AN EVALUATION OF THE REMOVAL METHOD FOR ESTIMATING BENTHIC POPULATIONS AND DIVERSITY

by

Frank Louis Carle

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Approved:

O. Eugene Maughan

O. E. Maughan, Chairman

E. F. Benfield

E. F. Benfield

R. C. Hoehn

R. C. Hoehn

May, 1976

Blacksburg, Virginia 24061

COLLEGE OF AGRICULTURE AND LIFE SCIENCES

VIRGINIA POLYTECHNIC INSTITUTE AND STATE UNIVERSITY

Blacksburg, Virginia 24061

DIVISION OF FORESTRY AND WILDLIFE RESOURCES (703) 951-5481

DEPARTMENT OF FISHERIES AND WILDLIFE SCIENCES (703) 951-5573

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To the memory of

Eugene W. Surber

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INTRODUCTION

Public concern over increasing amounts and types of agricultural, industrial, and domestic wastes entering aquatic ecosystems has resulted in the enactment of the Water Pollution Control Act (PL84-660) in 1966. This act required each state to establish and enforce water quality criteria. Standards based on these criteria were to enhance the quality of our aquatic resources for their "...use and value for public water supplies, propagation of fish and wildlife, recreational purposes, agricultural, industrial, and other legitimate uses. Numerical values should be stated for quality characteristics where available and applicable. Biological or bioassay parameters may be used where appropriate." (Federal Water Pollution Control Administration 1966).

Pollution assessment in the past has been accomplished primarily by chemical methods rather than biological methods related to community structure. Chemical methods are easily defined and implemented, while considerable variation exists among biological methods (Wilhm 1972). However, chemical methods of pollution evaluation are limited. Disadvantages inherent in the chemical assessment of pollution are: (1) chemical data indicate only conditions at the time and place of sampling, (2) chemical substances which affect water quality are numerous and act in a range of concentrations which vary continuously and erratically (Wilhm and Dorris 1968), and (3) chemical substances often act synergistically causing discrepancies between predicted and actual pollution effects. The further development of biological methods is a logical step in the improvement of pollution assessment procedures.

Benthic populations are especially suitable for evaluating pollution and other stress conditions in aquatic ecosystems. The assessment of pollution stress using benthic populations is justified by their: (1) trophic position as food organisms for fish, (2) sensitivity to stress which results in altered community structure allowing evaluation of past stress conditions, and (3) relatively sedentary way of life. Benthic diversity expresses the result of environmental stresses on an aquatic ecosystem, and therefore, shows promise as a measure of pollution stress or other disturbance in aquatic communities.

Aquatic ecologists encounter many problems when sampling biological communities. Inconsistencies in the use and efficiency of sampling devices increase the variability of biological evaluations. A survey of water pollution specialists conducted by Bartsch and Ingram (1966) indicated that many biologists prefer their own assessment procedures. No single procedure is accepted by all biologists, and little agreement exists as to the logical course to pursue in further development of biological assessment procedures. Improvement and standardization in the biological assessment of pollution are necessary if the value of biological information is to be fully realized.

Inefficiency of benthic sampling devices has been demonstrated by Elliott (1971b), Flannagan (1970), Frost et al. (1970), Hughes (1974), and Kroger (1972). Benthic sampling problems which result in biased estimates include emigration, inconsistent sample delineation, differential catchability, and separation and identification errors.

Some attempts to improve the efficiency of sieving devices have employed an increase in sampling time. Although increasing the sample time for Surber and Kicknet sampling techniques increases the capture of slow-moving organisms, emigration would also increase for organisms which can drift, crawl, or swim from the sample area. Therefore, simply increasing sampling time will not necessarily improve efficiency.

Emigration, immigration, and sample delineation are sampling problems of sieving devices which can be eliminated in a similar fashion. Emigration can be reduced by decreasing mesh size on sample netting, completely enclosing the sample area, and increasing the sample area to sample edge ratio. Emigration as defined here includes all movement of organisms from the sample area or collecting net, whether passive or active. Area-to-edge ratio and sample delineation can be most efficiently improved by designing sampling devices with large circular sample areas. The Hess sampler (Hess 1941) is circular and can be turned into most medium-sized substrates to delineate a definite sample area. Circular samplers with a larger sample area than the Hess sampler further increase the area-to-edge ratio and can be easily turned into a wider range of substrate types. Larger samples also reduce the percent effect of separation errors, and facilitate the correct determination of taxa by increasing the probability of capturing undamaged mature larvae. The variability in actual sample size is least with Hess-type samplers, greater with the various grabs and Surber sampler, and maximized in the subjective sample delineation of the Kicknet method.

Differential catchability or the selective capture of one type of organism over another is responsible for considerable sampling bias. Catchability (the probability of capture per unit effort) can be expected to vary with species or life form, sampling device, collector, and environmental conditions. The diversity of stream environments alone require that a sampling device perform equally well under a wide range of current and substrate conditions. The correction of biased population estimates resulting from catchability differences necessitates the estimation of catchability for species or life forms in each sample. The removal sampling method described by Moran (1951) and Zippin (1956, 1958) yields data for the calculation of catchability coefficients and the estimation of populations. The depletion procedure involves taking multiple subsamples from the sample area with constant sampling effort. Catchabilities are then estimated from the successive decline in catch-per-unit effort for each species or life stage. The catchability is then used to estimate the proportion of the population captured. The estimated proportion captured is then divided into the total catch to obtain a maximum likelihood estimate for the sample. Improved methods for the estimation of populations from removal data have been presented by Carle and Strub (1976). To prevent biased depletion estimates the assumptions of the removal method must be met. These assumptions can best be met by a benthic sampling device which ensures: (1) that population fluctuations during sampling are caused only by the successive capture of benthic organisms from the sample area, (2) the probability of capture is the same for each member of a population, and (3) the probability of capture for each species or life stage remains constant during the sampling period. With reference to assumption (2), Seber and Whale (1970) have shown that removal estimates and the variances of these estimates are fairly insensitive to variations in the probability of capture among individuals of the sample population.

REVIEW OF BENTHIC SAMPLING METHODS

Most benthic investigations are either extensive faunal surveys or intensive quantitative studies (Elliott 1971a). Therefore, benthic sampling methods for collecting qualitative and quantitative data have been developed. Qualitative methods are used to obtain information indicating the wealth of species and also to collect species for which the degree of pollution tolerance is known. Samples are collected with a wide variety of methods and devices that include the hands, scoops, rakes, posthole diggers, screens, kicknets, dipnets, and quantitative devices. The advantage of qualitative methods is that several devices may be used in a study, each suited for sampling a particular habitat. The most important objections to qualitative methods are: (1) subjective collecting techniques, (2) emigration and immigration of benthic invertebrates, and (3) the inability to estimate benthic populations, production, or diversity. Efficiency of a qualitative technique has been shown by Frost et al. (1970) who found that in kicknet samples about 60% of the fauna captured in ten 1-minute kicks were captured in the first kick. The escape of organisms around the net was acknowledged, but not quantified.

Quantitative sampling methods are used to obtain population and biomass estimates per unit area. Species composition, species diversity, dominance diversity, and production may also be determined from quantitative samples. Other advantages of quantitative methods are increased precision and an increased validity of comparisons between the results of different investigators. However, quantitative devices are limited as to the kind of habitat a given device can sample. The types of quantitative sampling devices fall into the categories of artificial substrates, grabs, corers, and sieving devices.

Artificial substrates are probably the most versatile sampling devices used, and include plate, webbing, and basket samplers. Artificial substrates may be used in many environments where it is impossible to collect with other methods. Higher precision is often obtained with artificial substrates when estimating the number of individuals and taxa because replicate substrates are essentially identical. An added advantage of artificial substrates is that less extraneous material is collected which reduces processing time in the lab. Hughes (1974) used trays filled with colonized substrate removed from the sample sites as "artificial" substrates and reported that this method collected more organisms and species and gave more consistent results than other methods tested. A further standardization of natural substrates for tray samplers would, of course, result in even more precise estimates. However, caution should be exercised when evaluating results from natural substrates used artificially in foreign environments. Unfortunately artificial substrates have limited utility since they do not yield data representative of the actual biological communities of lakes and streams. Hilsenhoff (1969), Fullner (1971). and Dickson et al. (1971) have recommended artificial substrates as good samplers for collecting most of the species at a given site, demonstrating their value as qualitative sampling devices. Dickson et al. (1972) reported species selectivity and high variability between replicate samples taken with 3M's #200 conservation webbing. Although the biological communities of artificial substrates can be considered artificial they may be useful in pinpointing pollution sources. Objections to artificial substrates include: (1) the long exposure time necessitates sturdy anchorage and protection from vandalism, (2) conditions cannot be monitored prior to the placing of substrates, (3) organisms are lost during retrieval, and (4) problems related to successional rates, species selectivity, season of placement, and in general, the failure to estimate actual stream community parameters.

Grabs are generally used to sample lakes, and also rivers where the depth exceeds 1 meter. The basic principle is for the grab to penetrate the substrate, either by virtue of its weight or by being pushed with a pole, and then for the jaws to close. The jaws are closed either by spring or gravity activated mechanisms. The grab is then retrieved and its contents preserved for later analysis. The more common devices include the Ekman, Shipek, Smith-McIntyre, Peterson, Orange peel, Ponar, Franklin-Anderson, and Dietz-Lafond grabs. In a study conducted by Beeton et al. (1965), the Smith-McIntyre grab was found to be more efficient than either the Peterson or Orange peel devices. Flannagan (1970) found the Dietz-Lafond, Franklin-Anderson, and Shipek grabs to be inferior to the Ponar grab, which Powers and Robertson (1967) found was as efficient as the Smith-McIntyre grab. Flannagan reported that the Ponar and Shipek grabs could sample mud, sand, or gravel substrates, although mud substrates were most efficiently sampled with the Ekman grab and sand substrates were most efficiently sampled with the Franklin-Anderson grab. Standardization of the depth of penetration is a problem when sampling variable substrates. Light weight devices such as the Ekman grab cannot penetrate sand or gravel substrates, and heavy devices such as the Franklin-Anderson grab penetrate too deeply in soft muds. Over-penetration may increase escapement during retrieval; and netting used to control escapement during retrieval captures organisms during descent, and also increases blowout. The blowout of surface materials and organisms is caused by the shock wave created from the impact of the falling device. In coarse substrates the failure of the jaws to close will also lead to the loss of organisms during retrieval. A built-in objection to many grabs is the bite or angle of closure. In the Orange peel grab this problem leads to considerable underestimation of organisms living within the substrate. In summary, sampling problems include: (1) wash out of organisms before impact, (2) depth of penetration, (3) angle and completeness of jaw closure, and (4) capture of organisms during descent and the loss of organisms during retrieval.

Corers and the more elaborate multiple coring devices are used primarily for sampling the soft muds of deep lakes. The corer is dropped into the substrate and then retrieved; the sample is retained by the combined effects of suction and compaction. Standard devices include the Benthos and Alpine corers, and the Kajak and FRB multiple corers. Shallow lentic habitats from 1 to 3 meters in depth are usually sampled with inverting devices such as the Dendy inverting sampler. Depths of less than 1 meter are generally sampled with stovepipe samplers such as the Wilding sampler. The small size of core samples results in high intersample variability. Intersample variability is often compensated for by using a multiple coring device. The depth of penetration in hard substrates is also a problem, and Flannagan (1970) reported the failure of a modified Kajak sampler to function properly. Flannagan found underestimation of benthic populations with the Alpine and Benthos corers, and found that the FRB multiple corer gave comparable results to diver's cores for all taxa except the chironomidae. In summary, limitations of coring devices include: (1) the inability to sample a wide range of substrates, (2) the lack of penetration in hard substrates, (3) the loss of material during retrieval, (4) the blowout of organisms, and (5) small sample sizes resulting in reduced precision.

