by all species of fish, the nearshore data are not always appropriate for direct use in the model. Estimates of the biomass supported by average habitat were made by averaging the near-shore biomass data with main channel biomass approximations. Approximations of main channel biomass for redhorse, sunfish, basses, and walleye/sauger were obtained by multiplying their near-shore biomass estimates by open-water conversion factors (0.83, 0.59, 0.2, and 0.54, respectively) from Davies and Shelton (1983). Production and consumption data were likewise adjusted and averaged. This resulted in a two sets (near-shore and main channel) of biomass/production/consumption estimates for each of the above species. Weighted averages of these sets were then determined based on the relative proportions of each habitat type in each river segment. These proportions were estimated from bathymetric recordings of Kanawha River cross sections (United States Army Corps of Engineers, Huntington District, unpublished data). Near-shore and main channel classifications comprised 43.2 and 56.8% of total habitat at

UW and 21.4 and 78.6% of total habitat at LW, respectively. Biomass/production/consumption estimates for those trophic groups which included one or more of the species above were then recalculated based on the average "system" biomass estimates. These adjustments had the net effect of reducing the standing stocks, production, and consumption estimates used by the model for three trophic groups: benthic invertivores, crayfish/piscivores, and piscivores.

Our estimate of midwater invertivore production was not nearly sufficient to support total consumptive demand by predators, even after the above reductions in key predatory groups were made. The various shiners and young-of-the-year fishes which dominate the midwater invertivore trophic group were apparently underrepresented in our collections and young-of-the-year were not included in the production calculations. Small fish (<100 mm) could not be collected with the same efficiency as larger individuals by electroshocking. As greater confidence was placed on our estimates of predator demands than prey supply, we resolved this imbalance by increasing both the standing stock and energy flows through the midwater invertivore group by ten fold.

Production was adjusted by weighting the observed turnover ratios of the major fish species in each trophic group according to relative contribution to total group biomass, and multiplying this weighted average P/B ratio with the revised (habitat-weighted) biomass estimates.

Consumption estimates were obtained indirectly from production, and consequently these also required recalculation. First a composite assimilation efficiency was established based on the proportions of various food types in the diets, assuming that animal foods, vegetable foods, and detrital foods are 70%, 30%, and 10% assimilated (Table II.7). The energy of non-assimilated food was directed to F.P.O.M. X(5) as waste products. A net production efficiency of 30% was assumed (Kozlofsky 1968) to complete the calculation.

Fish consumption of aquatic insects was consistently in excess of insect production estimates. It was concluded that this consumption originated from both benthic and drifting insects, in which case the drift might be considered an input to the system. Since there was no way to reliably determine the source of insects found in the fish stomachs, we assumed the proportion of insects eaten directly out of the water column based on a general

Table II.7. Weighted assimilation efficiencies for fish trophic groups.

Trophic Group	Name	<u>Composite efficiency</u>	
		UW	LW
X(14)	Benthic Invertivores	0.6778	0.6514
X(15)	Omnivores	0.4885	0.5056
X(16)	Crayfish/Piscivores	0.7000	0.7000
X(17)	Herbivore/Detritivores	0.1480	0.1576
X(18)	Midwater Invertivores	0.6320	0.6320
X(19)	Piscivores	0.7000	0.7000

knowledge of the feeding strategies used by the most common species. For example, it was assumed that common carp took only 30% of their insect food out of the drift and 70% directly from the bottom. In contrast, 100% of the insects found in the diet of longnose gar were assumed to come from the drift. Such percentages for the 19 most common fish species were then weighted according to their contribution to total trophic group biomass. The resultant (trophic group) percentages of total insect consumption originating in the drift ranged from 30% for omnivores to 88% for piscivores. In all cases in which a fish group consumed aquatic insects, the total energy flow was then partitioned between drift and benthic sources (with only the benthic portion supplied by the insect trophic groups).

Production in excess of consumptive demand (surplus) was partitioned between natural mortality (fated to $X(4)$) and harvest losses. Harvest was assumed to be 25, 50, and 50% of the production surplus for omnivores, crayfish/piscivores, and piscivores, respectively.

Model Output

The program generates two types of model output for each river segment. The first type is a time series of

standing stock values for all trophic groups during the simulation, along with the percentage change between initial and final values. The second form of program output is a set of energy budgets for each trophic group. Budgets detail all sources and sinks of energy flow through each trophic group and may be calculated for pre- and/or post-simulation conditions as a user option.

Ecosystem Flow Analyses

While energy budgets can be used to organize the flows involving individual trophic groups, they do not provide a ready means of integrating flows throughout the entire ecosystem. This information was obtained with flow analyses (Finn 1976,1980). Flow analyses evaluate pathways of energy flow linking trophic groups, and trace the ultimate origins and fates of energy from the perspective of individual groups. The "ultimate" aspect of the analyses is their ability to associate the flow of energy through any model component with flows to or from all other components, regardless of whether or not these are linked directly. In other words, energy flows are integrated throughout the entire ecosystem. A matrix is produced in each analysis which yields a concise and useful summary of all possible energy pathways in the ecosystem.

The first analysis deals with linkages between donors and recipients from the perspective of the donor. The product of this analysis is a matrix, hereafter referred to as "N **". The N ** matrix details the eventual fates of energy flows passing through all trophic groups. Each element of the N ** matrix, $N^{**}(I,J)$, pertains to a donor trophic group (J) and a recipient group (I). The value of $N^{**}(I,J)$ is the percentage of the total energy flux passing through donor group (J) which (directly or indirectly) reaches recipient group X(I). Looked at another way, $N^{**}(I,J)$ gives the units of flow "pushed" through recipient group X(I) as a result of 100 units of flux into donor group X(J). Column J of N **, then, is the vector of energy flows reaching all X(I) as a result of 100 units of inflow into trophic group X(J). Thus the N ** matrix provides a quantitative expression of the extent to which flow through any chosen trophic group eventually (directly or indirectly) supports flow in any other.

In a simple cascading model in which all energy flow proceeds directly out of the system, the elements of the N ** matrix would all be less than or equal to 100. In more complex models, however, energy flows may (directly or indirectly) pass through a trophic group more than once. In

these cases elements in excess of 100 result in the matrix indicating that internal cycling is involved.

The N^{**} matrix is derived by first defining an energy flow matrix F where element $F(I,J)$ represents the annual flow of energy from trophic group $X(J)$ to trophic group $X(I)$. Second, we define a vector T , where element $T(J)$ represents the total flow of energy passing through the donor trophic group $X(J)$ per year. The F matrix is then divided (in elementwise fashion) by the T vector to produce a Q' matrix:

$$Q'(I,J) = F(I,J) / T(J) \quad (1)$$

The N^{**} matrix is then calculated first by subtracting the Q' matrix from an appropriately dimensioned identity matrix I and inverting the difference:

$$N^{**} = \text{INV} (I - Q'(I,J)) \quad (2)$$

The second analysis addresses the linkages between donors and recipients from the perspective of the recipient. The product of this analysis is a second matrix, hereafter referred to as " N^* ". In contrast to the matrix above, N^* details the sources or origins of energy flow passing through all trophic groups. The analysis is not limited to

the other groups on which a particular group directly feeds. As before, each element of the N^* matrix, $N^*(I,J)$, involves a donor group $X(J)$ and a recipient group $X(I)$. The value of $N^*(I,J)$ is the percentage of the total energy flux passing out of recipient group $X(I)$ which (directly or indirectly) reached it by passing through donor group $X(J)$. Looked at another way, $N^*(I,J)$ gives the units of flow "pulled" through donor group $X(J)$ which would result from 100 units of flux out of recipient group $X(I)$. Row I of N^* , then, is the vector of energy flows coming from all $X(J)$ which when combined result in 100 units of outflow from trophic group $X(I)$. Thus the N^* matrix provides a quantitative expression of the extent to which flow through any chosen trophic group is (directly or indirectly) supported by flow in any other.

In a simple, non-branching food chain model, the elements of the N^* matrix would all be 100 or 0. In more complex models, however, energy flows may (directly or indirectly) pass through a trophic group more than once. In these cases elements in excess of 100 result in the matrix indicating that internal cycling is involved.

The N^* matrix is obtained using a derivation similar to the one above. The first difference is in the original

flow matrix used. In the second derivation, the F matrix defined above is expanded to a square matrix by adding an extra row and column. The "new" last column can be considered as a column vector D whose elements D(J) are the total flow of energy entering the ecosystem through trophic group X(J). Elements of the "new" last row are null (this done only to maintain a square matrix). Again we define an energy flow matrix in which any element F(I,J) of the matrix represents the annual flow of energy from trophic group X(J) to trophic group X(I), but now the vector T is defined with elements T(I) represents the total flow of energy passing through the recipient trophic group X(I) per year. The expanded flow matrix is then divided (in elementwise fashion) by the T vector to produce a Q' matrix:

$$Q' (I,J) = F(I,J) / T(I) \quad (3)$$

The N* matrix is calculated by subtracting the Q' matrix from an appropriately dimensioned identity matrix I, and inverting the difference:

$$N^* = \text{INV} (I - Q' (I,J)) \quad (4)$$

The information contained in the N* matrix can be used both to interpret, and to some extent predict, the simulation results obtained by using the model. In theory,

the most successful trophic groups are those in position to take advantage of the most prevalent energy source(s). As a test of this, the N * matrix will specify the sources of energy supporting the dominant organisms of the Kanawha River.

RESULTS

Estimation of Standing Stocks

The three greatest 'standing stock' estimates are for the particulate organic matter groups S.P.O.M., C.P.O.M., and F.P.O.M.. Phytoplankton biomass exceeds periphyton biomass at both sites. Both primary producer groups are more abundant at LW than at UW, particularly phytoplankton. Zooplankton biomass exceeds phytoplankton biomass at each site. Collector gatherers comprise the bulk of insect biomass at both UW and LW. Collector filterers are second in abundance among the insects at UW, but third behind predators at LW. Scraper grazers and shredders are the least abundant insects at both sites.

Herbivore/detritivores and omnivores dominate the fish community at both sites, followed by midwater invertivores. Benthic invertivores, piscivores, and crayfish/piscivores are the least abundant fishes. Both benthic invertivores and crayfish/piscivores are more abundant at UW than LW, while the reverse is true for piscivores. Average standing stock estimates as well as annual energy throughput for the 19 trophic groups of the model are given in Table II.8.

Table II.8. Model values for standing stocks (kcal/m²) and total energy flux (kcal/m²/yr) of trophic groups.

Trophic Group	Name	UW		LW	
		standing stocks	energy flux	standing stocks	energy flux
X(1)	Phytoplankton	1.797	1640.000	3.688	1438.000
X(2)	Periphyton	1.084	271.200	1.154	208.000
X(3)	SPOM	75.000	53919.412	100.000	46641.997
X(4)	CPOM	450.000	42509.820	350.000	32212.326
X(5)	FPOM	500.000	22488.630	500.000	22445.356
X(6)	Zooplankton	18.690	375.780	18.690	974.010
X(7)	Coll/Gatherers	2.734	1094.388	6.064	1039.592
X(8)	Coll/Filterers	1.197	150.496	0.203	22.778
X(9)	Scraper Grazers	0.010	0.200	0.120	0.600
X(10)	Invt Shredders	0.029	3.529	0.025	2.813
X(11)	Invt Predators	0.153	18.702	0.328	52.040
X(12)	Molluscs	9.750	510.320	9.750	510.320
X(13)	Crayfish	3.313	16.564	2.994	14.972
X(14)	B. Invertivores	3.823	8.346	1.535	4.925
X(15)	Omnivores	11.240	39.577	13.433	45.255
X(16)	Cray/Piscivores	0.862	3.748	0.217	0.808
X(17)	Herb/Detritivores	16.275	311.689	15.480	297.241
X(18)	M. Invertivores	6.480	53.930	4.980	41.450
X(19)	Piscivores	1.569	5.743	2.143	7.899

Estimation of Energy Flows

There are two major and three minor sources of energy flow entering the ecosystem (Table II.9). The major sources of energy driving the ecosystem are S.P.O.M. and gross primary production by phytoplankton and periphyton. Utilization of S.P.O.M. (roughly 30,000 kcal/m²/yr) is the single greatest flow of energy modeled at each site. This flow was defined as the net difference between S.P.O.M. captured and utilized and the amount of S.P.O.M. generated within (and subsequently lost from) a river segment. The flow does not represent the absolute amount of S.P.O.M. in transport, roughly estimated from seston data in VPI&SU (1985) as one billion kcal/m²/yr, or about four orders of magnitude greater than the amount which is actually utilized. The efficiency of S.P.O.M. utilization, that is the amount captured out of suspension relative to that available, is only 0.003%.

Gross primary production by phytoplankton (1640, 1438 kcal/m²/yr at UW and LW, respectively) and periphyton (271.2, 208 kcal/m²/yr) combined represent approximately 5.53 and 5.15% of all energy sources available and utilized in the UW and LW ecosystems. Annual incident light energy (AILE) was estimated from field data as approximately 1.2591

Table II.9. Matrices of energy flows entering system
(kcal/m²/yr).