Sieving devices are used extensively in stream environments when the water is less than a meter deep. The substrate in a standard sample area is disturbed with the hands or feet for a specified interval of time. Agitating techniques have included the use of compressed air and electroshocking. Substrate material and organisms dislodged through agitation then drift downstream into a collecting net. The organisms are later removed and stored for analysis. Standard sieving devices include the Hess, Surber, and Kicknet samplers. Kroger (1972) has reported underestimation of benthic populations with the Surber sampler, and Frost et al. (1970) have shown the inefficiency of Kicknet methods. However, Hughes (1974) reported similar results for Surber and "artificial" substrates and suggested that emigration was probably not significant for Surber samples. Electroshocking techniques have been found to be highly selective (Elliott 1971b), especially in the capture of Ephemeroptera, and Hughes (1974) has demonstrated considerable underestimation of benthic populations by electroshocking methods. Problems with sieving devices include: (1) the failure to define a definate sample area, (2) variation as to the depth of substrate disturbance, (3) the back wash of organisms around and out of the sieving net, (4) the drift of organisms into and out of the sample area, and (5) the failure of organisms to drift from the sample area into the collecting net.

OBJECTIVES

The objectives of this study were as follows:

(1) Determine differences in the probability of capture among benthic invertebrates.

  (a) Investigate the effect of collector experience and current velocity on the probability of capture of benthic invertebrates.

  (b) Test the hypothesis that the probability of capture is not constant between removal periods.

(2) Compare the efficiency of depletion sampling to that of Hess type, Surber, and Kicknet samplers.

(3) Investigate the effect of sampler efficiency on the estimation of species and dominance diversity.

(4) Develop a measure of evenness diversity for biological collections based on information theory.

(5) Develop a computer program to facilitate the rapid calculation of population and diversity estimates from removal data.

METHODOLOGY

The Removal Method of Population Estimation

The removal method of population estimation involves a depletion procedure in which multiple catches are taken from the sample area with constant effort. Under the assumptions of the removal method, the catch data contain information that can be used to estimate the probability of capture, and more importantly, to estimate the segment of the population remaining to be captured. The assumptions of the removal method are that: (1) population fluctuations during sampling are caused only by the successive capture of organisms from the sample area, (2) the probability of capture is the same for each member of a population, and (3) the probability of capture for each population is constant for all removal periods.

To aid in the understanding of the removal method, a brief derivation of its mathematical model will be given to help illustrate how probabilities of capture and populations are estimated. From the assumptions of the removal method, it can be seen that the probability of a particular catch for a given probability of capture (p) and population size (N) follows a binomial distribution and may be expressed as

$$P(C_1|N,p) = \frac{N!}{C_1!(N-C_1)!} p^{C_1}(1-p)^{N-C_1} ,$$

Where C_1 is the catch in the first removal period. Since the population remaining after the first catch period is $N-C_1$, and the population remaining after the second catch period is $N-C_1-C_2$, the probability of any three catches for a given p and N is

$$P(\underline{C}|N,p) = \frac{N!}{C_1!(N-C_1)!}\frac{(N-C_1)!}{C_2!(N-C_1-C_2)!}\frac{(N-C_1-C_2)!}{C_3!(N-C_1-C_2-C_3)!} \cdots$$

$$\cdots p^{C_1}p^{C_2}p^{C_3}(1-p)^{N-C_1}(1-p)^{N-C_1-C_2}(1-p)^{N-C_1-C_2-C_3} .$$

Taking the general case of k removal periods and simplifying, the model becomes

$$P(\underline{C}|N,p) = \frac{N!}{C_1!\ldots C_k!(N-T)!} p^T q^{KN-X-T} , \quad (1)$$

where,

$\underline{C}$ = vector of individuals in successive catches,

$P(\underline{C})$ = probability of occurrence of the vector $\underline{C}$,

N = population size,

p = probability of capture,

q = 1-p; probability of escape,

C_i = number of individuals in the i^{th} removal period,

k = total number of removal periods,

$T = \sum_{i=1}^{k} C_i$; total number of individuals captured, and

$X = \sum_{i=1}^{k} (k-1)C_i$

Moran (1951) maximized $P(\underline{C})$ with respect to p and obtained a maximum likelihood estimator for the probability of capture when N is known, which is

$$\hat{p} = \frac{T}{KN-X} . \quad (2)$$

After maximizing $P(\underline{C})$ with respect to N and substituting in the maximum likelihood estimate of p, Moran obtained an asymptotic maximum likelihood estimator for N. Moran obtained estimates iteratively utilizing an expression equivalent to

$$\hat{N} = \frac{T}{1-q^k} .$$

Zippin (1956, 1958) presented a graphical method for the rapid determination of maximum likelihood estimates from removal data. Carle and Strub (1976) presented improved methods of estimation and recommended the following inequality for the determination of population size from removal data

$$\frac{N+1}{N-T+1} \frac{KN-X-T+1}{KN-X+2} \cdots \frac{KN-X-T+K}{KN-X+(K+1)} - 1 \leq 0 \ . \tag{3}$$

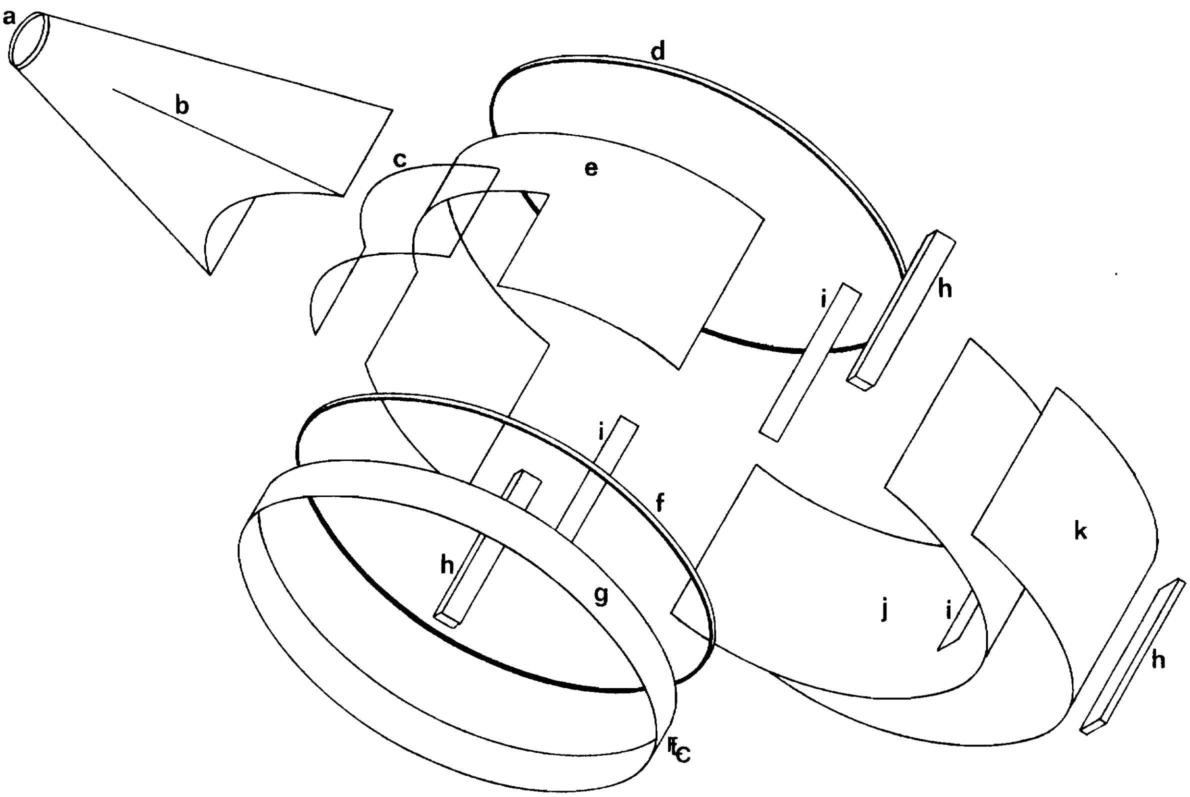
The estimated population size is the smallest integer equal to or greater than the total catch which satisfies inequality (3). Estimates may be determined easily with a desk calculator or more rapidly utilizing a computer. Equation (2) and inequality (3) were used to obtain estimates of the probability of capture and population estimates in this study, respectively.

Design of the Circular Depletion Sampler

The design of a particular depletion sampler is not important as long as the device ensures that: (1) population fluctuations during sampling are negligible within the sampling area, (2) the probability of capture is the same for each member of a population, and (3) the probability of capture remains constant throughout all removal periods. Additionally, the sampling device should be durable, lightweight, stable in fast currents, easily set into a wide range of substrates, and large in sample area.

The Circular Depletion Sampler (CDS), a sampler designed to meet the assumptions of the removal method, is shown in Fig. 1. The backing plate, penetration ring, and screening retainers of the sampler were made of 0.08 cm galvanized sheet metal. Side supports were 3.18 cm by 1.27

Fig. 1. Expansion view showing the parts of the Circular Depletion Sampler, collecting jar not shown; a) threaded flange, b) collecting net, c) net retainer, d and f) upper and lower circular supports, e) backing plate, g) penetration ring, h) side supports, i) screen retainers, j) support screening, and k) fine front netting.


a
b
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cm by 29 cm, and circular supports were 1.27 cm square and approximately 205 cm in length. The overall height of the sampler was 38.10 cm. The inside circumference and diameter were 204.64 and 65.14 cm, respectively. Total sample area was one-third square meter. The total weight of the sampler was approximately 15 kg. The coarse support screening was galvanized wire with 1.6 meshes per cm. The fine front screening was stainless steel wire with 7 meshes per cm. The small screening extended over the entire front opening of the sampler. The collecting net was made of 17 mesh per cm nylon netting with a bottom of cloth. The forward opening of the collecting net was approximately 19 by 40 cm and the length of the net was approximately 35 cm. The collecting net tapered toward the rear to a round opening 10 cm in diameter. The forward opening of the net was fitted with a 19.05 by 40.64 cm wire frame which held the collection net to the body of the sampler. A 0.5 by 1.3 cm band of foam rubber sealed the interface between the collecting net and the backing plate. The back of the collecting net was fitted with a flange 10 cm in diameter that allowed a collecting jar to be attached to the collecting net. A 3.79 liter plastic collecting jar was modified by replacing one side with 17 mesh per cm nylon netting. A funnel which could be attached to the collecting jar was used to allow the rapid removal of benthos and other collected material from the collecting jar.

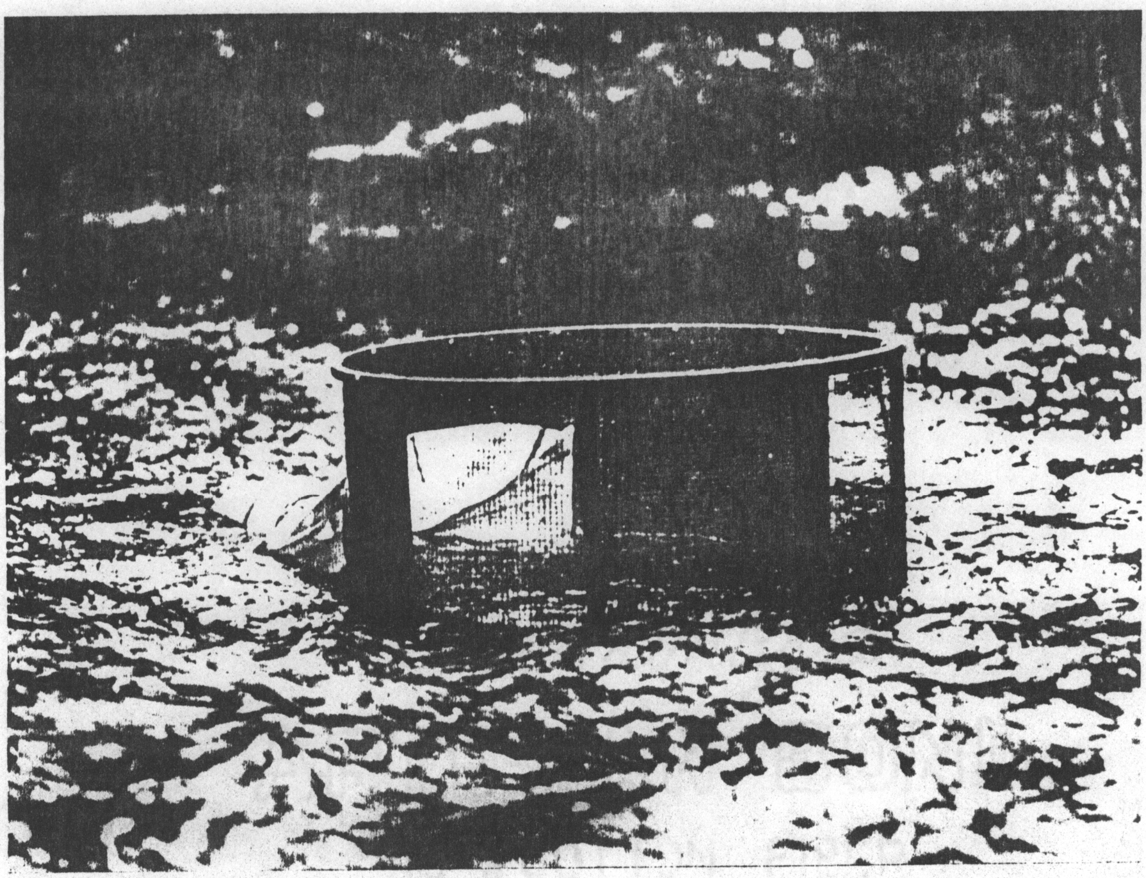
The Depletion Sampling Technique

The placement procedure for the CDS during sampling involved two steps. The collector selected the exact sample location by projecting the sample area onto the stream bottom to ensure that large rocks did not intersect the sample edge. The sampler was then rapidly thrust down and turned into the substrate. If the sample area was not delineated within 3 seconds or if the sampler was not stable the site was abandoned. After firmly imbedding the sampler 5 to 10 cm into the substrate, the collecting net and jar were lowered into the water. Fig. 2 shows the CDS properly placed before initiation of the depletion procedure. The substrate within the sample area then was continuously agitated with the hands to a depth of from 10 to 20 cm for 1 minute. In samples taken from the Roanoke Creek drainage a modification of the agitation procedure involved the use of the feet and hands. The procedure described allows the collector to meet the assumption of equal sampling effort only if the substrate is disturbed to the same depth during each removal period. Difficulties related to depth of agitation may be overcome by increasing the time per removal period to allow complete agitation in each sample period. Where current velocity was low the hands were also used to promote the flow of water through the sampler. After 1 minute of sampling effort the collecting net was cleaned by rubbing the net between the hands while directing all netted material into the collecting jar. The mouth of the collecting jar was then lifted from the water and the jar unfastened from the sampler. A second collection jar was attached to the sampler and the procedure repeated until three or more subsamples were taken. The subsamples were labeled in the sequence taken and stored separately in 95% ethanol.

Evaluation of Sampling Methods

Two ecologically similar sampling stations were selected on the Jackson River, Virginia. The upstream sampling station (Station 3), was

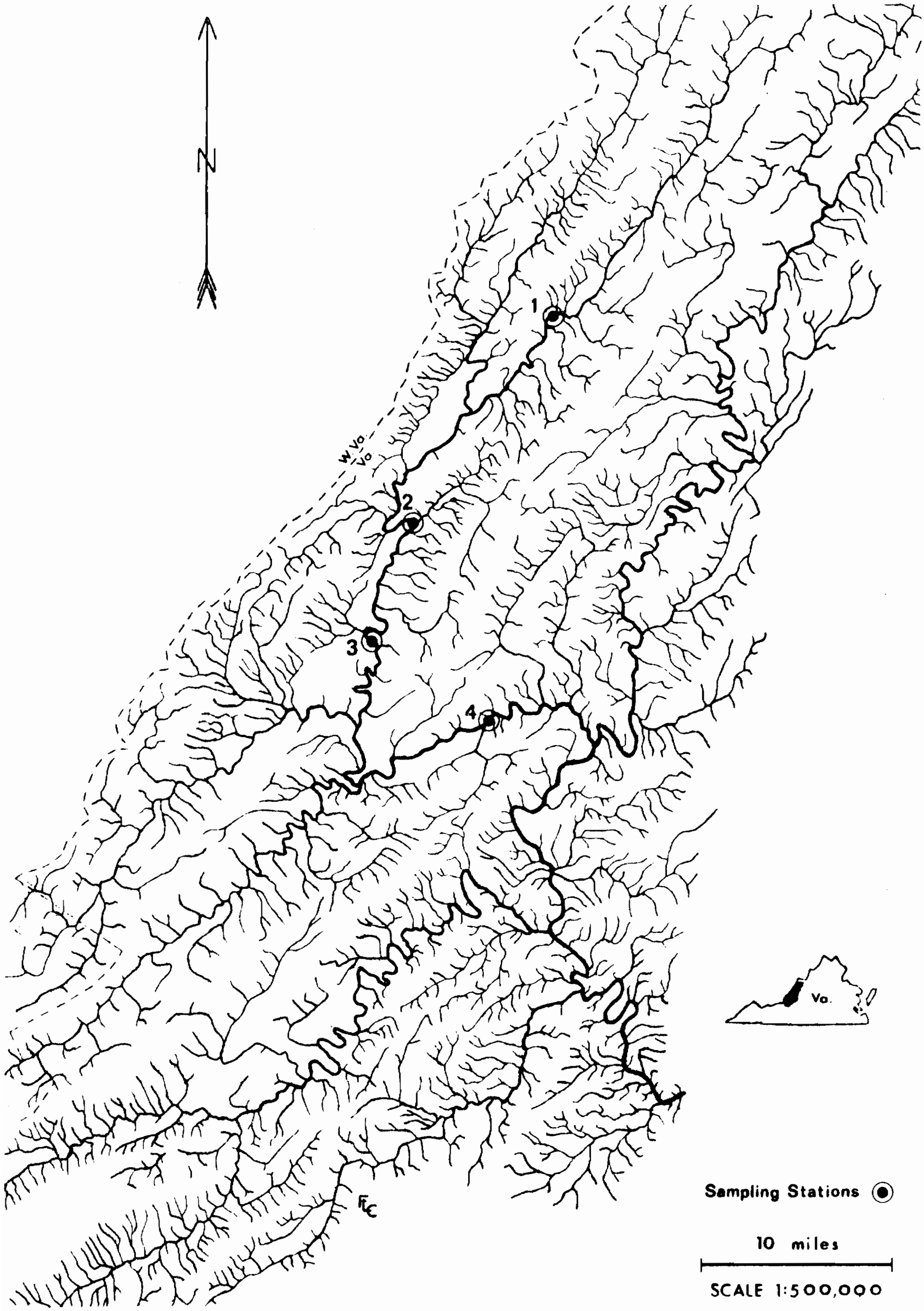
Fig. 2. The Circular Depletion Sampler properly placed in a stream before the initiation of the depletion procedure.



located 12 miles above a pollution outfall at Covington, Virginia, and the second station (Station 4), was located 8 miles below the outfall (Fig. 3). Station 4 was located far downstream from the pollution source to allow the comparison of sampling methods in a moderately stressed benthic community. The increased diversity also enabled the evaluation of catchability for a greater number of benthic species. Sampling stations were stratified into 25-square foot sections. A sample was taken from these sections with Depletion, Modified Hess (first depletion catch), Surber, Kicknet, and Substrate Removal Kicknet sampling methods. Samples in each section were taken in random order in an upstream direction. Sample sites in each section were selected to minimize the environmental differences of current velocity, stream depth, and substrate conditions. Current velocities were measured with the Gurley current meter at 0.6 the total depth, and substrate conditions were categorized according to Roelofs (1944) and Wentworth (1922). Four sections were sampled above the outfall (20 samples), and 16 sections were sampled below the outfall (80 samples). Further evaluation of the Depletion sampling technique involving the probability of capture and determination of diversity included a sample taken above (Station 1), and below (Station 2), the construction of the Gathright Dam on the Jackson River, Virginia (Fig. 3), and samples taken in the Roanoke Creek drainage, Virginia.

Samples for each sampling method were taken consistently in the same manner; a brief summary of each technique follows. Depletion samples were taken with the Circular Depletion Sampler by the method described in the previous section. Modified Hess samples were considered to equal the catch from the first removal period of CDS samples (standard

Fig. 3. Location of sampling stations, Upper James River basin, Virginia.


N
W.Va.
Va.
1
2
3
4
Va.
Sampling Stations
10 miles
SCALE 1:500,000

Hess samples are one square foot in area). Surber samples were taken by carefully moving with the hands as much material as possible from the 929 sq cm sample area into the Surber collecting net in 1 minute. Kicknet samples were taken with a rectangular kicknet (45.72 by 15.24 cm), that incorporated a Turtox collecting net with netting replaced with no. 270 nylon netting. The area in front of the kicknet was disturbed with the feet for 1 minute without attempting to collect substrate material. Sampling extended to a distance of about 40 cm upstream from the net. Multiple samples were not taken because of potential bias related to the emigration and immigration that occurs during and between sampling intervals. Substrate Removal Kicknet samples were taken in the same manner as Kicknet samples except that the substrate was moved from the sample area into the kicknet. Both Kicknet and Substrate Removal Kicknet sampling techniques sampled approximately 1858 sq cm.

The separation of benthos from substrate was accomplished using the following procedure. First, the larger rocks and detrital material were separated from the samples with the use of a sieve with a mesh size of 1 cm. The fine material was then put in a pan and hot water was added to aid in the flotation of organisms. Following flotation the organisms were decanted into Petri dishes for separation under a dissecting scope. After all lighter material had been decanted and separated, small amounts of the remaining sand and gravel were decanted and scanned for additional organisms. Separation was continued until all substrate material had been scanned. Each Petri dish of material was scanned several times to reduce bias related to the observability of organisms. Effort during each scanning remained essentially constant, therefore, it was possible after two scannings to make a quick estimate of the probability that an organism is not observed. An estimate of the probability of unobservability U, is obtained by dividing the number of a particular species separated from substrate material in the second scan period S_2, by the number separated from substrate material in the first scan period S_1,

$$\hat{U} = \frac{S_2}{S_1} .$$

An estimate of the total number of a species to be separated (NS) can be obtained with the formula

$$NS = \frac{S_1^2}{S_1 - S_2} .$$

These values can be computed very quickly and give the separator an idea of the amount of scanning necessary before the sample is "completely" separated.