Trophic Group	Name	Flows into System				
		net import	GPP	leaf fall	terr insect	drift insect
Upper Winfield						
X(1)	Phytoplankton	-	1,640.0	-	-	-
X(2)	Periphyton	-	271.2	-	-	-
X(3)	SPOM	32,559.7	-	26.6	-	-
X(14)	B. Invertivores	-	-	-	0.2	1.0
X(15)	Omnivores	-	-	-	5.4	1.6
X(16)	Cray/Piscivores	-	-	-	-	0.2
X(17)	Herb/Detritivores	-	-	-	-	0.5
X(18)	M. Invertivores	-	-	-	-	23.2
X(19)	Piscivores	-	-	-	-	tr
Lower Winfield						
X(1)	Phytoplankton	-	1,438.0	-	-	-
X(2)	Periphyton	-	208.0	-	-	-
X(3)	SPOM	30,260.5	-	54.8	-	-
X(14)	B. Invertivores	-	-	-	0.8	0.8
X(15)	Omnivores	-	-	-	8.0	1.1
X(16)	Cray/Piscivores	-	-	-	-	tr
X(17)	Herb/Detritivores	-	-	-	-	0.6
X(18)	M. Invertivores	-	-	-	-	17.8
X(19)	Piscivores	-	-	-	-	tr

$\times 10^6$ and 1.2058×10^6 kcal/m²/yr for UW and LW, respectively (Lizotte 1984, pers. comm.). If we assume (after Lind 1979) that photosynthetically active radiation (PAR) constitutes 50% of total solar radiation, then the photosynthetic efficiency of all primary producers combined is 0.304, 0.272% at UW and LW, respectively.

Direct leaffall and blow-in combined (26.6, 54.8 kcal/m²/yr) represents less than 0.001% of the energy entering the system. Total terrestrial insect fall per mile for UW and LW was estimated as 903.7 and 1662.5 kcal/yr. With conversion to average square meters, however, these inputs become only 0.003 and 0.005 kcal/m²/yr. This is much less than the estimated consumptive demand of fish predators using this resource (5.6, 8.7 kcal/m²/yr). It was assumed that this demand is met by drowned terrestrial insects from upstream reaches supplementing the local additions. Drifting aquatic insects (26.48, 20.313 kcal/m²/yr) contributed less than 0.01% to the total energy input. As with terrestrial insects, this source was assumed to be the amount required to support consumptive demands.

Comparing the system inputs at each site, we find utilization of S.P.O.M. slightly higher at UW (32,559.7 kcal/m²/yr) than at LW (30,260.5 kcal/m²/yr), although this

may be merely an artifact of the gross methods used in their estimation. Total primary production is greater at UW than at LW (1,911, 1,646 kcal/m²/yr). Leaf inputs at LW are over twice this same flow at UW, and utilization of terrestrial insects by fish is also greater at LW than UW. Utilization of drifting aquatic insects by fish is generally greater at UW than LW, the sole exception being for herbivore/detritivores.

The estimates for all intra-system energy transfers are shown in Tables II.10 and II.11 for UW and LW, respectively. One fundamental difference between reaches involves the flow of energy representing resuspension of C.P.O.M. to S.P.O.M.. This flow in the upper, more lotic reach was assumed to be approximately twice the same flow in the lower reach. This is one of the fundamental differences between energy flows in the two reaches. The other is the dependence of invertebrate predators on meiofauna at LW, as described in the methods. Other energy flows, while differing between sites, are not fundamentally different. In what follows, UW flows are reviewed. Energy flows in the two sites will be compared in the presentation of flow analyses results.

By far the most thoroughly integrated groups (highest connectivity) are C.P.O.M. and F.P.O.M.. The highest

Table II.11. LW matrix of energy flows between model components.

$F(i,j)$ = average annual flow (kcal/m²/yr) from donor X(i) to recipient X(j)
(energy flows and their analyses by individual trophic groups are found in Appendix Tables B.1-19.)

FLOW	C(1)	C(2)	C(3)	C(4)	C(5)	C(6)	C(7)	C(8)	C(9)	C(10)	C(11)	C(12)	C(13)	C(14)	C(15)	C(16)	C(17)	C(18)	C(19)	
R(1)	-	-	509.201	-	-	146.102	17.730	1.792	-	-	38.274	-	-	-	-	-	-	-	-	-
R(2)	-	-	-	42.748	20.800	-	-	-	0.600	-	-	-	4.492	-	10.722	-	69.508	7.050	-	-
R(3)	-	-	-	32122.137	1.0xE04	827.908	-	20.664	-	-	459.288	-	-	-	-	-	-	-	-	-
R(4)	-	-	5357.001	-	10714.002	-	20.612	-	2.813	-	-	2.246	0.335	5.026	-	4.128	-	-	-	-
R(5)	-	-	1.0xE04	-	1001.202	-	-	-	-	-	-	0.748	0.064	2.489	-	218.175	-	-	-	-
R(6)	-	-	460.657	-	0.048	0.322	-	-	-	-	12.758	-	-	-	-	3.708	-	-	-	-
R(7)	-	-	-	9.564	928.356	-	-	-	-	-	18.136	5.211	0.152	0.975	-	0.116	3.128	0.001	-	-
R(8)	-	-	-	0.228	19.954	-	-	-	-	-	-	0.007	0.031	-	-	0.307	1.050	-	-	-
R(9)	-	-	-	0.032	0.042	-	-	-	-	-	-	-	0.028	-	-	-	-	-	-	-
R(10)	-	-	-	0.021	2.532	-	-	-	-	0.005	-	-	-	0.119	-	-	-	-	-	-
R(11)	-	-	-	4.428	15.612	-	-	-	-	7.858	-	2.268	0.280	0.856	-	0.191	0.280	-	-	-
R(12)	-	-	-	22.511	443.978	-	-	-	-	-	-	-	0.726	4.241	-	0.412	12.110	-	-	-
R(13)	-	-	-	0.749	7.486	-	-	-	-	-	-	-	1.206	1.314	0.379	-	-	-	-	0.095
R(14)	-	-	-	0.419	1.719	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.543
R(15)	-	-	-	4.672	22.356	-	-	-	-	-	-	-	0.028	-	0.214	-	-	-	-	0.392
R(16)	-	-	-	0.084	0.241	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R(17)	-	-	-	2.415	250.277	-	-	-	-	-	-	-	-	-	6.257	0.029	-	-	-	3.353
R(18)	-	-	-	1.488	15.254	-	-	-	-	-	-	-	0.489	2.195	0.178	-	-	-	-	3.510
R(19)	-	-	-	0.830	2.369	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

volumes of energy flow (> 1000 kcal/m²/yr) exclusively involve organic matter groups. Flows in the range of 500 to 1,000 kcal/m²/yr also include organic matter groups as either a donor or recipient. Thus the majority of all energy being transferred directly involves organic matter (Tables II.8, II.10,11).

The importance of organic matter is further confirmed by the major role it plays at all of the higher trophic levels. Among the insect invertebrates, the major energy transformation is between collector gatherers X(7) and F.P.O.M. X(5). For noninsect invertebrates mollusc X(12) utilization of S.P.O.M. X(3) and subsequent conversion to F.P.O.M. X(5) are the major energy flows. The dominant flow among fish groups is herbivore/detritivore X(17) consumption of F.P.O.M. X(5).

Flows of energy from primary producers to the heterotrophic groups are generally less than those from organic matter groups (Tables II.10-11). Energy flows from phytoplankton X(1) lead primarily to intermediate trophic level groups (e.g. zooplankton X(6), collector gatherers X(7), collector filterers X(8), and molluscs X(12)). In comparison, flows from periphyton X(2) lead to higher trophic level groups (e.g. crayfish X(13), omnivores X(15),

herbivore/detritivores X(17), and midwater invertivores X(18)) (Table II.10-11).

The greatest flows of energy provided by invertebrate groups come from the collector-gatherers X(7), collector-filterers X(8), and from molluscs X(12). Energy flows involving the herbivore-detritivores X(17) and midwater invertivores X(18) are generally among the largest from the fish trophic groups (Table II.10-11).

Energy flows exiting the system at UW and LW are listed in Tables II.12 and II.13, respectively. Respiration losses of energy dominate the energy flows leaving the system at both sites. In comparison, emergence of adult insects and fish harvest are relatively minor sinks of energy. Phytoplankton and zooplankton both demonstrated a net surplus of energy which was exported downstream (Tables II.12-13).

Energy Flow Analyses

Energy flow analyses (Tables II.14-17) were conducted to test two hypotheses. The first of these was the previously unquantified expectation of higher dependence on allochthonous rather than autochthonous sources of energy.

Table II.12. UW matrix of extrasystem energy flows
(kcal/m²/yr).

Trophic Group	Name	Flows out of System			
		resp	emergence	harvest	net transport
X(1)	Phytoplankton	410.000	-	-	405.234
X(2)	Periphyton	67.800	-	-	-
X(3)	SPOM	767.700	-	-	-
X(4)	CPOM	21,254.910	-	-	-
X(5)	FPOM	11,244.315	-	-	-
X(6)	Zooplankton	160.386	-	-	25.190
X(7)	Coll/Gatherers	58.201	8.493	-	-
X(8)	Coll/Filterers	7.804	1.224	-	-
X(9)	Scraper Grazers	0.040	-	-	-
X(10)	Invt Shredders	0.157	0.007	-	-
X(11)	Invt Predators	6.906	0.236	-	-
X(12)	Molluscs	26.342	-	-	-
X(13)	Crayfish	4.141	-	-	-
X(14)	B. Invertivores	3.960	-	-	-
X(15)	Omnivores	13.514	-	1.313	-
X(16)	Cray/Piscivores	1.837	-	0.394	-
X(17)	Herb/Detritivores	32.291	-	-	-
X(18)	M. Invertivores	23.854	-	-	-
X(19)	Piscivores	2.814	-	0.603	-

Table II.13. LW matrix of energy flows leaving system
(kcal/m²/yr).

Trophic Group	Name	Flows out of system			net transport
		resp	emergence	harvest	
X(1)	Phytoplankton	359.500	-	-	365.401
X(2)	Periphyton	52.000	-	-	-
X(3)	SPOM	3,212.000	-	-	-
X(4)	CPOM	16,106.163	-	-	-
X(5)	FPOM	11,222.678	-	-	-
X(6)	Zooplankton	415.724	-	-	80.793
X(7)	Coll/Gatherers	71.560	2.393	-	-
X(8)	Coll/Filterers	1.144	0.057	-	-
X(9)	Scraper Grazers	0.120	-	-	-
X(10)	Invt Shredders	0.131	0.005	-	-
X(11)	Invt Predators	19.158	1.109	-	-
X(12)	Molluscs	26.342	-	-	-
X(13)	Crayfish	3.743	-	-	-
X(14)	B. Invertivores	2.244	-	-	-
X(15)	Omnivores	16.035	-	1.558	-
X(16)	Cray/Piscivores	0.393	-	0.084	-
X(17)	Herb/Detritivores	32.910	-	-	-
X(18)	M. Invertivores	18.336	-	-	-
X(19)	Piscivores	3.870	-	0.830	-

The second hypothesis was that the structure and function of the river ecosystem would reflect this higher dependence, specifically that the most abundant trophic groups (both overall and at each trophic level) would derive the majority of their energy from the system's major energy source.

Primary Producers

Viewed from the N * perspective (Tables II.16,17) all phytoplankton X(1) throughflow at either site originates from incident solar radiation. Seen from the N ** perspective (Tables II.14,15) most of this throughflow later passes through organic matter groups S.P.O.M. (68, 63%), C.P.O.M. (54, 44%), and F.P.O.M. (34, 34%), or through zooplankton (10, 11%).

As with phytoplankton, periphyton X(2) throughflow at both sites is derived wholly from incident solar radiation. Most of this throughflow is fated to pass through organic matter groups S.P.O.M. (46, 42%), C.P.O.M. (72, 51%), or F.P.O.M. (64, 74%), collector gatherers (3, 3%), crayfish (2, 2%), omnivores (4, 7%), herbivore/detritivores (23, 34%), and midwater invertivores (3, 3%).

Table II.14. LM NEM matrix. Elements give the percentage of energy flow through X(i,j) destined to support flow in X(i), rounded to first decimal place. tr = trace (< 0.1%). E = aquatic insect emergence. H = fish harvest.

	NEM(i,j) = element in row(i), column(j)																						
	C (1)	C (2)	C (3)	C (4)	C (5)	C (6)	C (7)	C (8)	C (9)	C (10)	C (11)	C (12)	C (13)	C (14)	C (15)	C (16)	C (17)	C (18)	C (19)	C (E)	C (H)		
R (1)	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
R (2)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
R (3)	67.7	46.3	161.6	59.2	75.7	77.3	69.6	69.5	57.1	70.4	36.0	69.4	47.2	35.0	45.1	20.9	66.8	36.9	28.9	0.0	0.0	0.0	0.0
R (4)	53.5	72.2	127.1	146.6	59.7	60.9	58.3	58.4	48.8	56.7	36.2	57.5	44.5	43.7	45.6	33.3	55.6	40.8	33.3	0.0	0.0	0.0	0.0
R (5)	33.6	63.5	66.7	50.8	136.5	36.5	123.7	123.4	100.8	126.2	60.5	123.4	81.1	54.1	75.6	46.3	110.7	59.9	46.3	0.0	0.0	0.0	0.0
R (6)	10.3	0.2	0.6	0.2	0.3	100.3	0.3	0.3	0.2	0.3	0.1	0.3	0.2	0.1	0.2	0.1	0.3	0.1	0.1	0.0	0.0	0.0	0.0
R (7)	4.1	2.9	3.1	2.4	6.1	1.7	105.6	5.5	4.5	5.7	2.7	5.6	3.7	2.5	3.4	2.1	5.3	2.7	2.1	0.0	0.0	0.0	0.0
R (8)	0.9	0.1	0.4	0.2	0.2	0.9	0.2	100.2	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.0	0.0	0.0	0.0
R (9)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R (10)	tr	tr	tr	tr	tr	tr	tr	tr	tr	100.0	tr	tr	tr	tr	tr								
R (11)	0.1	tr	0.1	tr	0.1	tr	1.6	1.7	0.1	1.2	107.6	0.1	0.1	tr	0.1	tr	0.1	tr	0.1	tr	tr	tr	tr
R (12)	3.3	0.4	1.4	0.5	0.7	4.1	0.6	0.6	0.5	0.6	0.3	100.6	0.4	0.3	0.4	0.3	0.6	0.3	0.3	0.0	0.0	0.0	
R (13)	tr	1.9	tr	tr	0.1	tr	0.7	0.8	tr	0.5	3.4	tr	100.0	tr	tr	tr	tr	tr	tr	tr	tr	tr	tr
R (14)	tr	0.1	tr	tr	tr	tr	tr	0.2	0.1	7.5	tr	1.6	1.0	2.7	100.0	tr	tr	tr	0.3	tr	tr	tr	tr
R (15)	0.1	3.5	0.1	tr	0.1	0.1	0.4	0.5	0.1	2.0	2.1	1.7	2.9	tr	100.0	tr	1.0	1.4	tr	0.0	0.0	0.0	0.0
R (16)	tr	0.3	tr	tr	tr	tr	0.1	0.1	tr	1.3	0.8	0.1	13.6	tr	0.7	100.0	tr	1.8	tr	0.0	0.0	0.0	0.0
R (17)	0.5	23.1	0.7	0.6	1.5	1.2	1.3	1.5	1.1	1.4	0.8	1.4	1.0	0.6	0.6	0.5	101.3	0.7	0.5	0.0	0.0	0.0	0.0
R (18)	0.1	3.4	0.1	tr	tr	0.1	0.5	0.7	tr	0.2	14.5	3.1	tr	tr	tr	tr	tr						
R (19)	tr	0.4	tr	tr	tr	tr	tr	0.1	0.4	tr	0.8	tr	1.0	4.7	0.7	tr	0.8	4.7	100.0	0.0	0.0	0.0	0.0
R (E)	tr	tr	tr	tr	0.1	tr	0.8	0.9	tr	0.3	1.4	tr	tr	tr	tr	tr							
R (H)	tr	0.2	tr	0.2	0.2	0.1	1.6	0.5	3.5	10.5	0.1	0.7	10.5	tr	tr	tr	tr						

Table II.15. LM Nnn matrix. Elements give the percentage of energy flow through X(i,j) destined to support flow in X(i), rounded to first decimal place. tr = trace (< 0.1%). E = aquatic insect emergence. H = fish harvest.

	Nnn(i,j) = element in row(i), column(j)																				
	C(1)	C(2)	C(3)	C(4)	C(5)	C(6)	C(7)	C(8)	C(9)	C(10)	C(11)	C(12)	C(13)	C(14)	C(15)	C(16)	C(17)	C(18)	C(19)	C(E)	C(H)
R(1)	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(2)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(3)	63.2	41.0	150.5	48.6	70.5	72.3	64.4	64.7	53.4	65.6	33.5	64.7	44.6	31.6	40.2	26.3	61.2	32.5	26.3	tr	tr
R(4)	43.8	50.7	103.8	133.5	48.7	49.9	45.6	45.9	42.7	46.5	33.8	49.3	37.8	31.5	39.2	28.6	43.5	27.7	28.6	tr	tr
R(5)	34.1	74.1	71.8	58.2	138.8	36.1	126.3	126.8	103.0	128.7	62.0	125.6	85.2	58.7	75.3	47.8	120.0	62.1	47.7	tr	tr
R(6)	11.3	0.7	2.7	0.9	1.3	101.3	1.1	1.1	0.9	1.1	0.6	1.1	0.8	0.6	0.7	0.5	1.1	0.6	0.5	tr	tr
R(7)	2.8	3.3	3.3	2.7	6.2	1.6	105.7	5.7	4.6	5.8	2.8	5.6	3.8	2.6	3.4	2.2	5.4	2.8	2.1	tr	tr
R(8)	0.2	tr	0.1	tr	tr	0.1	tr	100.0	tr												
R(9)	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(10)	tr	tr	tr	tr	tr	tr	tr	tr	tr	100.0	tr										
R(11)	0.1	0.1	0.1	0.1	0.1	tr	2.2	0.1	0.1	0.3	117.8	0.1	0.1	0.1	0.1	tr	0.1	0.1	0.1	tr	tr
R(12)	3.4	0.4	1.5	0.5	0.7	2.0	0.6	0.6	0.6	0.5	0.7	0.3	100.7	0.4	0.3	0.4	0.3	0.6	0.3	0.3	tr
R(13)	tr	2.2	tr	tr	tr	tr	0.6	0.1	tr	0.1	5.2	tr	100.0	tr							
R(14)	tr	0.2	tr	tr	tr	tr	0.1	0.2	4.7	tr	1.1	0.2	8.1	100.0	0.1	tr	tr	1.2	tr	tr	tr
R(15)	0.1	6.5	0.1	0.1	0.1	0.1	0.3	0.4	0.1	4.3	2.5	1.0	8.8	tr	100.0	tr	2.8	5.3	tr	tr	tr
R(16)	tr	0.1	tr	0.1	tr	2.6	tr	tr	100.0	tr	tr	tr	tr	tr							
R(17)	0.4	34.2	0.7	0.6	1.4	0.7	1.3	2.6	1.0	1.3	1.0	1.3	0.8	0.6	0.7	0.5	101.2	0.6	0.5	tr	tr
R(18)	0.1	3.4	tr	tr	tr	0.1	tr	4.6	tr	0.7	2.4	tr	tr	tr	tr	tr	100.0	tr	tr	tr	tr
R(19)	tr	0.8	tr	tr	tr	tr	0.1	0.4	0.5	0.1	0.2	0.2	1.6	11.0	0.9	tr	1.2	8.7	100.0	tr	tr
R(E)	tr	tr	tr	tr	tr	tr	0.3	0.3	tr	0.2	2.5	tr	100.0	tr							
R(H)	tr	tr	tr	tr	tr	tr	0.1	0.1	0.2	0.1	0.1	0.1	0.7	1.2	3.6	10.5	0.2	1.1	10.5	tr	100.0

Table II.16. UM NM matrix. Elements give the percentage of energy flow through X(j) destined to support flow in X(i), rounded to first decimal place. tr = trace (< 0.1%). E = aquatic insect emergences. H = fish harvest.

	NM(i,j) = element in row(i), column(j)																				
	C(1)	C(2)	C(3)	C(4)	C(5)	C(6)	C(7)	C(8)	C(9)	C(10)	C(11)	C(12)	C(13)	C(14)	C(15)	C(16)	C(17)	C(18)	C(19)	C(E)	C(H)
R(1)	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(2)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(3)	2.1	0.2	161.6	46.7	31.6	0.5	1.4	1.9	tr	tr	tr	0.7	tr								
R(4)	2.1	0.5	161.2	146.7	31.6	0.5	1.5	0.2	tr	tr	tr	0.7	tr	tr	tr	tr	tr	0.4	0.1	tr	tr
R(5)	2.5	0.6	160.0	96.1	136.5	0.6	6.0	0.8	tr	tr	0.1	2.8	0.1	tr	0.1	tr	1.6	0.1	tr	tr	tr
R(6)	45.2	0.1	90.5	26.2	17.7	100.3	0.8	0.1	tr	tr	tr	0.4	tr	tr	tr	tr	tr	0.2	tr	tr	tr
R(7)	6.1	0.7	154.0	95.0	126.0	0.6	105.6	0.8	tr	tr	tr	2.6	0.1	tr	0.1	tr	1.5	0.1	tr	tr	tr
R(8)	9.7	0.2	149.0	43.1	29.1	2.2	1.3	100.2	tr	tr	tr	0.6	tr	tr	tr	tr	0.4	tr	tr	tr	tr
R(9)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(10)	2.1	0.5	161.2	146.6	31.6	0.5	1.5	0.2	tr	100.0	tr	0.6	tr	tr	tr	tr	0.4	tr	tr	tr	tr
R(11)	6.6	0.7	153.4	88.2	113.0	0.8	91.6	13.9	tr	0.2	107.6	2.3	tr	tr	tr	tr	1.4	0.1	tr	tr	tr
R(12)	10.5	0.2	147.7	42.7	28.9	3.0	1.3	0.2	tr	tr	tr	100.6	tr	tr	tr	tr	0.4	tr	tr	tr	tr
R(13)	3.7	30.4	108.9	70.9	68.0	0.5	46.3	7.0	tr	tr	3.8	1.4	100.0	tr	0.1	tr	0.8	tr	tr	tr	tr
R(14)	7.5	2.5	124.8	48.5	44.5	1.9	19.8	1.7	0.2	tr	3.5	60.1	5.4	100.0	0.2	tr	0.5	2.1	tr	tr	tr
R(15)	3.5	23.9	89.5	50.7	38.8	0.9	10.2	1.7	tr	tr	1.0	21.8	1.2	tr	100.0	tr	7.3	1.9	tr	tr	tr
R(16)	3.5	24.3	89.2	53.7	49.6	0.6	31.3	4.9	tr	tr	3.8	9.9	60.1	tr	7.0	100.0	1.2	25.5	tr	tr	tr
R(17)	2.4	20.1	127.1	77.1	107.0	1.5	4.8	0.7	tr	tr	tr	2.3	tr	tr	0.1	tr	101.3	0.1	tr	tr	tr
R(18)	3.8	17.1	59.6	21.8	20.3	1.0	9.9	1.9	tr	tr	5.0	29.6	tr	tr	tr	tr	0.2	100.0	tr	tr	tr
R(19)	3.4	18.0	95.2	49.3	60.2	1.2	9.3	1.5	tr	tr	2.6	19.1	2.9	6.8	4.9	tr	42.9	44.1	100.0	tr	tr
R(E)	6.6	0.7	153.4	88.5	113.7	0.8	92.3	13.3	tr	0.1	2.6	2.3	tr	tr	0.1	tr	1.4	0.1	tr	100.0	tr
R(H)	3.5	22.4	90.9	50.8	46.3	1.0	13.5	2.2	tr	0.3	1.9	19.1	11.7	1.8	59.3	17.1	15.6	16.9	26.1	tr	100.0

Table II.17. LM NH matrix. Elements give the percentage of energy flow through X(j) destined to support flow in X(i), rounded to first decimal place. tr = trace (< 0.1%). E = aquatic insect emergence. H = fish harvest.