After identification to species or the lowest possible morphological group and enumeration, the data were stored on computer cards by station and species. Species identification was facilitated by rearing and association. The different sample sizes of the various sampling methods necessitated that data be standardized for 1 square foot sample area before the statistical analysis. A nonparametric multiple comparisons statistical procedure was used which considered the CDS samples as controls and the remaining sampling methods as treatments.

The Measurement of Diversity

Diversity may be considered to include the components of richness and evenness. Species or richness diversity involves the relationship between species and numbers. The validity of species richness indices is doubtful when comparing communities because the relationship between species and numbers is different in different communities. Therefore, it was decided to compare the ability of sampling methods to determine species diversity with the use of species area curves. The average number of species captured was graphed against the area sampled for each sampling method to allow comparisons.

Evenness or dominance diversity involves determining the relative sizes of the populations comprising the community. A diverse community is characterized by a fairly even distribution of individuals among its species, and a non-diverse community is characterized by the dominance of one or more species. There has been much confusion as to the proper use of information theoretical measures of diversity. Therefore, the diversity of the collections and not estimates of diversity for the stream stations were compared. Therefore, it is correct to use the expression for the diversity per individual (H) of Brillouin (1962)

$$H = \frac{1}{N} \ln \frac{N!}{N_1!N_2!\ldots.N_s!} ,$$

where,

N = the total number of individuals captured,

N_i = the number of individuals in the i^{th} species, and

s = the total number of species.

For a given N and s, the minimum diversity per individual may be expressed as

$$H_{min} = \frac{1}{N} \ln \frac{N!}{(N-s+1)!} ,$$

and the maximum diversity per individual may be expressed as

$$H_{max} = \frac{1}{N} \ln \frac{N!}{\frac{N}{S}!^{s}} .$$

The evenness compnent of diversity may be partitioned with a redundancy equation. Therefore, the evenness component of diversity was calculated using the following equation

$$1 - r = \frac{\ln \sum_{i=1}^{s} N_i! - \ln(N-s+1)!}{s \ln \frac{N}{S}! - \ln(N-s+1)!} . \tag{4}$$

The value of equation (4) varies between 0 and 1 with maximum evenness when 1-r is equal to 1. Because populations are generally estimated to the nearest individual, $s \ln \frac{N}{S}!$ may be determined by $(s-R) \ln m! + R \ln(m+1)!$, where m is the integer part of $\frac{N}{S}$ and R is the remainder. The problem of information units is circumvented when calculating 1-r evenness because the base of the logarithms is irrelevant. The natural log of a factorial of a number increases slower than the square of a number, therefore, 1-r evenness diversity is expected to be less dependent on sample size than indices incorporating square weighting.

RESULTS AND DISCUSSION

The Probability of Capture

Sample population estimates for quantitative benthic sampling methods other than grabs and cores are generally considered to equal the number of individuals captured during a specified interval of time. In the 1-minute time interval which is generally used, 80% or more of benthic populations are considered to be captured (Benfield, personal communication). Expressing this method mathematically

$$\hat{N} = C/\text{minute} \ ,$$

where $\hat{N}$ is the population estimate and C is the catch. The expected value of the catch per minute may be expressed as the product of the true population size N, and the probability of capture p, where for convenience the probability of capture is defined for a 1-minute sampling interval. Therefore

$$E(C) = pN \ .$$

It is obvious that this method of estimation is negatively biased when the probability of capture (p) is less than 100%.

The probability of capture for a given sample population may be influenced by the size, shape, and weight of the individuals comprising a population and also by their ability to swim, cling, or burrow. Other factors influencing the probability of capture include the experience of the collector, the type of sampler, and environmental differences such as current velocity, substrate type, and water depth. The possible combinations of factors that may result in different probabilities of capture for benthic invertebrates are essentially unlimited.

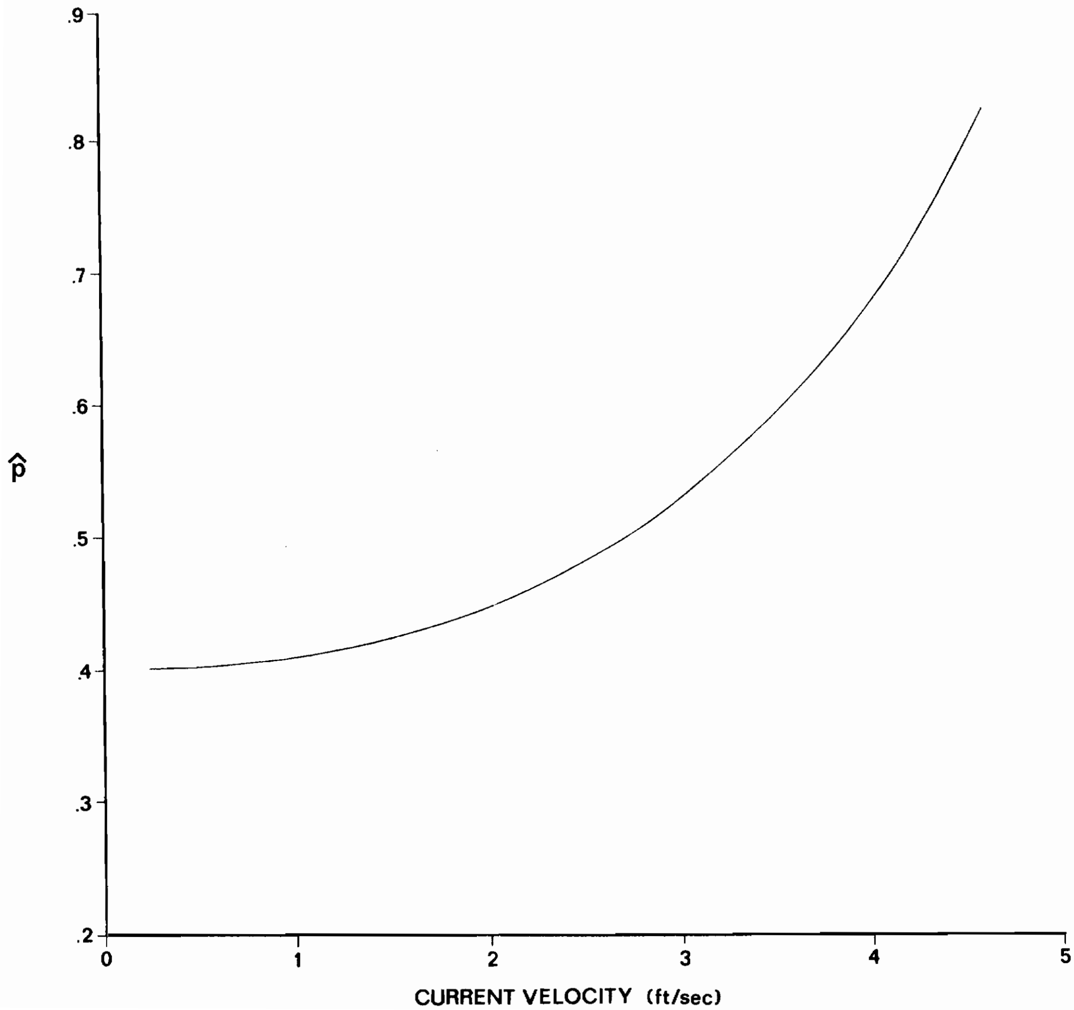
The morphology and behavior of an organism determines its catchability. Therefore, it is reasonable to expect differences in catchability for different developmental stages of the same species. If groups such as adults and larvae of the same species are not estimated separately, the estimate of the probability of capture will be positively biased and the population estimate will be negatively biased. An example of catchability differences between developmental stages is illustrated by adult and larval Riffle beatles (Elmidae) collected in a sample taken from the Jackson River, Virginia. The larvae of *Optioservus trivitatus* are smaller, denser, and live deeper in the substrate than the adults; their catchability was 0.181 whereas the catchability of the adults was 0.603. It is apparent that organisms should not only be separated to species, but also separated into catchability groups before estimation. Final population estimates for species with larvae and adults in the same sample are simply the sum of larval and adult estimates.

The probabilities of capture for selected taxa collected from the upper James and Roanoke River drainages, Virginia, are reported in Appendix Table 3. The highest catchabilities are generally exhibited by the Chironomidae (particularly the smaller species), and the non-burrowing Ephemeroptera. Taxa generally found to be intermediate in catchability included the free-living and net-building Trichoptera, Odonata, Megaloptera, Plecoptera, Nematoda, and Crustacea. Taxa showing low catchabilities included the case-building Trichoptera, and various Diptera, Coleoptera, Mollusca, and Annelida. Exceptions do occur for these general catchability groups. For example the Naididae of the Annelida have relatively high catchabilities.

Current velocity and collector experience clearly showed a relationship to catchability. Catchabilities for the organisms collected in faster currents were consistently higher than those for organisms collected in slower currents (Fig. 4). Catchability of specific groups increased at current velocities above about 2 ft per second. Catchabilities of the same groups tended to level off below this velocity. The leveling off of catchability at low current velocity was expected because at low current flows the collector used his hands in an attempt to increase the flow of water through the sampler. Catchabilities for organisms collected by an experienced collector were higher than the catchabilities of organisms collected by a novice collector (Fig. 5). Differences in catchability for organisms collected by novice and experienced collectors were greater at lower current velocities and for organisms that burrow into the substrate. These data suggest that the novice collector needed to increase current flow through the sample at low current flow, and also needed to disturb the substrate more vigorously. It is advantagous for the collector to increase the probability of capture of a population because this will increase the precision of population estimates.

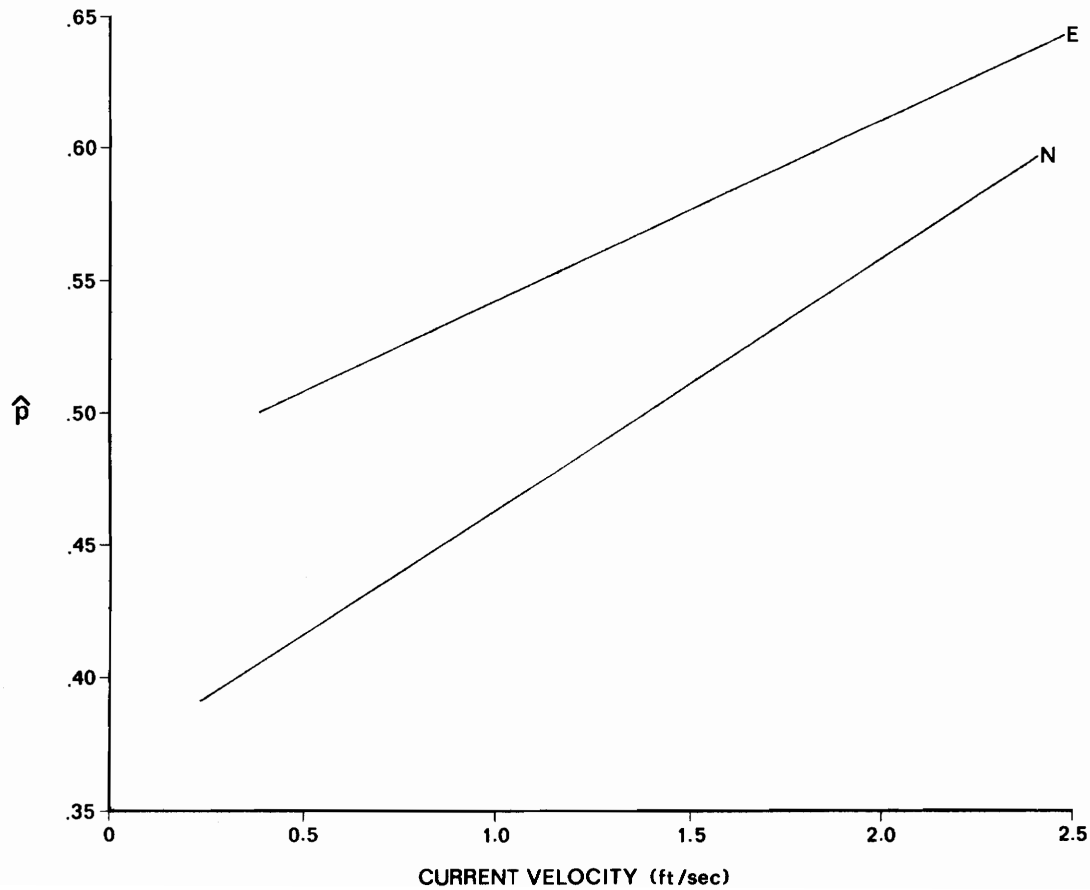
An important advantage of the removal method is the opportunity to estimate the probability of capture, which when low suggests a modification of sampling techniques. This opportunity for feedback enables the novice collector to eventually improve his sampling technique while allowing optimum utility to be made of information contained in poorly collected samples. After some experience, the collector learns to make a conscious effort to increase the catchability of organisms which are difficult to capture. For example, more care is taken when removing

Fig. 4. Average catchability and current velocity for selected taxa collected above and below Covington, Virginia.