	NH(i,j) = element in row(i), column(j)																				
	C(1)	C(2)	C(3)	C(4)	C(5)	C(6)	C(7)	C(8)	C(9)	C(10)	C(11)	C(12)	C(13)	C(14)	C(15)	C(16)	C(17)	C(18)	C(19)	C(E)	C(H)
R(1)	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(2)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(3)	1.9	0.2	150.5	33.5	33.9	1.5	1.4	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
R(4)	2.0	0.3	150.3	133.5	33.9	1.5	1.5	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.0
R(5)	2.2	0.7	149.2	83.6	136.8	1.6	5.8	0.1	0.0	0.0	0.1	2.9	0.1	0.0	0.2	0.0	1.6	0.1	0.0	0.0	0.0
R(6)	16.7	0.2	127.9	28.5	28.8	101.3	1.2	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
R(7)	3.9	0.7	144.7	83.1	134.3	1.5	105.7	0.1	0.0	0.0	0.1	2.8	0.1	0.0	0.1	0.0	1.5	0.1	0.0	0.0	0.0
R(8)	9.9	0.2	136.3	30.8	31.2	2.8	1.3	100.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
R(9)	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
R(10)	2.0	0.3	150.3	133.5	33.9	1.5	1.5	0.0	0.0	100.0	0.1	0.8	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.0
R(11)	1.6	0.3	60.2	34.1	55.2	0.6	43.4	0.0	0.0	0.0	117.8	1.1	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
R(12)	9.7	0.2	136.7	30.9	31.3	3.9	1.3	0.0	0.0	0.0	0.0	100.7	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
R(13)	2.0	30.4	90.2	58.3	67.2	0.9	43.9	0.1	0.0	0.0	17.9	1.4	100.0	0.0	0.1	0.0	0.8	0.1	0.0	0.0	0.0
R(14)	2.7	10.0	69.4	35.5	34.9	1.2	17.7	0.9	0.6	0.0	11.2	18.4	24.5	100.0	0.6	0.0	0.1	10.0	0.0	0.0	0.0
R(15)	1.9	29.9	68.6	39.2	40.1	1.2	6.2	0.2	0.0	0.3	2.8	11.6	2.9	0.0	100.0	0.0	18.7	4.9	0.0	0.0	0.0
R(16)	2.3	27.0	77.4	43.9	50.7	1.1	24.5	0.7	0.0	0.1	9.4	10.4	48.1	0.0	26.7	100.0	9.1	23.9	0.0	0.0	0.0
R(17)	1.9	29.9	68.6	39.2	40.1	1.2	6.2	0.2	0.0	0.0	0.2	2.3	0.0	0.0	0.1	0.0	101.2	0.1	0.0	0.0	0.0
R(18)	3.4	17.1	55.5	16.3	20.4	1.3	8.7	2.6	0.0	0.0	0.8	29.6	0.0	0.0	0.0	0.0	0.2	100.0	0.0	0.0	0.0
R(19)	2.6	20.3	82.2	39.4	58.0	1.8	7.8	1.3	0.0	0.0	1.6	16.0	3.1	6.9	5.1	0.0	44.0	48.4	100.0	0.0	0.0
R(E)	3.2	0.5	119.6	67.1	107.9	1.3	84.5	1.7	0.0	0.2	36.8	2.2	0.0	0.0	0.1	0.0	1.2	0.1	0.0	100.0	0.0
R(H)	2.2	26.6	73.5	39.4	46.4	1.4	7.4	0.6	0.0	0.2	2.6	13.1	4.5	2.3	65.7	3.4	26.9	19.1	33.6	0.0	100.0

Organic Matter Groups

In general energy flowing through the organic matter groups X(3-5) is strongly cycled, but most is ultimately derived from upstream sources. The fate of this energy is further downstream transport, with only a small fraction retained through the actions of filtering and collecting organisms. Throughflow in S.P.O.M. X(3) at both sites originates mainly from downstream transport and/or internal cycling (162, 151%), C.P.O.M. (47, 34%), and F.P.O.M. (32, 34%). The majority of this throughflow is fated to cycle and/or pass through organic matter groups S.P.O.M. (61, 51%), C.P.O.M. (127, 104%), or F.P.O.M. (67, 72%), zooplankton (0.6, 2.7%), collector gatherers (3.1, 3.3%), and molluscs (1.4, 1.5%).

At both UW and LW, throughflow in C.P.O.M. X(4) is derived primarily from S.P.O.M. (161, 150%), internal cycling (47, 34%), and F.P.O.M. (32, 34%). Most of this throughflow is destined to cycle and/or pass through organic matter groups S.P.O.M. (59, 49%), C.P.O.M. (47, 34%), or F.P.O.M. (51, 58%), and collector gatherers (2.4, 2.7%).

Throughflow in F.P.O.M. X(5) at both sites originates mainly from the settling of S.P.O.M. (160, 149%), breakdown of C.P.O.M. (96, 84%), and internal cycling (37, 39%). The

majority of this throughflow is destined to cycle and/or pass through organic matter groups S.P.O.M. (76, 71%), C.P.O.M. (60, 49%), or F.P.O.M. (137, 139%), collector filterers (6.1, 6.2%), and herbivore/detritivores (1.5, 1.4%). The degree of energy flow cycling through F.P.O.M. (37, 39%) is similar to that observed for C.P.O.M..

By way of comparison, the fates of primary producer groups X(1,2) differ from the fates of organic matter groups X(3-5) in that there is no cycling in the former and considerable cycling in the latter. Only a small fraction of the throughflow in either set of groups reach higher trophic levels, although relatively larger fractions of primary producer throughflow reach some of these (e.g. crayfish X(13), omnivores X(15), herbivore-detritivores X(17), and midwater invertivores X(18)).

Invertebrates

As intermediates in the food web, flows of energy through invertebrates do not provide direct evidence to support or refute the first hypothesis and are therefore only summarized briefly here. The most important sources of energy flows through invertebrate groups X(6-13) are the organic matter groups. A common analysis demonstrates almost total dependence on X(3-5) as exemplified by

collector gatherers X(7), invertebrate shredders X(10), invertebrate predators X(11), and molluscs X(12). Slightly less commonly the pattern shows highest dependence on organic matter groups but also significant dependence on primary producers (e.g. zooplankton X(6), collector filterers X(8), crayfish x(13)). Scraper grazers X(9) are unique among the invertebrate groups in that they are wholly dependent on a primary producer group (periphyton, X(2)). Cycling of energy flows within an invertebrate group is usually slight, with the exception of invertebrate predators X(11).

Fish

At both UW and LW throughflow in benthic invertivores X(14) is derived mainly from periphyton (2.5, 10%), the organic matter groups S.P.O.M. (125, 69%), C.P.O.M. (49, 36%), or F.P.O.M. (45, 35%), collector gatherers (20, 18%), invertebrate predators (3.5, 11%), molluscs (60, 18%), crayfish (5.4, 25%), and midwater invertivores (2.1, 10%).

Omnivore X(15) throughflow at both sites originates mainly from periphyton (24, 30%), the organic matter groups S.P.O.M. (90, 69%), C.P.O.M. (51, 39%), or F.P.O.M. (39, 40%), collector gatherers (10, 6.2%), molluscs (22, 12%), and herbivore detritivores (7.3, 19%).

Throughflow in crayfish/piscivores X(16) at both sites is derived primarily from periphyton (24, 27%), the organic matter groups S.P.O.M. (89, 77%), C.P.O.M. (54, 44%), or F.P.O.M. (50, 51%), collector gatherers (31, 25%), invertebrate predators (3.8, 9.4%), molluscs (9.9, 10%), crayfish (60, 48%), omnivores (7, 27%), and midwater invertivores (26, 24%).

At both sites throughflow in herbivore detritivores X(17) originates mainly from periphyton (20, 24%), and the organic matter groups S.P.O.M. (128, 114%), C.P.O.M. (77, 64%), or F.P.O.M. (107, 103%). Cycling of energy flow through this group (1.3, 1.2) was slight.

Midwater invertivore X(18) throughflow at both sites is derived primarily from periphyton (17, 17%), the organic matter groups S.P.O.M. (60, 56%), C.P.O.M. (22, 16%), or F.P.O.M. (20, 20%), collector gatherers (9.9, 8.7%), and molluscs (30, 30%).

Throughflow in piscivores X(19) originates mainly from periphyton (18, 20%), the organic matter groups S.P.O.M. (95, 82%), C.P.O.M. (49, 39%), or F.P.O.M. (60, 58%), molluscs (19, 16%), herbivore detritivores (43, 44%), and midwater invertivores (44, 45%).

Aquatic Insect Emergence

Outflow leaving the river ecosystem as aquatic insect emergence (AIE) originates mainly from the organic matter groups S.P.O.M. (153, 120%), C.P.O.M. (89, 67%), or F.P.O.M. (114, 108%), collector gatherers (92, 85%), collector filterers (13, 1.7%), and invertebrate predators (2.6, 37%).

Fish Harvest

Outflow into fish harvest is derived primarily from periphyton (22, 27%), the organic matter groups S.P.O.M. (91, 74%), C.P.O.M. (51, 39%), or F.P.O.M. (46, 46%), collector gatherers (14, 7%), molluscs (19, 13%), crayfish (12, 4.5%), omnivores (59, 66%), crayfish/piscivores (17, 3.4%), herbivore detritivores (16, 27%), midwater invertivores (17, 19%), and piscivores (26, 34%).

Navigation Impact Assessment

Four different levels of tow traffic were tested for their effects on the biota of the Kanawha River. These included simulations of traffic corresponding to baseline (1982-83), future (2040) without project, Winfield replacement, and both Marmet and Winfield replacements. All

trophic groups (at both UW and LW) responded to the increased tow traffic perturbation with declines in standing stock (Table II.18). Overall these were not large reductions, even in Scenario #4. The largest single declines were predicted for phytoplankton X(1) and for periphyton X(2), both of which were reduced by 15.3% at UW and 18.1% at LW. The least affected trophic group was the invertebrate shredders X(10) (-0.4, -0.4%), as illustrated in Figures II.3a,b.

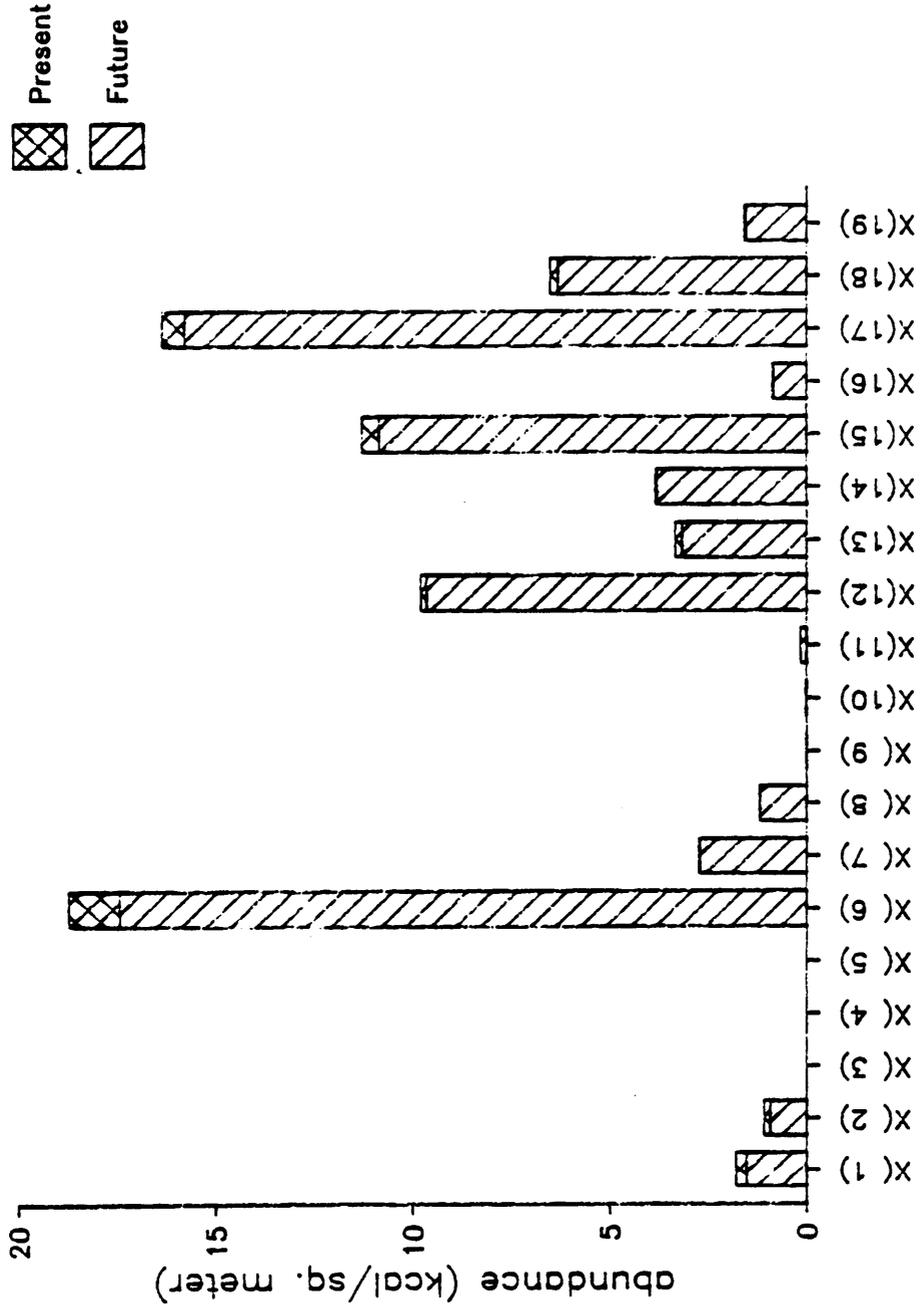
If the trophic groups are aggregated into general classes and averaged at each site, the general trend of predicted declines is as follows: primary producers, (-15.3,-18.1%), followed by crayfish (-5.1,-5.8%) or zooplankton (-6.9,-3.0%), fish (-3.1,-4.0%), molluscs (-1.6,-1.8%), insect invertebrates (-1.0,-0.8%), and lastly the organic matter groups (-0.4,-0.4%). Scraper grazer declines (15.3, 18.1%) were not included in the insect invertebrates class above, since this group is essentially represented by snails and these declines would greatly bias the class averages.