.9
.8
.7
.6
p̂
.5
.4
.3
.2
0
1
2
3
4
5
CURRENT VELOCITY (ft/sec)

Fig. 5. Catchability for *Microtendipes* sp. A and current velocities for samples collected in the Roanoke Creek drainage, Virginia; for E) experienced, and N) novice collectors.


.65
.60
.55
.50
.45
.40
.35
$\hat{p}$
0
0.5
1.0
1.5
2.0
2.5
CURRENT VELOCITY (ft/sec)
E
N

snails and case-building Trichoptera from rocks and large Mollusks are readily identified as such and collected.

Thus far, only closed samples have been considered, that is samples taken without emigration or immigration. Samples taken properly with the CDS and Hess type samplers are closed samples, but samples taken with Surber and Kicknet samplers allow emigration and immigration, and are, therefore, termed open samples. Immigration for Surber and Kicknet samples is largely invertebrate drift. Drift density during sampling on the Jackson River, Virginia, was low (6×10^{-4}cc/cu m/min), and was considered to be negligible over the 1-minute sampling period. Thus, the new model for the expected value of the catch becomes

$$E(C) = (p-e)N \ , \tag{5}$$

where e is the probability of emigration. Solving equation (5) for the probability of emigration

$$e = p - \frac{C}{N} \ . \tag{6}$$

Emigration as defined here includes all movement of organisms from the sample area or collecting net, whether passive or active. In contrast, the probability of escape applies, as in closed samples, to those organisms which are not collected and remain in the sample area. It is possible, after making a few assumptions, to estimate a minimum escapement probability from equation (6). The assumptions necessary to estimate a minimum probability of emigration are that: (1) the depletion estimate of N is not significantly larger than the true N, which is generally the case particularly at high probabilities of capture, and (2) the probability of capture for Surber and Kicknet samples is equal to or greater than the probability of capture calculated for the CDS. The latter assumption is reasonable since CDS samples involved the same sampling time but a larger sample area. The estimate of p for equation (6) was obtained from CDS samples using equation (2), and N was estimated from CDS samples using equation (3). Admittedly estimates of emigration obtained by this method will be imprecise, but meaningful comparisons between open sampling methods are possible. The probabilities of emigration for selected taxa collected with the Surber and Kicknet sampling methods are reported in Table 1. Kicknet samples showed the highest rates of escapement for all taxa compared. Substrate Removal Kicknet samples generally showed higher rates of escapement than Surber samples. High emigration rates for the Kicknet sampler can be attributed to: (1) the use of the feet to disturb the substrate, (2) the absence of sample confining flanges, (3) the clogging of sampler netting, and (4) the shallow collecting net. Scarcity of small organisms in Kicknet samples suggest that organisms might be washed from the collecting net by back currents formed as the net clogs with detritus. In general, species with low probabilities of capture have a low propensity to drift and therefore, show low emigration rates (Table 2). Species which show the highest probabilities of capture for closed sample methods are often entirely absent from samples taken with open sampling devices. These observations suggest that the drift of organisms from the sample area is responsible for much of the underestimation found for open sampling methods. Dividing emigratibility by catchability results in a relative index which indicates the degree of active emigration. Aquatic insects showed the highest index values indicating that the emigration of the

Table 1. Probabilities of emigration for open sampling methods for selected taxa collected from the Jackson River, Virginia.

Taxa	Probability of Emigration Method Surber	 S-R Kicknet	 Kicknet
ANNELIDA			
HIRUDINEA			
Arhynchobdellida			
Erpobdellidae	0.000	0.000	0.615
OLIGOCHAETA			
Plesiopora			
Tubificidae	0.120	0.718	0.718
Prosopora			
Lumbriculidae	0.045	0.000	0.241
ARTHROPODA			
ARACHNIDA			
Acari	0.589	0.607	0.622
CRUSTACEA			
Isopoda			
Asellidae	0.000	0.000	0.257
INSECTA			
Coleoptera			
Elmidae	0.068	0.326	0.551
Hydrophilidae	0.027	0.078	0.507
Psephenidae	0.000	0.000	0.385
Diptera			
Chironomidae	0.280	0.484	0.615
Empididae	0.181	0.533	0.644
Tipulidae	0.262	0.113	0.527
Ephemeroptera			
Baetidae	0.717	0.502	0.626
Ephemerellidae	0.723	0.749	0.837
Heptageniidae	0.475	0.568	0.691
Megaloptera			
Corydalidae	0.000	0.000	0.432
Plecoptera			
Perlidae	0.278	0.382	0.589
Perlodidae	0.524	0.706	0.768
Trichoptera			
Hydropsychidae	0.066	0.219	0.443
Philopotamidae	0.037	0.347	0.594
MOLLUSCA			
GASTROPODA			
Basommatophora			
Ancylidae	0.000	0.071	0.406
Physidae	0.000	0.003	0.590
Planorbidae	0.000	0.000	0.342
Mesogastropoda			
Pleuroceridae	0.000	0.000	0.000
NEMATODA	0.555	0.555	0.766

Table 2. Probability of capture from CDS samples and average probability of emigration from open sampling methods for selected taxa collected from the Jackson River, Virginia.

Taxa	Catchability	Emigratibility	E/C
Heptageniidae	0.921	0.578	0.628
Ephemerellidae	0.879	0.770	0.876
Physidae	0.786	0.198	0.252
Perlidae	0.761	0.416	0.547
Lumbriculidae	0.753	0.095	0.126
Chironomidae	0.718	0.460	0.641
Hydropsychidae	0.680	0.243	0.357
Corydalidae	0.671	0.144	0.215
Ancylidae	0.649	0.159	0.245
Tipulidae	0.559	0.301	0.540
Psephenidae	0.557	0.128	0.230
Pleuroceridae	0.136	0.000	0.000

Mollusca and Annelida was relatively more passive.

Validity of Assumptions

The degree to which the assumptions of the removal method are met in practice determine its utility as a method of sample population estimation. The assumption of no emigration or immigration during sampling presents no problem for closed sampling devices such as the CDS. The assumption of equal probability of capture for all individuals in a population is a problem of separating populations into catchability groups before estimation. Examples of populations comprised of different catchability groups include populations containing larvae and adults and also populations containing different age classes. In benthic communities the Coleoptera are generally the most important when considering catchability differences related to lifestage; and the Megaloptera, Odonata, Decapoda, and Mollusca present the largest catchability differences related to age classes. The larvae of the Coleoptera have lower catchabilities than the adults, and in contrast the catchability of earlier age classes for other groups is generally higher than that of older age classes. The separation of populations into catchability groups based on age class is generally only necessary when the aquatic life stage is longer than one year, for example third, fourth, and fifth instars would constitute a catchability group and ninth, tenth, and eleventh instars would comprise another. The separation of species into catchability groups may be ignored in cases where the expected value of the population remaining after sampling is small. Variation in the catchability among members of the same catchability group can be considered to be negligible since Seber and Whale (1970) have shown the removal method to be fairly insensitive to these variations.

A collector using the removal method also assumes that the probability of capture remains constant between removal periods. The catchability of benthic invertebrates is largely dependent on current velocity and collector experience, and is not affected by the organisms' learning. Therefore, it is reasonable to assume a constant probability of capture between removal periods when the interval of sampling time is constant. To test the hypothesis that the probability of capture was not constant among removal periods for a particular species in the sample community, the following expression of Zippen (1956) may be used.

$$\chi^2 = \sum_{i=1}^{k} \frac{(C_i - N_{pq}{}^{i-1})^2}{N_{pq}{}^{i-1}} + \frac{(N-T-N_q{}^k)^2}{N_q{}^k} \tag{7}$$

Equation (7) is asymptotically distributed as Chi-square (χ^2) with k-2 degrees of freedom. The χ^2 may be calculated for one species or all species individually and compared with the critical tabular value to decide if the probability of capture was constant at a selected level of significance for each species. The most serious problem related to variable sample effort was the tendency of novice collectors to disturb substrates less deeply in earlier removal periods. This failure results in positively biased estimates for organisms living within the substrate and was characterized by significantly more of these organisms in catch two relative to catches one and three.

Comparison of Population Estimation Methods

Negative bias in the estimation of benthic populations results primarily from emigration out of the sample area and the failure of organisms to move from the sample area into the collecting net. The relative importance of the probability of emigration and of the probability of escape (1-p), has been discussed, but it is left to show the effect of these probabilities on the estimation of populations based on different sampling techniques.

The means, standard errors of the means, and coefficients of variation for the total number of organisms estimated from 20 Depletion, Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet samples taken from the Jackson River, Virginia, are reported in Table 3. Compared with the Depletion method, all other methods showed significantly lower estimates for the total number of organisms present. The percent of the total organisms estimated with the Depletion method, which were estimated by the Hess, Surber, Substrate Removal Kicknet, and Kicknet sampling methods were 69.7, 53.1, 37.4, and 15.8, respectively. Surber and Substrate Removal Kicknet estimates were 75.7 and 53.4% of Modified Hess estimates, respectively, indicating agreement with the results of Frost (1970). Coefficients of variation were greatest for Kicknet estimates and smallest for Depletion estimates. These data indicate that the Depletion method increases precision by eliminating the effects of variable catchability. High cofficients of variation were expected for all methods because comparisons were made over a wide range of substrate and current conditions.

Using only the first two methods in determining Depletion estimates resulted in an average of 120.1 organisms to be estimated per sample compared to 119.9 when three catches were used. This result suggests that the two-catch method is suitable for estimating benthic populations.

Table 3. Means, standard errors of the means, and coefficients of variation for the total number of organisms estimated per sq ft from 20 Depletion, Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet samples from the Jackson River, Virginia.

Method	Mean	Coefficient of variation
Depletion	119.9 ± 26.8[a]	57.58
Modified Hess	83.5 ± 18.7**	60.94
Surber	63.7 ± 14.2***	64.02
Substrate Removal Kicknet	44.8 ± 10.0***	69.30
Kicknet	19.0 ± 4.2***	85.84

[a]Standard error of the mean.
**Significantly less than depletion estimates at $\alpha<0.05$.
***Significantly less than depletion estimates at $\alpha<0.001$.