Within some of these general classes are additional trends. Among the insect class the order of declines, greatest to least, is: collector filterers X(8)

Table II.18. Percentage declines in standing stock of trophic groups for each traffic scenario¹.

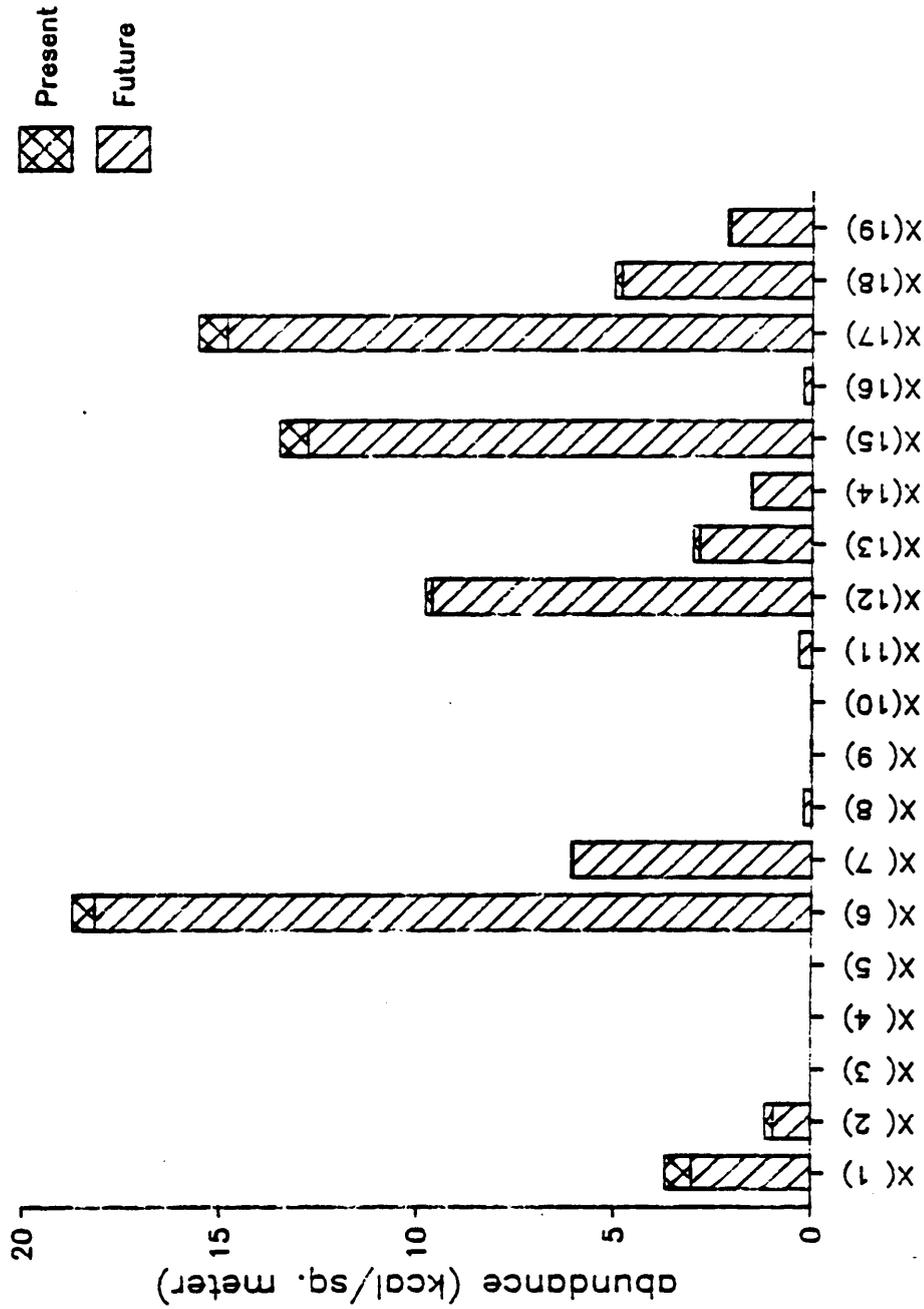
Trophic Group	Name	Tow Traffic Scenarios					
		S2		S3		S4	
		UW	LW	UW	LW	UW	LW
X(1)	Phytoplankton	4.9	6.9	5.6	9.7	15.3	18.1
X(2)	Periphyton	4.9	6.9	5.6	9.7	15.3	18.1
X(3)	SPOM	0.1	0.2	0.1	0.2	0.4	0.4
X(4)	CPOM	0.1	0.2	0.1	0.2	0.4	0.4
X(5)	FPOM	0.2	0.2	0.2	0.3	0.5	0.5
X(6)	Zooplankton	2.2	1.2	2.5	1.6	6.9	3.0
X(7)	Coll/Gatherers	0.3	0.3	0.4	0.4	1.0	0.8
X(8)	Coll/Filterers	0.5	0.7	0.6	1.0	1.5	1.8
X(9)	Scraper Grazers	4.9	6.9	5.6	9.7	15.3	18.1
X(10)	Invt Shredders	0.1	0.2	0.1	0.2	0.4	0.4
X(11)	Invt Predators	0.4	0.1	0.4	0.2	1.1	0.3
X(12)	Molluscs	0.5	0.7	0.6	1.0	1.6	1.8
X(13)	Crayfish	1.6	2.2	1.9	3.1	5.1	5.8
X(14)	B. Invertivores	0.4	0.8	0.5	1.1	1.2	2.0
X(15)	Omnivores	1.3	2.1	1.4	2.9	4.0	5.4
X(16)	Cray/Piscivores	1.2	1.7	1.4	2.4	3.8	4.5
X(17)	Herb/Detritivores	1.1	1.8	1.3	2.5	3.4	4.7
X(18)	M. Invertivores	1.0	1.4	1.2	2.0	3.2	3.7
X(19)	Piscivores	0.9	1.4	1.1	2.0	3.0	3.8

¹ 0.0% change in standing stocks for baseline scenario (S1)



UW Trophic Groups

Figure II.3a. Pre- and post- simulation abundance of K.R.E.A.M. components at UW.



LW Trophic Groups

Figure II.3b. Pre- and post- simulation abundance of K.R.E.A.M. components at LW.

(-1.5,-1.8%), followed by collector gatherers X(7) (-1.0,-0.8%), invertebrate predators X(11) (-1.1,-0.3%), and invertebrate shredders X(10) (-0.4,-0.4%). In the fish class the greatest declines were predicted for omnivores X(15) (-4.0,-5.4%), followed closely by cray/piscivores X(16) (-3.8,-4.5%) or herbivore detritivores X(17) (-3.4,-4.7%), midwater invertivores X(18) (-3.2,-3.7%) or piscivores X(19) (-3.0,-3.8%), and finally the benthic invertivores X(14) (-1.2,-2.0%).

Comparing the two reaches, it appears that declines in standing stock within the general classes of trophic groups are more often greater at LW. Exceptions to the above trend include zooplankton and invertebrate insects (greater declines at UW) and organic matter (no difference between sites). Collector filterers X(8) are the only insect group to decline more at LW than at UW, while fish groups X(14-19) consistently experience greater declines at LW.

DISCUSSION

In the course of model building, decisions regarding what is to be included or omitted from the model are made which greatly influence model predictions. This section of the discussion is provided to centralize these considerations of scope and to identify and evaluate limitations or perceived shortcomings of the model.

Although models provide a useful framework for organizing information concerning a system, they never include all the aspects of the complex problem they were called upon to solve. In this instance the complex problem requiring a solution concerned the biota of a large river previously developed for navigation. The problem statement becomes: what will happen to the complex biological community of the river given an additional traffic load? It was recognized (after Karr and Dudley, 1981) that there are four general categories of environmental variables that affect ecological integrity. In addition to energy sources and fates, water flow regime, habitat structure, and water quality may all be influenced by navigation. In the case of the Kanawha River however, it appears that Karr and Dudley's (1981) latter three categories are most directly influenced by other factors (e.g. impoundment to form the navigation

pools, or by proximity to the Charleston municipal and industrial complex), and not by tow traffic.

The major impacts caused by barge traffic were identified by the Academy of Natural Sciences of Philadelphia (1980) as 1) sediment resuspension and resultant decreased primary production, 2) altered insect abundance and distribution, and 3) direct mortality of larval fish in the sailing line. The energy flow modeling approach was designed to evaluate only the indirect effects of additional tow traffic, principally decreased primary production.

Since the energy flow methodology used does not accommodate all concerns of increased traffic, a review of specific limitations is in order. In its present form, the model does not address direct impacts on zooplankton, benthos, or larval and/or adult fish. These were not ignored but were omitted from the model when the results of specific investigations in these areas did not reveal any significant direct impacts (VPI&SU, 1985). The model does not presently evaluate changes in sight-feeding or recruitment success, although these are not so much mathematical limitations as they are difficult-to-fill gaps in our biological knowledge. The model is not capable of integrating the effects of toxic spills or the impacts of ancillary economic growth. It does

not evaluate every possible area of concern related to increased tow traffic. Provided that its limitations are clearly understood, it is a powerful and flexible tool for assessing certain aspects of the study problem.

Having discussed why this overall approach was taken, we may now consider more specific limitations. The equations of the model used simple linear donor control. Other more complex and realistic formulations are available yet linear donor control is sufficient for estimating system-level impacts (Patten 1975) and provides a stable, well behaved model. Linear donor control incorporates the advantage of generality. More complex equations greatly increase the number of parameters requiring estimation, and are well beyond what present databases for large rivers can support.

Another shortcoming of the model is its use of annual average flows of energy as constants in simulations. Ideally, energy flows throughout the model would be seasonal in nature. The model program includes mechanisms to accomodate time and temperature dependence but only a small portion of the data needed to run the model were available in sufficient detail to utilize these features. Unless all flows can be simulated seasonally nothing is gained from the exercise.

Some concerns might be raised regarding the aggregation of species or the absence of certain groups. Aggregation is not a matter of choice but rather a necessity for doing system level studies. It is neither possible nor desirable (Warren 1971) to explicitly represent individual species. What is lost in aggregating species in order to do whole ecosystem studies is hopefully compensated for by the holistic potential which is gained. One aggregation problem in the model is the lack of size classes in the S.P.O.M. group, X(3). This was not due to any lack of data on what sizes of S.P.O.M. are present (VPI&SU 1985) but rather the uncertainty about precisely what sizes of seston are utilized by each of the various consumer groups.

It should be made clear that larval fish were intentionally omitted from the model. Larval fish would have been included had there been evidence that tow passage was significantly affecting recruitment, although considerable study would be needed to estimate production and mortality rates.

One may be concerned by the approach used to reconcile production/consumption discrepancies, for example the consumption of some benthic invertebrate groups (especially filterers and shredders), midwater invertivores, and

periphyton by fish groups. In those cases where "Allen's paradox" (Allen 1951, Morgan et al. 1980, Benke 1984) was encountered in this study, the original lower trophic level estimate was assumed to be an underestimate and was expanded to satisfy the demand. In all cases the fish groups exerted more predatory pressure than could be supported by the lower trophic level. It appears justifiable to expand energy flows involving the lower level groups because fish abundance and production estimates were well within reported values from other rivers. The discrepancy involving benthic invertebrates might also be related to the lack of sampling in snag habitats, although these are not especially abundant in the Kanawha. An additional factor to consider is the uncertainty with which artificial substrates reflect benthic production. One final difficulty was to estimate the degree to which fish consumed invertebrates from the drift versus the substrate. The rate with which benthos drifts through the pool (an unknown) might easily explain the discrepancy. Rapid colonization of artificial substrates which was observed (VPI&SU 1985) suggesting this rate may be substantial.

In the discrepancy involving periphyton, the original production estimate was derived using average annual photic depth and the areal extent of the river bed suitable for

periphyton colonization. This estimate did not take irregular surfaces or snag substrates into account and so as a first approximation was known to be low.

The last production/consumption discrepancy involved consumption of forage fish. Because only adult fish and not larvae or young of the year were included in the model there was not sufficient production to support the combined consumptive demands of piscivorous groups. It became necessary to artificially inflate abundance, production, and consumption by midwater invertivores (the primary forage fish in the model) to meet this demand. Undoubtedly larvae and juvenile fish supplied much of the difference between total consumptive demand for and supply of "forage fish", since the majority of total fish population production occurs in these age classes. Larval fish were not found in significant numbers in fish stomachs but this may be due to rapid digestion. In addition, the monthly sampling interval may have overlooked short but intense periods during which larval fish were consumed in large quantities.