However, tests of equal probability of capture cannot be made from two catches. Population estimates made from two catches are also less precise than those based on three catches.

The proportion of organisms estimated for Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet samples relative to Depletion estimates for various taxa are reported in Table 4. The results indicate that the removal method is more efficient than other sampling methods. All taxa were significantly (α=0.05) underestimated by the Kicknet sampling technique. Therefore, the Kicknet method does not appear reliable for quantitative sampling. Open sampling methods generally showed considerable underestimation for taxa with high catchabilities compared to Hess and Depletion estimates. Hess and Depletion estimates were not significantly different for these taxa. The high probabilities of capture and emigration rates of these taxa suggested drift from the sample area as the causative factor of underestimation. The non-burrowing Ephemeroptera are a good example of organisms with high probabilities of capture and high emigration rates that are underestimated when using open sampling techniques (Table 2). The burrowing Ephemeroptera, in contrast, show low catchabilities and low emigration rates. Like the burrowing Ephemeroptera, the Mollusca and Annelida estimates from Substrate Removal and Surber samples were generally not significantly less (α=0.1) than Depletion estimates. This finding supports the contention that species with low catchabilities have a low propensity to drift, and therefore, have low emigration rates. Therefore, species with low catchabilities are estimated better by open sampling methods than species with high catchabilities.

Table 4. Proportion of Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet estimates relative to Depletion estimates, per sq ft, for selected taxa collected from the Jackson River, Virginia.

Taxa	Hess	Surber	S-R Kicknet	Kicknet
ANNELIDA	74.6**	71.4	79.9	48.8***
OLIGOCHAETA	75.0***	70.4	80.1	49.5***
Terricolae (Lumbricidae)	75.5***	70.8	82.8	51.2***
HIRUDINEA	0.5	134.5	67.3	0.0***
Arhynchobdellida	0.5	134.5	67.3	0.0***
ARTHROPODA	70.1**	49.5***	31.8***	12.9***
INSECTA	70.6*	46.6***	30.0***	12.1***
Coleoptera	67.1***	59.2***	42.3***	12.8***
Elmidae	69.1**	59.6***	34.1***	11.9***
Hydrophilidae	69.0*	67.7***	60.6***	17.7***
Psephenidae	56.1**	56.0*	76.1*	15.8***
Diptera	67.0*	44.3***	21.5***	9.9***
Chironomidae	66.4**	43.5***	21.3***	10.0***
Empididae	75.6	56.1***	20.9***	9.8***
Tipulidae	41.7*	29.9**	44.8	1.2***
Ephemeroptera	88.4*	24.3***	22.8***	10.8***
Baetidae	82.7	14.4***	35.9**	23.9***
Ephemerellidae	87.8	15.7***	13.1***	4.3***
Ephemeridae	59.3	13.3**	86.4	13.3**
Heptageniidae	92.5	38.9***	29.6***	17.3***
Megaloptera (Corydalidae)	68.5***	74.7***	80.1**	24.0***
Odonata (Gomphidae)	61.5	13.8**	48.3**	13.8**
Plecoptera	81.4**	36.8***	19.5***	9.5***
Capniidae	93.3	71.8	0.0**	0.0**
Perlidae	75.0	48.3***	37.9**	12.2***
Perlodidae	81.4	30.4**	12.2***	6.1**
Trichoptera	65.6***	63.7***	46.4***	22.2***
Hydropsychidae	68.1***	61.5***	46.1***	23.7***
Limnephilidae	56.0*	100.5	50.2**	35.9***
Philopotamidae	55.2	61.9	30.9	6.2**
CRUSTACEA	63.9	133.1***	82.0***	36.8***
Isopoda (Asellidae)	63.9	133.1***	82.0***	36.8***
ARACHNIDA	58.6	3.6**	1.8*	0.0***
Acari	58.6	3.6**	1.8*	0.0***

Table 4. Proportion of Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet estimates relative to Depletion estimates, per sq ft, for selected taxa collected from the Jackson River, Virginia (continued).

Taxa	Hess	Surber	S-R Kicknet	Kicknet
MOLLUSCA	55.9***	91.8	78.8***	24.5***
GASTROPODA	55.5***	93.4	78.6***	24.9***
Basommatophora (Planorbidae)	66.8***	96.4	63.1***	23.9***
Mesogastropoda (Pleuroceridae)	15.0**	82.5	134.5	28.7**
PELECYPODA	75.0	0.0***	89.7	0.0***
Heterodonta (Sphaeridae)	75.0	0.0***	89.8	0.0***
NEMATODA	70.6	21.1***	21.1***	0.0***
SECRENETA	70.6	21.1***	21.1***	0.0***
Rhabditida	70.6	21.1***	21.1***	0.0***

*Significantly less than depletion estimates at $\alpha<0.100$.
**Significantly less than depletion estimates at $\alpha<0.050$.
***Significantly less than depletion estimates at $\alpha<0.025$.

An apparent inconsistency appeared in the data for the Surber sample method for the Ascellidae (Table 4). In this case, more organisms were captured with the Surber method than with the Depletion method, although the Surber estimates were found to be significantly lower than those of the Depletion method. This apparent discrepancy is easily explained in the multiple comparison nonparametric analysis because all but one Depletion sample exceeded Surber estimates; the one Surber sample representing a large aggregation of organisms.

Species Diversity Determination

The total number of species represented in a sample can be negatively biased. From equation (1) it can be shown that the probability a species will be represented (R) in a sample for a given population size and probability of capture is

$$P(R|N,p) = 1-q^{kN} ,$$

where k is the number of removal periods. When using the one-catch method of estimation it can be seen that the probability of species representation is dependent upon the probability of capture and population size. The probability of representation is generally high when the population size is large even when the probability of capture is relatively small; however, difficulties arise for small sample populations. The problem of negative bias when estimating the number of species per sample becomes significant because the largest proportion of species in a sample is generally represented by one individual, the second largest proportion by two individuals, and so forth. One solution to this problem is to increase sample population sizes; but because the relationship between species and numbers varies among communities, the utility of increasing sample size is difficult to determine. An increase in the number of removal periods, however, will increase the probability of representation by a predictable amount for a given population size and probability of capture. As the number of removal periods increase, the probabilities of representation for different species can be seen to converge. For example, if we consider a population size of 1, it can be seen from Table 5 that increasing the number of removal periods will decrease differences in the probabilities of representation between species with different initial probabilities of capture.

The average number of species captured per sample, standard errors of the means, coefficients of variation, and percent difference between upstream and downstream collections are reported in Table 6. Depletion samples contained the most species and showed the lowest coefficients of variation for the number of species collected in both downstream and upstream communities. Closed sampling methods showed the largest differences of the number of species collected between upstream and downstream communities. Kicknet samples showed the lowest number of species and high coefficients of variation. Surber samples also showed a low number of species and high coefficients of variation, but these results were expected for the relatively smaller Surber samples.

The cummulative average number of species captured for Depletion, Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet samples is reported in Fig. 6. Depletion, Modified Hess, Surber, and Kicknet samplers sampled a total of 6.67, 6.67, 1.86, and 3.72 square meters,

Table 5. Increase in the probability of representation with successive catch periods for species represented by one individual and various probabilities of capture.

Probability of capture	Removal period 1	2	3	4	5
	Probability of representation				
0.8	0.800	0.960	0.992	0.998	0.999
0.6	0.600	0.840	0.936	0.974	0.990
0.4	0.400	0.640	0.784	0.870	0.922

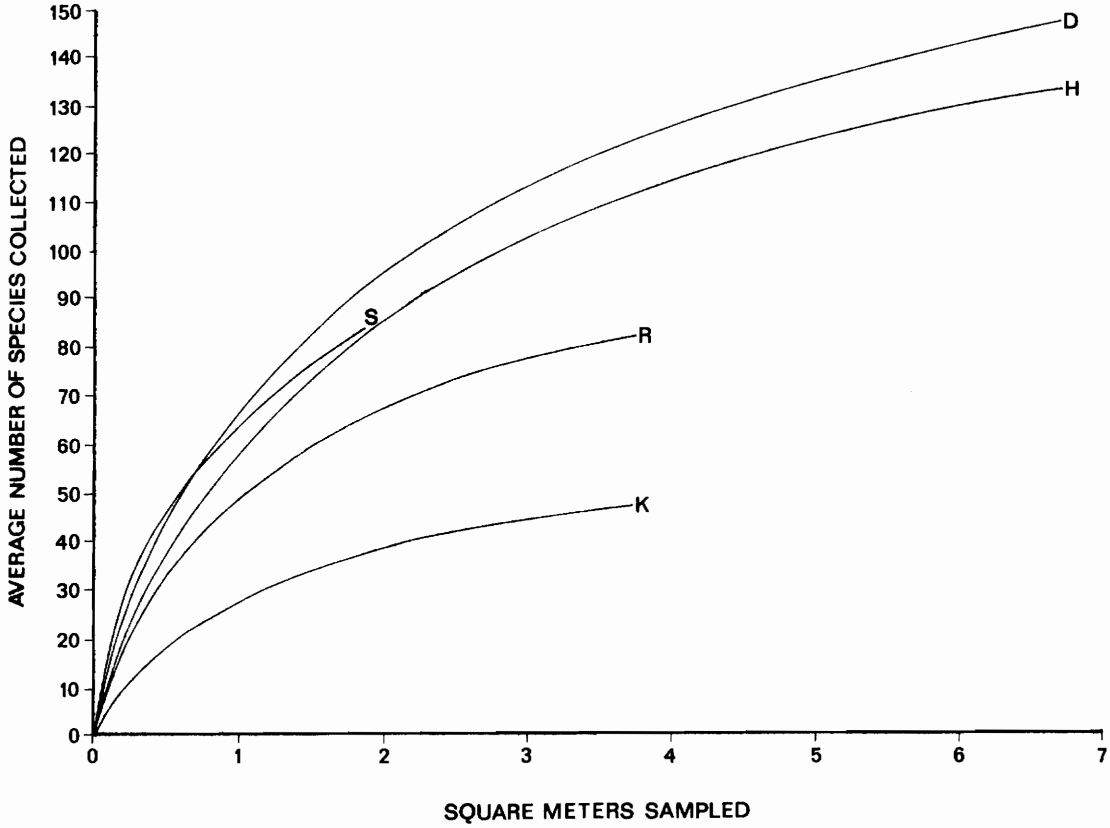
Table 6. Means, standard errors of the means, and coefficients of variation for the number of species and 1-r evenness diversity from 4 diverse and 16 nondiverse collections taken with Depletion, Modified Hess, Surber, Substrate Removal Kicknet, and Kicknet sampling methods.