A conservative feature of the model is the nature of the interruption to photosynthesis. The model assumes that no photosynthesis occurs for a period approximately twice the length of time Hochstein and Adams (1985) predicted for

materials suspended by tow passage to settle out. Furthermore, the zone of the river channel which experiences temporary pulses of increased turbidity has been estimated as about a third of the total river's width (Hochstein and Adams 1985), while the model assumes complete cessation of primary production throughout the entire reach. In essence all tows passages are considered by the model to be worst case and there is little concern that the potential impact of additional tow traffic on energy flow in the ecosystem via primary production has been underestimated.

Navigation Impact Assessment

Given that the ecosystem is dependent mainly on detrital energy sources, one would expect minimal impacts on energy flow to the higher trophic levels from the projected increases in navigation use. This expectation was confirmed by each of the tow traffic simulations performed using the model. Since the various simulations differed only in the frequency of tow passage, the following comments pertain to the results of the worst case traffic scenario in which both Winfield and Marmet locks are upgraded. Other traffic levels tested (future without-project conditions, and replacement of Winfield only) demonstrated intermediate

results between baseline (1982-83) and the worst case simulation.

Even under the highest projections of future traffic conditions, the reductions in standing stocks predicted by the model were relatively minor. The greatest reductions in standing stock were, as would be expected, for primary producers (phytoplankton and periphyton). Periodic interruptions of photosynthesis caused by tow passage reduced phytoplankton biomass by 15.28% at UW and 18.06% at LW. Periphyton was predicted to decline by these same amounts since energy flows to both primary producers were assumed to be reduced by the same proportions. The larger reductions predicted for LW were a result of greater tow frequencies simulated over this portion of the pool. The direct effects of tow traffic on primary producers, while in and of themselves appreciable, were predicted to cause only slight declines in biomass for other trophic groups of the ecosystem. These indirect effects will be discussed for three categories of trophic groups: invertebrates, vertebrates, and organic matter groups.

The greatest reductions in biomass among invertebrates were for zooplankton (UW 6.92%, LW 3.04%), collector filterers (UW 1.52%, LW 1.81%), scraper grazers (UW 15.28%,

LW 18.06%), molluscs (UW 1.63%, LW 1.78%), and crayfish (UW 5.13%, LW 5.75%). Larger reductions were expected for these groups since their diets include direct consumption of primary producer organisms. Other food sources (especially S.P.O.M.) are both available and utilized however, and these continued to support the above-mentioned groups at near baseline levels. Other invertebrate groups, for example the collector gatherers, shredders, and invertebrate predators, did not depend on autochthonous food sources to as large an extent, and consequently did not experience appreciable declines in standing stock under the heaviest traffic conditions.

Similar results were predicted by the model for the vertebrate groups, namely that those organisms most directly dependent on autochthonous sources of energy were the most affected. All fish trophic groups remained within six-percent of baseline abundances. Omnivores and herbivore/detritivores were predicted to decline by the greatest amounts due to higher utilization of periphyton by these fish groups.

Suspended particulate, benthic coarse, and benthic fine organic matter all declined by quite small amounts (< 0.52%). Since only a small fraction of the total available

organic matter transported downstream is captured and utilized to begin with, these reductions are inconsequential with respect to ecosystem functioning. Overall then, trophic groups which directly depend on phytoplankton and/or periphyton were predicted to decline by fairly small amounts, while the majority of the trophic groups experienced even lower declines. Such minor impacts were expected in an ecosystem which functions almost entirely on allochthonous sources of energy which are transported from upstream reaches. As a detritus-based system then, the Kanawha River is relatively insensitive to the small reductions in the rates of primary production by photosynthesizers caused by the maximum increment of tow passage frequencies.

Independent of tow traffic impact assessment, however, it should be noted that larger reductions in primary production (from whatever cause) could have greater negative effects on the system. It is important at this point to clearly distinguish between the periodic and temporary interruptions of photosynthesis caused by traffic on the river and the complete absence of photosynthesis in the system. Should the physical conditions of the pool continuously and severely reduce photosynthesis, a different set of conclusions would be reached.

In considering the effects of this more radical (and theoretical) impact, we must distinguish between phytoplankton and periphyton, since the latter is sessile, while the former is part of the continuously replaced seston. Assuming that the condition which impaired primary production was limited to the pool itself, some amount of phytoplankton would continue to be transported from upstream reaches and this would remain available for organisms to consume. However, periphyton would be eliminated and would not be able to recolonize if the physical environment allowed no photosynthesis to occur.

The model assumes that the only difference between the quantity of phytoplankton entering and leaving any segment of the pool is caused by production, consumption, or non-consumptive mortality. Constant replenishment of phytoplankton from the upstream reaches is not included explicitly as an energy source in the model, although constant downstream removal from each segment is explicitly modeled. In this sense the model's predictions are quite conservative since heterotrophs in the modeled ecosystem only benefit from in situ primary production and not from import.

Replenishment via transport is not a feature of the periphyton, however. Larger reductions in periphyton production rates would have a more serious effect on consumers than the same reductions in phytoplankton productivity. It is especially important to consider here that of the two primary producers, the higher level trophic groups depend more critically on periphyton for support. Thus protection and/or enhancement of healthy periphyton communities would appear to be more beneficial to the system as a whole than maintaining existing phytoplankton production. Other than increased turbidity reducing primary production, tows could potentially impact the periphyton via scouring, although this was not observed. Excepting scraper grazers, dependence on periphyton production was estimated as high as 30.4% (by crayfish). Omnivores X(15), crayfish/piscivores X(16), and piscivores X(19) directly or indirectly rely on periphyton for (23.9, 29.9%), (24.3, 27.0%), and (18.0, 20.3%) of the energy which reaches them at UW and LW, respectively. These are precisely the percentages of fish biomass which the model would predict would be lost in the complete absence of periphyton production.

Ecosystem Structure and Function

The following section focuses attention on the character of energy flows which are internal to the ecosystem and seeks to identify from this the structure and function of the Kanawha River ecosystem. A later section will emphasize the fates of, and reliance upon, the major energy sources entering the system from outside.

The major energy flow pathways internal to the ecosystem were determined by comparing the magnitude of total energy flows through each of the trophic groups (Table II.8, Figure II.4) and then observing the relationships between these flow-dominant groups. Flow dominance by a trophic group is a measure of importance or success in the ecosystem, since the function of the system is energy processing. The most significant flows within each class of trophic groups are all clearly related to detritus, either as suspended or benthic materials. The fluxes through SPOM are the largest flows in the entire system, suggesting that much of the biological activity revolves around allochthonous materials originating from upstream areas. These findings support the second hypothesis that the ecosystem is heterotrophic with most of the energy provided from particulate organic matter, as predicted in the river continuum concept (Vannote et al. 1980).

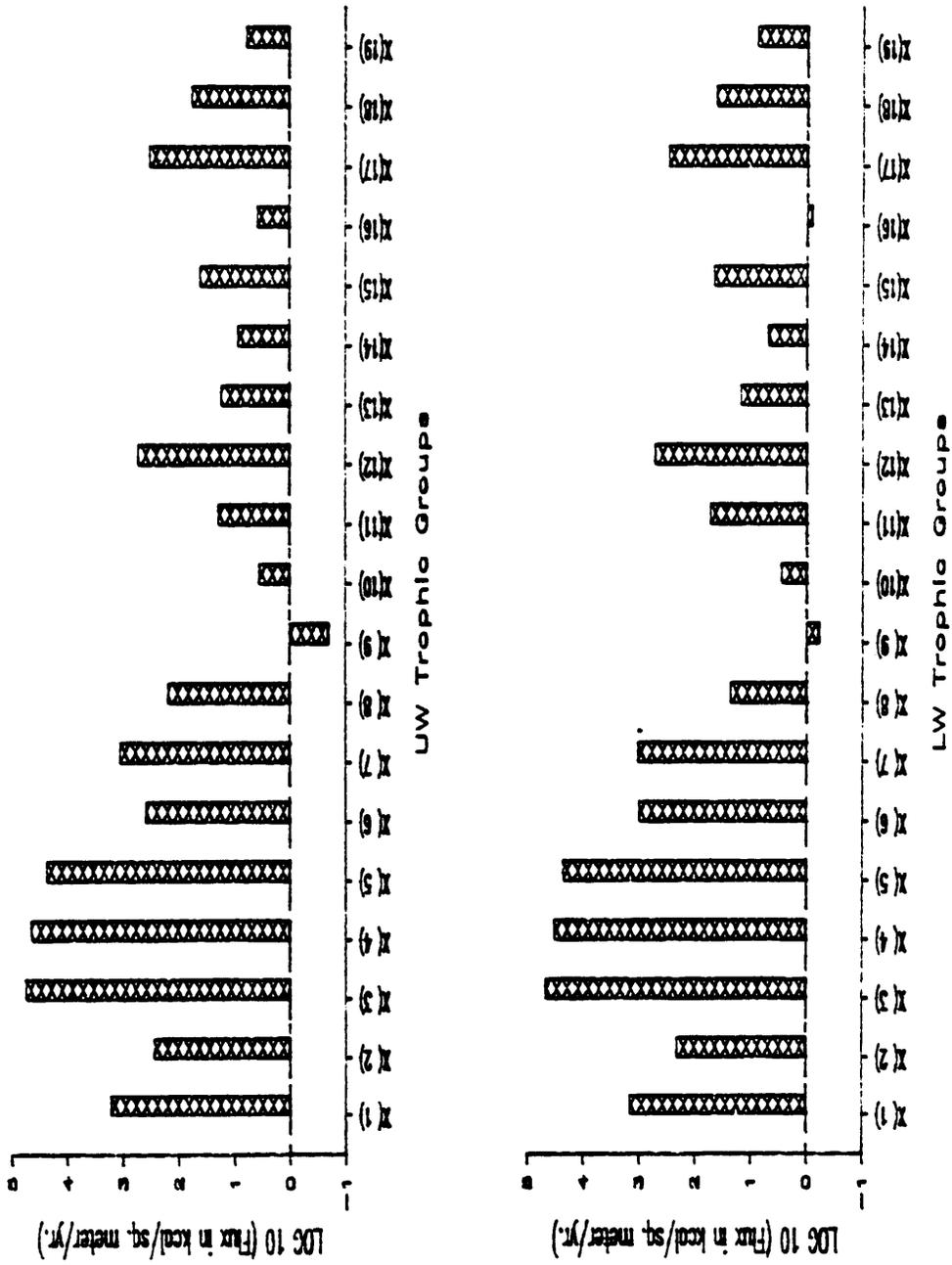


Figure II.4. Annual energy fluxes through K.R.E.A.M. components.

Zooplankton, in a class by themselves, rely more on S.P.O.M. than on phytoplankton, especially at LW. While this group processes relatively large amounts of energy, they are not significantly relied upon as a source of energy for any other trophic group in the model. One explanation for this paradox is that the average turbidity of the Kanawha in combination with the small size of the zooplankton might reduce the efficiency of foraging on this group relative to other available food types. Gardner (1981) showed that bluegill reduced their feeding rates on zooplankton as turbidity increased in the lab. Vinyard and O'Brien (1976) demonstrated that the reactive distances of bluegill to Daphnia were reduced by turbidity. These and other studies suggest that turbidity will reduce the utilization of zooplankton if visual senses are impaired. This may explain the lack of appreciable planktivory among fish groups in the Kanawha.

Among the insects, the dominance of collector gatherers as processors of energy is apparent. Collector gatherers consistently mediate more energy flow to invertebrate insect predators, crayfish, and the fish groups than other insects. Collector filterers make a significant contribution as a channel of energy flow, especially at UW where solid

substrate and water currents are less limiting. These findings provide support for part of our second hypothesis that collectors would dominate the macroinvertebrate assemblage. Invertebrate shredders play only a minor role in the Winfield Pool ecosystem. Unlike a headwater system in which coarse terrestrial plant litter provides the major sources of energy (Fisher and Likens 1973), the pattern observed among the invertebrate groups in the Kanawha suggests that organic materials, which have already undergone appreciable processing (Cummins 1977), constitute the main energy source.

The ready availability of preprocessed organic material would explain the relatively large role of filtering molluscs (another collector), as well as the great success of the herbivore/detritivore fish, both of which subsist largely on fine particulates. The omnivores, the second most abundant group in the fish class, successfully function as trophic generalists which utilize detritus. The more specialized feeders which do not directly consume detritus (e.g. benthic invertivorous, crayfish/piscivores, midwater invertivores, and piscivores) were not nearly as abundant. Midwater invertivores, the third most abundant fish group overall, consume prey items which themselves have detritus (particularly S.P.O.M.) as their primary source of energy.