Sampling method	Upstream		Downstream		
	Mean	CV	Mean	CV	% dif.
			Number of species		
Depletion	64.25 ± 10.27[a]	31.98	27.56 ± 1.07	15.56	133
Mod. Hess	55.50 ± 9.32	33.60	23.63 ± 1.20	20.26	134
Surber	24.25 ± 6.18	50.99	13.63 ± 0.98	28.71	78
SR Kicknet	26.50 ± 6.02	45.44	16.56 ± 1.00	24.15	60
Kicknet	12.50 ± 2.10	33.63	7.81 ± 0.95	48.86	60
			Evenness diversity		
Depletion	0.7364 ± 0.0031	0.83	0.5696 ± 0.0287	20.17	29.3
Mod. Hess	0.7405 ± 0.0039	1.05	0.5620 ± 0.0331	23.57	31.8
Surber	0.5197 ± 0.1884	72.52	0.5894 ± 0.0418	28.38	-11.8
Surber[b]	(0.6930 ± 0.1049)	(26.21)			(17.6)
SR Kicknet	0.6558 ± 0.0501	15.28	0.6180 ± 0.0499	32.28	6.1
Kicknet	0.5478 ± 0.0599	21.85	0.4954 ± 0.0646	59.19	10.6

[a]Standard error of the mean.
[b]Excluding sample 3.

respectively. The ability of the various sampling methods to estimate the number of species present is reflected in different rates of species accumulation. The discrepancy between the Depletion species area curve and the species area curve of the Modified Hess samples (equal to the first depletion catch), resulted from the additional capture of rare species in removal periods two and three. It can be shown from Fig. 6 that when compared to Modified Hess samples the combined Depletion catch required 25% less area to be sampled to capture an equivalent number of species. Kicknet and Surber samples were expected to show higher rates of species accumulation when compared to Depletion samples because of the greater dispersion of samples for a given area sampled. Surber samples initially showed the highest rate of species accumulation, but as more samples were taken the rate of species accumulation dropped below that of Depletion samples. The average number of species collected in any three Depletion samples exceeded the average number of species captured in any 11 Surber samples, although both methods at this point had sampled approximately 1 square meter. Substrate Removal Kicknet and Kicknet samples showed species accumulation rates far lower than other methods. Kicknet samples had the lowest rate of species accumulation of all methods. The low rate of species accumulation was probably related to low catchabilities, and also to high emigration rates. This result raises doubt as to the suitability of Kicknet samplers for use as qualitative sampling devices.

Fig. 6. Species area curves for the cumulative average number of species collected with D) Depletion, H) Modified Hess, S) Surber, R) Substrate Removal Kicknet, and K) Kicknet samples.



150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
AVERAGE NUMBER OF SPECIES COLLECTED
0
1
2
3
4
5
6
7
SQUARE METERS SAMPLED
D
H
S
R
K

Dominance Diversity Determination

It is apparent from previous discussion that benthic population estimates can be seriously biased by either emigration or low catchability or both. Differences in the probability of capture among species can result in substantial bias when determining community evenness. Species with low probabilities of capture will have their importance underestimated relative to species with high probabilities of capture. It should be noted that if the percent bias in estimation of the populations comprising a community are approximately equal, there will be little effect on the final determination of dominance diversity. Nearly equal population sizes also further reduce the effect of biased estimates on the determination of dominance diversity. However, low population sizes will make the determination of evenness diversity very sensitive to biased population estimates. The most serious bias will occur in communities with a low number of species where the most abundant species are underestimated relative to the less common species. Therefore, a diverse community would be expected to be less susceptible to the biased estimation of evenness diversity than a nondiverse community, but could be very susceptible to the biased estimation of diversity if populations are low.

Evenness diversity for a pool sample taken above and below the Gathright Dam construction site on the Jackson River, Virginia, is presented in Table 7. Both upstream and downstream diversity decreased with an increase of information available from the Depletion procedure. Upstream and downstream diversities dropped by 14.5 and 34.6%, respectively. More importantly the difference between upstream and downstream diversities showed an increase with the use of Depletion information.

Table 7. Evenness diversities (1-r) for a pool sample taken above and a pool sample taken below the Gathright Dam construction site, Jackson River, Virginia.

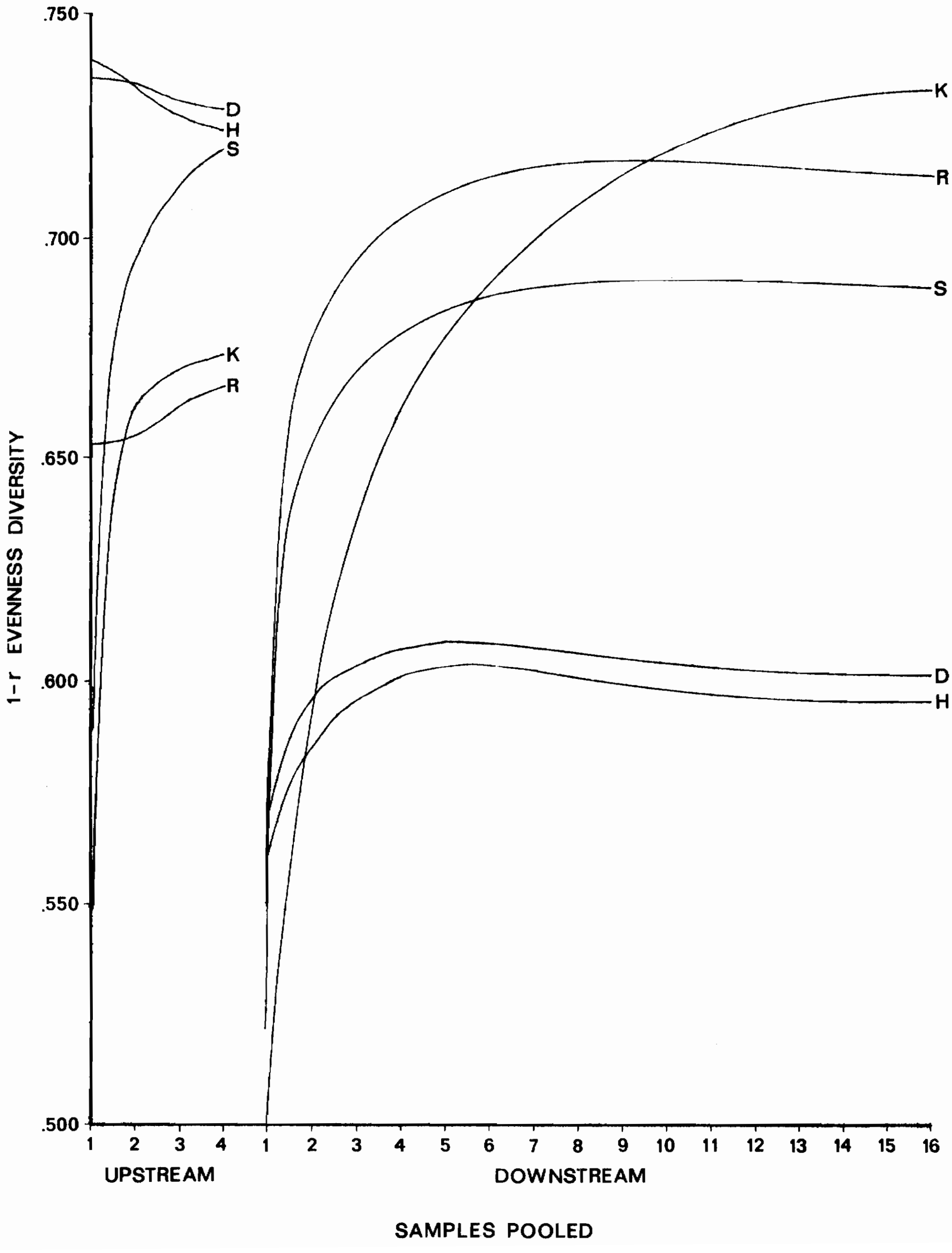
Data considered	1-r evenness diversity		
	Upstream	Downstream	Difference
C(1)	0.590	0.575	0.015
C(1)+C(2)	0.597	0.440	0.157
Est.[a]C(1)&C(2)	0.473	0.171	0.302
C(1)+C(2)+C(3)	0.562	0.399	0.223
Est.[a]C(1)&C(2)&C(3)	0.445	0.229	0.216

[a]1-r diversities calculated from the Depletion estimates of data shown.

The agreement between the diversity of the catches and Depletion estimates also increased as more Depletion information was included, indicating that the diversity estimates were becoming more accurate. The decrease in diversity as more Depletion information was included was primarily caused by low catchabilities for the most abundant species in each community. In the upstream community, the larvae of *Optioservus trivitatus* (the most abundant species) showed a catchability of 0.181. The low catchability is significant because the Elmidae often include the most abundant species in nonpolluted streams. These findings suggest that nonpolluted streams will generally have their evenness diversity overestimated by single catch methods. In the downstream community the snail *Mudalia carinata* was the most abundant species in the final Depletion estimates showing a catchability of 0.171, but the chironomid *Tanytarsus* sp. A was the most abundant species in the first catch showing a catchability of 0.933. These two species were responsible for much of the change in diversity with an increase in the use of Depletion information. Catchabilities less than 0.3 are not common for stream benthos except in areas of low current velocity such as pools. The data indicate that pool samples will show the greatest biases of dominance diversity when using conventional sampling methods. The improved accuracy and precision of diversity calculated using Depletion information demonstrate the value of the removal method for determining benthic diversity.

Fig. 7 presents the results of 1-r evenness diversity for cummulated populations for various sampling methods in pollution stressed and nonstressed communities. In the stressed community the open sampling methods

Fig. 7. Average 1-r evenness for cumulative samples for pollution stressed and nonstressed communities for various sampling techniques from the Jackson River, Virginia; D) Depletion, H) Modified Hess, S) Surber, R) Substrate Removal Kicknet, and K) Kicknet.


.750
.700
.650
.600
.550
.500
1-r EVENNESS DIVERSITY
D
H
S
K
R
K
R
S
D
H
1 2 3 4
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
UPSTREAM
DOWNSTREAM
SAMPLES POOLED

showed the highest evenness diversities, which were less precise than the diversities of closed sampling methods (Table 6). Cumulative populations estimated with the Depletion method showed the highest evenness diversity in the nonstressed community and nearly the lowest evenness diversity in the stressed community; these diversity values also stabilized more rapidly than for other methods. Differences between the evenness diversity of stressed and nonstressed communities were greatest for closed sampling methods. The evenness calculated from Hess samples was very close to that of CDS collections, although diversities calculated from Hess samples showed a slower rate of attaining stability and also lower precision. The reason for the lack of large differences between Hess and CDS evenness diversities is that the most abundant species had high catchabilities. The most abundant species in the stressed community was a predacious Chironomid of the genus Guttipelopia, whose free-living habit and small size gave it the high catchability of 0.807. If we consider the standing crop of populations as importance values rather than the number of individuals, the evenness diversity of the downstream community is considerably overestimated in Hess collections relative to CDS collections. This large difference in evenness diversity resulted from the low catchability of Corydalus cornutus which had by far the largest standing crop of all species collected.

Emigration rates for open sample methods were high because of the high catchability and associated high propensity to drift of the more common species, and resulted in reduced resolution between stressed and nonstressed communities. The evenness of Surber collections increased rapidly with increased pooling, and in the unstressed community eventually approximated the evenness of Hess collections. Population estimates derived from Kicknet methods exhibited higher evenness diversities in the stressed community than in the unstressed community. Evenness diversity differences for Kicknet methods resulted primarily from the emigration of the common species from samples taken in the stressed community.

Applications of the Removal Method in Aquatic Ecology

The removal method is suitable for any sampling situation for which it is suspected that the probability of capture is significantly less than 100%. In order to achieve meaningful estimates, the assumptions of a stable population and equal probability of capture must be upheld. Low precision is a limitation of the method when both the population and probability of capture are small, although accuracy will always be improved.