The relative abundance of the various groups was quantitatively explained by the second energy flow analysis. The most abundant (i.e. successful) groups show a decided dependence on organic matter. The N * matrix (Tables II.16 and II.17) provided a measure of the degree to which a trophic group depends on other trophic groups for energy flow. The highest values in any row are consistently found in the third through fifth columns, indicating that of all sources of energy flow, organic matter groups provide the greatest percentage of recipient group throughflow. In arriving at the final percentage dependence figure, the analysis integrated all avenues (direct as well as indirect) of energy flow to each trophic group. Thus even groups which do not consume detrital matter directly ultimately depend on it. For example 77.4% of flow through the crayfish/piscivore component once passed through the S.P.O.M. component. Crayfish/piscivores directly consume no detritus at all yet the invertebrates, crayfish, and other fish in their diet consume a fairly large proportion of detritus. The higher trophic level is indirectly supported by detritus in this case.

Another general observation is that for any donor group, a large percentage of the energy processed is ultimately destined to support one of the particulate

organic matter groups X(3-5) rather than living matter (Tables II.14,15). This means that nonliving organic matter, and not production, is the fate of most of the energy captured and retained by the ecosystem.

Comparison of Major Energy Sources

In this section we narrow our interest to only the major sources of energy flow into the system: phytoplankton, periphyton, and S.P.O.M. (X(1), X(2), and X(3), respectively). We wish to determine which trophic groups/levels in the ecosystem are most effectively supported by, and which are most critically dependent on, each source. Taking the first perspective, we establish the extent to which throughflow in X(1), X(2), and X(3) reaches the remaining trophic groups or levels in the system. Effectiveness is taken here to mean how well these throughflows are conserved as they pass through the system.

At both sites, energy flow entering via phytoplankton X(1) supports zooplankton X(6), invertebrate collector-filterers X(8), and molluscs X(12) more effectively than flow from either periphyton X(2) or S.P.O.M. X(3). At UW, collector-gatherers X(7) are also more effectively supported by phytoplankton than by either of the other sources (Tables

II.14,15). Except for X(7), these recipients all function by straining or sorting through the water column for food, and would generally be considered as belonging to the middle trophic levels.

Energy entering as S.P.O.M. X(3) is more effectively passed to S.P.O.M. itself, (via settling and subsequent resuspension), C.P.O.M. X(4) (via settling), and invertebrate shredders X(10) than energy entering through either of the primary producers (Tables II.14,15). These recipient groups are at or are near the base of the food web for the Kanawha River ecosystem.

Energy more effectively reaches scraper-grazers X(9), crayfish X(13) and virtually all of the fish groups X(14-19) from periphyton X(2) than from the other two major entry points at both sites. In addition throughflow in periphyton is more effectively channeled than that in phytoplankton or S.P.O.M. to F.P.O.M. X(5) at LW (Tables II.14,15). Both in terms of number and position in the ecosystem, then, it appears that energy entering via periphyton supports the highest trophic levels more effectively than either of the other major sources. Energy originating from periphyton is also more effectively passed out of the system as emerging insects or through fish

harvest than energy originating via phytoplankton or S.P.O.M..

It is important to note that such effectiveness does not necessarily equate with gross availability of energy to groups in the ecosystem. Over a year far more energy flows through the system as S.P.O.M. than as either of the primary producer groups: roughly one billion kcal per square meter (approximately 30,000 of which are biologically retained) as compared to 1500 and 250 kcal per square meter through phytoplankton and periphyton, respectively (VPI&SU 1985). Thus while the system may more effectively transfer energy originating as periphyton, even with low transfer effectiveness the larger volume of S.P.O.M. ultimately makes it the more important food source. Comparison of elements in the third column of N ** flow analyses (Tables II.14,15) provides additional confirmation of the importance of S.P.O.M. as an energy source.

Higher N ** values for the donor group X(3) correlate well with the most abundant trophic groups in each class (Tables II.14,15). This demonstrates that those trophic groups which are in a position to effectively take advantage of S.P.O.M. are precisely the ones which dominate their respective taxonomic classes. This same relation between

highest N ** values and the more successful trophic groups exists within most columns of the N ** matrices, including columns 1 and 2. This confirms the more general hypothesis that the ecosystem is more suitable (from an effectiveness standpoint) for supporting certain groups, and as a natural consequence these groups are successful.

Taking the second perspective, we wish to know how each trophic group or level is dependent on energy flows from the three major entry points. If, by way of simplification, we combine all primary producers and all organic matter groups, then Figure II.5 illustrates the balance of allochthonous and autochthonous sources of energy for the most abundant trophic groups in the river ecosystem. Energy flows between boxes are in units of kcal/m²/year, and the numbers in the lower right and left corners of each box are the biomass (kcal/m²) and total throughflow (kcal/m²/year), respectively. Energy budgets consistently demonstrate greatest dependence on detritus. The results of the flow analyses (Tables II.16,17) quantitatively show that the Kanawha River ecosystem is supported primarily on allochthonous sources of energy, particularly S.P.O.M.. Energy exiting the ecosystem through sixteen of the nineteen trophic groups originates predominantly in the form of S.P.O.M.. In approximately half of these cases, the element

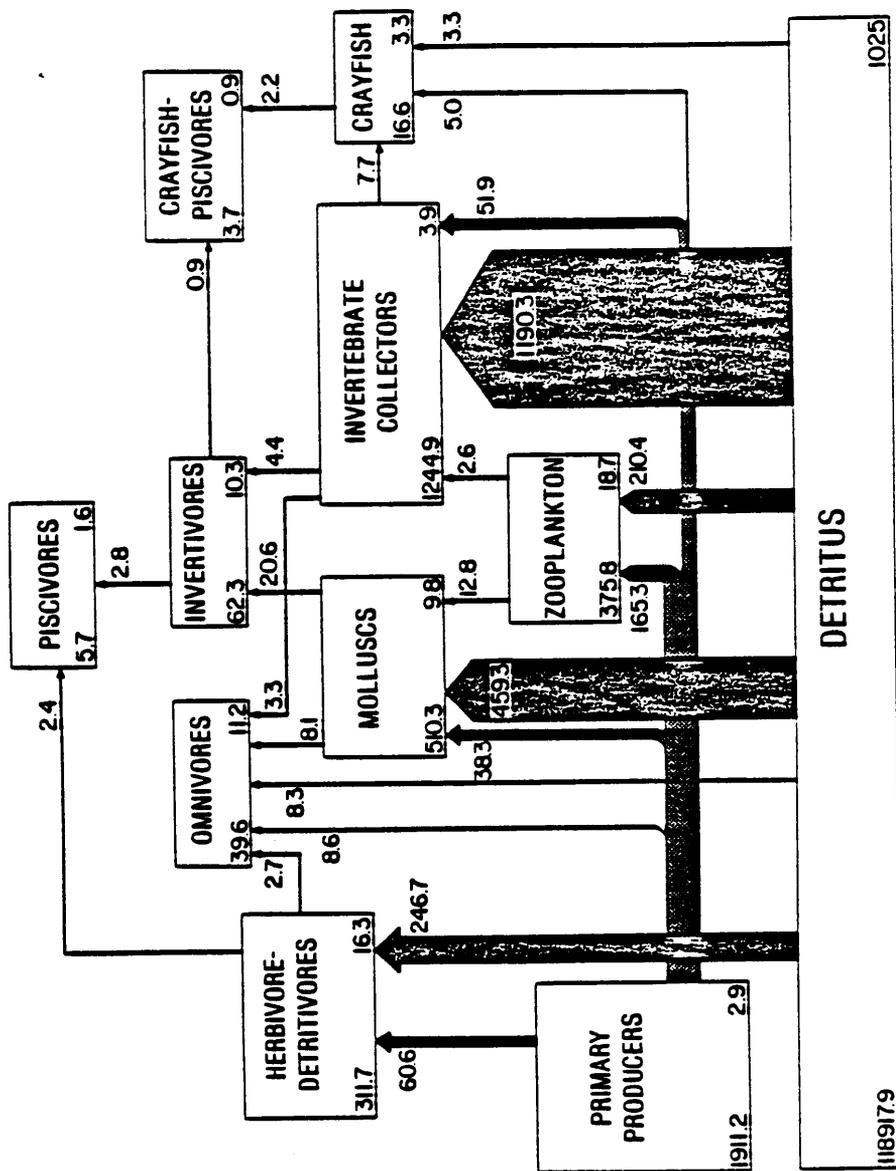


FIGURE II.5 Diagram of major trophic energy flows in the Winfield Pool ecosystem.

of the matrix exceeds unity, indicating that the energy on which these groups depend has cycled through the suspended matter class at least one time. In contrast, dependence upon primary producers is substantially less. Most trophic groups (exception zooplankton) rely on phytoplankton for less than ten percent of the energy flowing reaching them. Dependence on energy flow which originated through periphyton is greater (up to 30.4%), but still not of the same magnitude as dependence on organic matter sources. Phytoplankton, periphyton, and the invertebrate scraper grazers (with token representation) are the only trophic groups which depend more on autochthonous than allochthonous energy sources. All other groups and, consequently, all but the first trophic level of the ecosystem consistently depend more upon whatever S.P.O.M. or other organic matter can be retained and/or generated than on the other (autotrophic) sources.

One notes that different trophic levels exhibit differential dependence upon the two groups of primary producers. Insects rely more on phytoplankton-based energy sources than periphyton-based sources. In contrast, all of the fish trophic groups show a greater dependence on energy channeled through periphyton than through phytoplankton.

Variations in the expected feeding habits and abundances of certain groups indirectly suggest how little autotrophy contributes to this ecosystem. It is illuminating to note that a fish species such as the gizzard shad, which is physiologically adapted to utilize phytoplankton (Hendricks and Noble 1979, Pierce et al. 1981), opts instead to concentrate feeding on benthic deposits of organic matter in the Kanawha. Part of our second hypothesis suggested that planktivory would be observed as a feeding mode among fishes. There was very little evidence of such feeding. Gizzard shad did consume small quantities of zooplankton (probably limited more by turbidity than low availability; see above), but relied much more on benthic sources such as F.P.O.M.. Scraper grazer organisms, which are obligatory consumers of periphyton, were the least common of the benthic macroinvertebrates collected. It is doubtful that physical/chemical conditions in the river exclude or limit scraper grazers, since even some water quality-sensitive plecoptera were present in the river. Perhaps most stable substrates which could be colonized by periphyton are below the shallow photic zone. At present the structure and function of the ecosystem (i.e. its distribution of biomass and biological activity) is configured to process allochthonous sources of energy.

Comparisons with Other Large Rivers

The collection of detailed data on sources and fates of energy and productivity at all trophic levels in large rivers has limited progress in modeling. In fact, the advances in theoretical formulations and technical computing methods for river models have underscored the inadequacies in our data bases on large rivers. The studies by Mann (1964, 1965) and Mann et al. (1972) are the only published reports on productivity and patterns of energy flow at all trophic levels in a large river. These studies were done on the River Thames near Reading, England. In several ways the Thames and the Kanawha Rivers are similar: both are low gradient rivers, both are modified with locks and low dams, both are subject to considerable sewage enrichment, and consequently both support relatively rich phytoplankton populations.

Several conclusions from Mann et al. (1972) are in agreement with our findings. (1.) The two most abundant fish species, roach and bleak, rely heavily on benthic detritus. In their first year of life, these fish rely heavily on zooplankton (rotifers and cladocerans) and chironomid larvae, while older roach and bleak rely on organic detritus, terrestrial insects taken at the surface,

and algae. The common adult fish species of the Kanawha River demonstrated a similar dependence on detrital energy sources, terrestrial insects, and periphyton. (2.) Substantial periphyton production ($155 \text{ kcal/m}^2/\text{yr}$) occurred at depths up to 1 m, beyond which light was severely limiting. Periphyton production in the Kanawha River (271.2 and $208.0 \text{ kcal/m}^2/\text{yr}$) was somewhat higher, probably reflecting a slightly deeper photic depth for the Kanawha and/or a more southerly latitude with an associated longer growing season. (3.) Production of all benthic animals was 144.5 and $137.0 \text{ kcal/m}^2/\text{year}$ in the Thames above and below the confluence with the River Kennet, and 128.2 , $98.8 \text{ kcal/m}^2/\text{yr}$ for UW and LW, respectively. The slightly higher values for the Thames may be a result of greater sewage enrichment. In both rivers collectors dominated the benthos. (4.) Thames fish production was $198 \text{ kcal/m}^2/\text{year}$, of which roach and bleak accounted for $137 \text{ kcal/m}^2/\text{year}$ (70%). Adult fish production in the Kanawha averaged about $25 \text{ kcal/m}^2/\text{yr}$, with herbivore/detritivores and omnivores contributing approximately 80% to this total. The percentage of total production attributable to detritivorous fish are similar in each river. (5.) Nutrients derived directly from sewage effluents supported a very rich phytoplankton production ($1,907\text{--}4,388 \text{ kcal/m}^2/\text{year}$) in the Thames. Kanawha River

phytoplankton production was consistently lower, averaging 1640.0 and 1438.0 kcal/m²/yr. Perhaps a longer retention time in the navigation pools of the Thames during the growing season contributed to the higher primary productivity. (7.) Both lotic systems, as a whole, were heterotrophic. Thus many of the trends in our Kanawha River results are confirmed by earlier observations made by Mann (1964, 1965) and Mann et al. (1972) for the River Thames.

Management Implications

From a resource management perspective, the energy pathways leading to harvestable and/or gamefish groups (omnivores, crayfish/piscivores, and piscivores) take on special interest. Omnivores (for example, channel catfish) are directly dependent on periphyton, molluscs, C.P.O.M., herbivore/detritivores, and terrestrial insects for 76.5 and 80.1% of energy consumed at UW and LW, respectively. Omnivores depend mainly on periphyton and molluscs at UW, and on periphyton and herbivore/detritivores at LW. Crayfish, omnivorous fish, and midwater invertivores support 92.3 (UW) and 96.1% (LW) of the energy flow to the crayfish/piscivore group, which includes the spotted, smallmouth, and largemouth basses. Crayfish mediate the

most important energy pathway to these popular sportfish. Herbivore/detritivores (e.g. gizzard shad) and midwater invertivores (e.g. various shiners) supply 85.6 and 86.8% of the energy flow directly supporting the piscivore group (including walleye, sauger, and white bass) at UW and LW, respectively.

The estimated total harvest of fish from UW and LW (18.5, 19.8 kg/ha/yr) appears to be reasonable although there are few other reported estimates from large rivers with which to compare our results. These harvest estimates agree with the average harvest from U.S. reservoirs (Jenkins 1982). Total fish harvest estimates from smaller river and stream fisheries (where smallmouth bass were one of the most frequently caught species) have ranged from 6.6 to 40.2 kg/ha/yr (Austen 1984 cites Sanderson 1959, Turner 1967, Wollitz 1968, Fleener 1971, 1972, and 1975, Fleener et al. 1974, and Funk and Fleener 1974).

All fish groups and, consequently, all food and gamefish in the Kanawha River depend more upon whatever S.P.O.M. can be retained and/or generated by the ecosystem than on the other (autotrophic) sources. This suggests that to enhance energy flow to species of interest to sportsmen, the most effective management approach would be to increase

the system's ability to utilize S.P.O.M., perhaps by providing solid substrates for collector filterer insect colonization in areas exposed to current. Note that benthic macroinvertebrates at present do not directly provide critical support to any of the harvestable fish groups, perhaps because their overall availability is limited by suitable habitat. However, enhancement of invertebrate insect habitat through addition of rubble or snags might increase insect availability and some increase in gamefish utilization would likely result. Benke et al.(1985) showed that 78% of the drifting invertebrate biomass in the Satilla River originated from snag habitat, the primary hard substrate available. Addition of hard substrates may serve gamefish primarily as habitat and only secondarily through direct or indirect increases in food availability. Another benefit of additional solid substrates in the photic zone would be an increase in habitat for periphyton colonization.

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Table A.1. Historical record of the fish species (number of subspecies in parenthesis) in the Kanawa River

	Addair		Jenkins		ORSANCO		West Virginia		VPI
	Mainstem ¹	Minfield ²	Drainage basin	Minfield ³	London ³	Minfield ³	London ³	London ³	65 ⁴
Petromyzontidae									
<i>Ichthyomyzon bellium</i> , Ohio lamprey			X				X		X
<i>Lampetra septentr.</i> , Least brook lamprey			X						X
Polyodontidae									
<i>Polyodon spathula</i> , Paddle fish			X						
Lepisosteidae									
<i>Lepisosteus osseus</i> , Longnose gar	X		X		X		X		X
Anguillidae									
<i>Anguilla rostrata</i> , American eel	X		X		X				
Clupeidae									
<i>Alosa chrysochloris</i> , Skipjack herring			X		X		X		X
<i>Alosa pseudoharengus</i> , Alewife					X				
<i>Dorosoma cepedianum</i> , Gizzard shad			X		X		X		X
<i>Dorosoma petenense</i> , Threadfin shad			X		X				
Salmonidae									
<i>Salmo gairdneri</i> , Rainbow trout			X						
<i>Salmo trutta</i> , Brown trout			X						
<i>Salvelinus fontinalis</i> , Brook trout			X						
Esocidae									
<i>Esox masquinongy</i> , Muskellunge			X			X			X
<i>Esox niger</i> , Chain pickerel			X						

	Ackair		Jankins		ORSAHCO		Hasi Virginia		VPL	
	Mainstem ¹	Minfield ²	Drainage basin	Minfield ³	London ³	Minfield ³	London ³	Minfield ³	London ³	
Cyprinidae										
<i>Composita anomalum</i> (2), Stoneroller	X	X	X					X		X
<i>Carassius auratus</i> , Goldfish		X	X			X		X		X
<i>Cyprinus carpio</i> , Carp	X	X	X							
<i>Ericymba buccata</i> , Silverjaw minnow	X	X	X			X		X		X
<i>Hybopsis aestivialis</i> , Speckled chub	X		X			X		X		X
<i>Hybopsis amblope</i> , Bigeye chub	X	X	X			X		X		X
<i>Hybopsis dissimilis</i> , Streamline chub			X			X				X
<i>Hybopsis storeriana</i> , Silver chub			X			X				X
<i>Nocomis micropogon</i> , River chub			X			X				X
<i>Notemigonus crysoleucas</i> , Golden shiner			X			X				X
<i>Notropis anogenus</i> , Comely shiner			X			X				X
<i>Notropis atherinoides</i> , Emerald shiner	X	X	X			X		X		X
<i>Notropis bienni</i> , River shiner			X			X		X		X
<i>Notropis boops</i> , Bigeye shiner			X			X		X		X
<i>Notropis buchanani</i> , Ghost shiner			X			X		X		X
<i>Notropis chrysocephalus</i> , Striped shiner	X	X	X			X		X		X
<i>Notropis cornutus</i> , Common shiner			X			X		X		X
<i>Notropis hudsonius</i> , Spottail shiner			X			X		X		X
<i>Notropis photogenis</i> , Silver shiner			X			X		X		X
<i>Notropis rubellus</i> , Rosyface shiner	X	X	X			X		X		X
<i>Notropis spilopterus</i> , Spotfin shiner	X	X	X			X		X		X

	Addair		Jenkins		ORSAWCO		East Virginia	
	Mainstem ¹	Minfield ²	Drainage basin	Minfield ³	London ³	Minfield ³	London ³	VPI
<i>Notropis stramineus</i> , Sand shiner	X	X	X	X	X	X	X	X
<i>Notropis telescopus</i> , Telescope shiner							X	X
<i>Notropis umbratilis</i> , Redfin shiner			X					
<i>Notropis volucellus</i> (2), Mimic shiner	X	X	X	X	X	X	X	X
<i>Notropis whipplei</i> , Steelcolor shiner	X	X	X					X
<i>Phenacobius mirabilis</i> , Suckersouth minnow			X					
<i>Phoxinotus erythrogaster</i> , Southern redbelly dace	X		X			X	X	X
<i>Pimephales notatus</i> , Bluntnose minnow	X		X					
<i>Pimephales promelas</i> , Fathead minnow			X					
<i>Pimephales vigilax</i> , Bullhead minnow	X	X	X			X		X
<i>Rhinichthys atratulus</i> , Blacknose dace			X					
<i>Rhinichthys cataractae</i> , Longnose dace			X					
<i>Semotilus atromaculatus</i> , Creek chub	X	X	X					X
Calostomidae								
<i>Carpionotus carpio</i> , River carpsucker			X					X
<i>Carpionotus cyprinus</i> , Quillback			X			X		X
<i>Carpionotus velifer</i> , Highfin carpsucker			X					X
<i>Calostomus commersoni</i> , White sucker	X	X	X					X
<i>Hypentelium nigricans</i> , Northern hogsucker	X	X	X					X
<i>Ictiobus bubalus</i> , Seallmouth buffalo			X			X	X	X
<i>Ictiobus niger</i> , Black buffalo	X		X			X	X	X
<i>Minytrema melanops</i> , Spotted sucker			X				X	X

	Addair		Jenkins		ORSANCO		East Virginia		YPI
	Mainstem ³	Minfield ²	Drainage basin	Minfield ³	London ³	Minfield ³	London ³	Minfield ³	London ³
<i>Hoxostoma anisurum</i> , Silver redhorse			X			X		X	X
<i>Hoxostoma carinatum</i> , River redhorse			X			X		X	X
<i>Hoxostoma duquesnai</i> , Black redhorse			X						X
<i>Hoxostoma erythrum</i> , Golden redhorse	X		X			X		X	X
<i>Hoxostoma macrolepidotum</i> , Shorthead redhorse	X		X			X		X	X
Ictaluridae									
<i>Ictalurus furcatus</i> , Blue catfish			X						X
<i>Ictalurus melas</i> , Black bullhead			X			X			X
<i>Ictalurus natalis</i> , Yellow bullhead			X			X			X
<i>Ictalurus nebulosus</i> , Brown bullhead			X			X			X
<i>Ictalurus punctatus</i> , Channel catfish	X		X			X	X	X	X
<i>Noturus flavus</i> , Stonecat						X			
<i>Noturus gyrinus</i> , Tadpole madtom						X			
<i>Noturus miurus</i> , Brindled madtom			X						
<i>Pygidictis olivaris</i> , Flathead catfish	X		X			X	X	X	X
Percopsidae									
<i>Percopsis omiscomyces</i> , Trout-perch	X		X			X			
Atherinidae									
<i>Labidesthes sicculus</i> , Brook silverside	X		X			X			X
Percichthyidae									
<i>Morone chrysops</i> , White bass						X		X	X
Centrarchidae									
<i>Ambloplites rupestris</i> , Rock bass			X			X	X	X	X

	Addair		Jenkins		ORSANCO		Mess Virginia		YPL
	Mainstem ³	Minfield ²	Drainage basin	Minfield ³	London ³	Minfield ³	London ³		
<i>Lepomis cyanellus</i> , Green sunfish			X			X			X
<i>Lepomis gibbosus</i> , Pumpkinseed			X						X
<i>Lepomis gulosus</i> , Warmouth			X						
<i>Lepomis macrochirus</i> , Bluegill			X			X		X	X
<i>Lepomis megalotis</i> , Longear sunfish		X	X			X		X	X
<i>Lepomis microlophus</i> , Redear sunfish			X						X
<i>Micropterus dolomieu</i> , Smallmouth bass		X	X			X		X	X
<i>Micropterus punctulatus</i> , Spotted bass		X	X			X		X	X
<i>Micropterus salmoides</i> , Largemouth bass		X	X			X		X	X
<i>Pomoxis annularis</i> , White crappie		X	X			X		X	X
<i>Pomoxis nigromaculatus</i> , Black crappie			X			X		X	X
Percidae									
<i>Ammocrypta pellucida</i> , Eastern sand darter		X	X						
<i>Etheostoma blennioides</i> , Greenside darter		X	X						
<i>Etheostoma caeruleum</i> , Rainbow darter		X	X						
<i>Etheostoma caeruleum</i> , Bluebreast darter		X	X						
<i>Etheostoma flabellare</i> , Fantail darter			X						
<i>Etheostoma meculatum</i> , Spotted darter			X						
<i>Etheostoma nigrum</i> , Johnny darter		X	X						
<i>Etheostoma osburni</i> , Finescale saddle darter			X						
<i>Etheostoma tippecanoe</i> , Tippecanoe darter			X						
<i>Etheostoma variatum</i> , Variegated darter			X						
<i>Etheostoma zonale</i> , Banded darter			X						X

	Addair		Jenkins		ORSANCO		Hess Virginia		VPL
	Mainstem ¹	Minfield ²	Drainage basin	Minfield ³	London ³	Minfield ³	London ³	Minfield ³	London ³
<i>Percina caprodes</i> , Logperch	X	X	X	X	X	X	X	X	X
<i>Percina copelandi</i> , Channel darter	X								
<i>Percina evides</i> , Gilt darter			X						
<i>Percina macrocephala</i> , Longhead darter			X						
<i>Percina maculata</i> , Blackside darter			X				X		
<i>Percina oxyrhynchos</i> , Sharpnose darter			X						X
<i>Percina sciera</i> , Dusky darter			X						X
<i>Stizostedion canadense</i> , Sauger			X		X	X	X	X	X
<i>Stizostedion vitreum</i> , Walleye		X	X		X	X	X	X	X
Sciaenidae									
<i>Aplodinotus grunniens</i> , Freshwater drum			X		X	X	X	X	X
Cottidae									
<i>Cottus bairdi</i> , Mottled sculpin			X						X

- 1 Kanawha River mainstem below Kanawha Falls.
- 2 Based on five sampling locations in the Minfield Pool
- 3 One lock sampled at each indicated location.
- 4 Based on eight sampling locations in the Minfield Pool

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