The removal method has been used extensively by fisheries biologists, primarily to estimate the fish populations of small streams. An electroshocker is the most common device used, and as with benthic invertebrates, differences in the probability of capture for different species and size classes exist. The value of the removal method when used in conjunction with benthic sieving devices has been demonstrated. Results indicated improved efficiency with the CDS in the estimation of benthic populations and diversity. The successful use of the CDS in pool areas which lacked current suggest that the removal method could be used in lentic sampling. In water more than 0.5 meter in depth, a covered depletion device could be used to sample bottom substrates or macrophytes. Samples would be much larger than the standard stovepipe samples, and could be collected in about one-third the time, and would contain a comparably small amount of extraneous material. Divers could use the same device in deeper water, and less substrate material would be collected than with grabs or cores. A jet of water pumped from a boat could also aid the diver in sieving or a suction dome could be used to collect depletion data. Suction domes could be interfaced with a filtering device aboard ship and equipped with a backwash to enable the easy removal of samples.

Another application of the removal method is in the estimation of periphyton communities from collected substrate material. Removal estimates can be made if the periphyton is removed from substrates with equal effort over specified time intervals and if catches are recorded for each life form. The method would also indicate which forms had low catchability, and precision when low could be increased by increasing the number of removal periods.

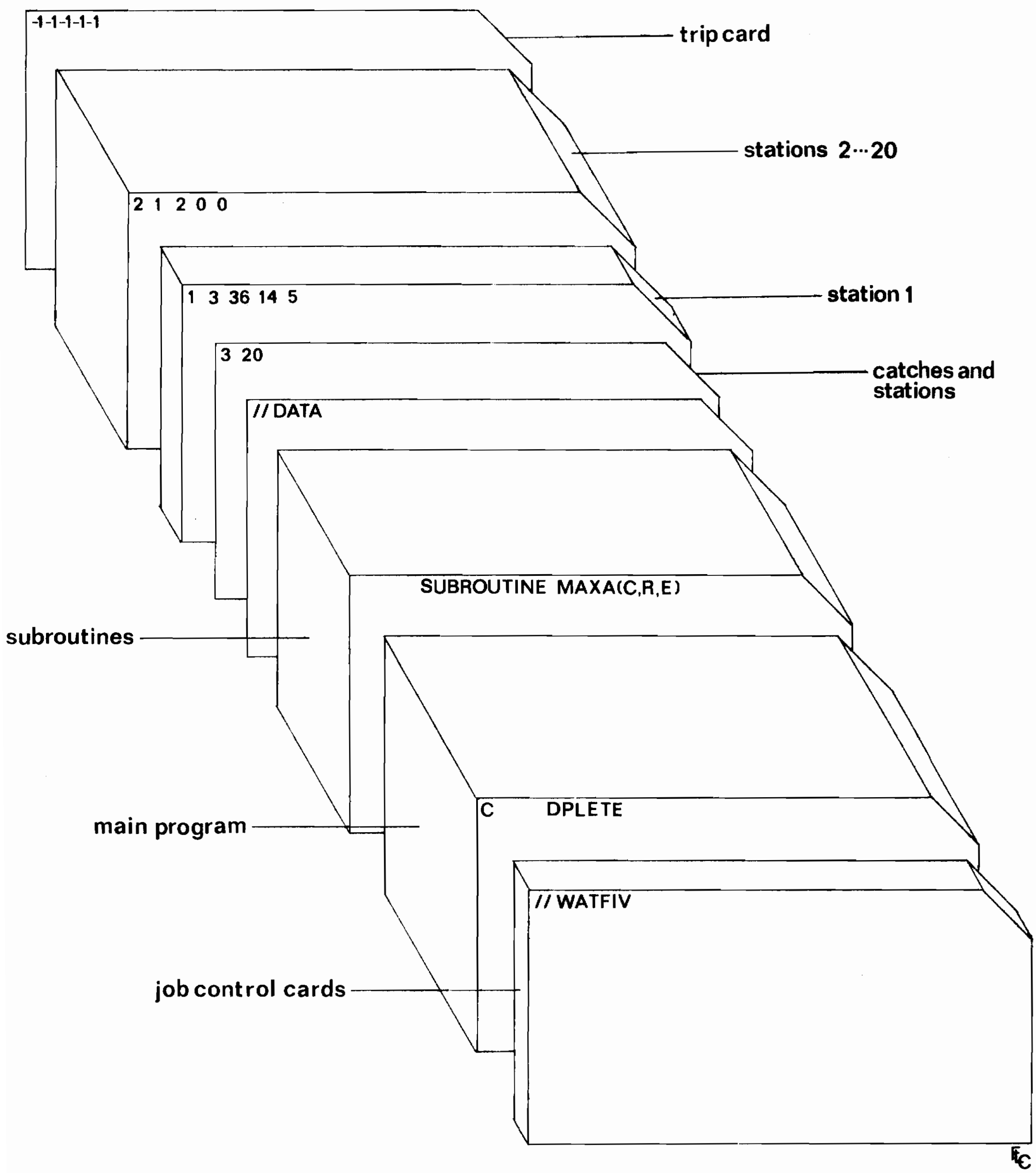
DPLETE, a Computer Program for Calculating Population Estimates and Diversity from Removal Data

The description of biological communities is a primary objective in most ecological studies. Indices of diversity, especially those involving information theory, require extensive calculation before analysis and use. Evenness diversity in this program was calculated with equation (4) and depletion estimates were determined using the method suggested by Carle and Strub (1976). The program was developed specifically for the analysis of benthic communities, but it can be used for any ecological study for which depletion information has been collected.

If a community of organisms is distributed randomly, random samples will provide unbiased estimates of population means and variances. However, if the community is characterized by populations with contagious distributions, as are benthic populations, evenness diversity will vary depending on the opposing effects of adding rare species and the effect of changing average population estimates for common species. A modification of a pooling method suggested by Pielou (1966) can be used to determine if the true diversity has, in fact, been attained. A reduction in variability is achieved over Pielou's method by using the average population estimates for each level of pooling to determine diversity. When several samples are taken the average of all possible combinations of samples becomes prohibitive. Therefore, the program made random sample combinations for each pooling level, determined diversity, and printed the result to allow the determination of when the averages became stabilized.

The program will accept up to 20 samples and 200 species with 3 catches for each sample/species combination. The program utilizes the format-free input option so that a space between each data entry is the only format required. The first data card specifies the number of catch periods used and also the number of samples taken. All following data cards contain actual species catch data. The first entry on following data cards is the sample number (ST), the second is the species number (SP), and finally the catches in successive order from catch 1 to catch 3. Examples of data cards are shown in Fig. 8 for sample 1,

Fig. 8. Arrangement of program deck and data cards for DPLETE.


-1-1-1-1-1
trip card
stations 2···20
2 1 2 0 0
1 3 36 14 5
station 1
3 20
catches and stations
// DATA
SUBROUTINE MAXA(C,R,E)
subroutines
C DPLETE
main program
// WATFIV
job control cards

species 3, and successive catches 36, 14, and 5; and for sample 2, species 1, and successive catches 2, 0, and 0. The last data card is the trip card and should contain 5 negative ones. The main calling program and subroutines of DPLETE are presented in Appendix D.

SUMMARY AND CONCLUSIONS

The estimation of populations and the determination of community structure are generally biased by sampling inefficiency. Bias in the estimation of benthic populations can be attributed to emigration, inconsistent sample delineation, and differential catchability. Catchability can be different for each species or developmental stage and is influenced by collector, sampler, and environmental differences. In an attempt to eliminate these sampling biases, a one-third square meter Circular Depletion Sampler (the CDS), was constructed and equipped with a detachable collecting bottle. Multiple 1-minute subsamples were taken with equal effort at each sample location and used to calculate catchability coefficients and sample population estimates.

The sampling efficiencies of the CDS were compared to the efficiencies of standard sieving devices. The methods were compared on several ecologically-matched sample sites. Sample estimates for benthic organisms determined from data collected with the CDS were consistently higher and less variable than estimates from Modified Hess, Surber, and Kicknet samples. Probabilities of capture were calculated for selected taxa collected in CDS samples. The lowest catchabilities were found for the case-building Trichoptera, and various Diptera, Annelida, and Mollusca. The highest catchabilities were found for the smaller Chironomidae and the nonburrowing Ephemeroptera. Probabilities of emigration were determined for open sampling methods and were generally highest for those taxa with high catchability. Pooled diversity estimates calculated from Modified Hess, Surber, and Kicknet samples were significantly affected by differences in catchability or emigration or both. Diversity estimates made from CDS samples are adjusted for differences in catchability, not affected by emigration or immigration, and also have an increased probability of correctly representing the rare species in a community. The efficiency of the CDS and improved accuracy of depletion estimates ideally suit the removal sampling method for estimating benthic populations, for evaluating pollution stress in aquatic communities, and for ecological research in general where the probability of capture is less than 100% and tagging is unfeasible.

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APPENDIX A

Benthic Data

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods.

	(Sample site 1)					
	DEP					
Taxa	CH1 (Hess)	CH2	CH3	SUR	SRK	KIC
ANNELIDA						
OLIGOCHAETA						
Opisthopora						
Lumbricidae						
Eiseniella spp.	1	2	0	0	1	0
ARTHROPODA						
ARACHNIDA						
Acari						
Hygrobatidae						
Atractides(atractides)	0	1	0	0	0	0
Hygrobates(hygrobates)	0	1	1	0	0	0
Sperchonidae						
Sperchon sp. A	11	3	2	0	0	0
Torrenticolidae						
Tottenticola(rusetria)	21	16	8	0	0	0
CRUSTACEA						
Amphipoda						
Talitridae						
Hyalella azteca	0	0	0	0	1	0
Decapoda						
Astacidae						
Cambarus longulus	1	0	0	0	0	0
Isopoda						
Asellidae						
Asellus militaris	1	1	0	0	0	0
INSECTA						
Coleoptera						
Elmidae						
Dubiraphia quadrionotata	4	1	2	2	1	1
Limnius lativsculus	112	22	16	0	1	3
Macronychus galabratus	1	0	0	0	1	0
Optioservus trivitatus	26	8	3	15	38	0
Promorsia tardella	4	1	1	1	3	0
Stenelmis sandersoni	3	1	0	2	2	0
Hydrophilidae						
Paracymus sp. A	1	0	0	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 1)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Psephenidae						
Ectoparia nervosa	1	0	0	0	1	0
Psephenus herichi	23	9	8	11	45	2
Diptera						
Blepharoceridae						
Blepharocera sp. A	0	1	0	0	1	0
Chironomidae						
Cardiocladius obscura	3	2	0	0	0	0
Chironomus sp. A	1	0	0	0	0	0
Cricotopus sp. A	4	3	0	0	0	0
Cricotopus sp. B	6	0	0	1	0	0
Cricotopus sp. C	0	0	0	2	0	0
Cricotopus sp. D	3	0	0	0	0	0
Cryptochironomus sp. A	1	0	0	0	0	0
Eukiefferiella sp. A	2	2	0	3	0	0
Microtendipes sp. A	1	0	0	1	2	0
Nanocladius sp. A	2	0	0	0	0	0
Orthocladius sp. A	0	0	1	0	0	0
Prodiamesa sp. A	2	0	0	0	0	0
Pseudochironomus sp. A	0	1	0	0	2	0
Thienemanniella sp. A	4	0	0	0	0	0
Tribelos sp. A	0	0	0	0	0	0
Empidiae						
Roederiodes sp. A	1	0	0	0	0	0
Rhagionidae						
Atherix variegata	1	0	0	0	1	0
Tipulidae						
Dicranota sp. A	1	0	0	0	0	0
Hexatoma sp. A	1	0	0	0	0	0
Limonia sp. A	0	1	0	0	0	0
Tipula abdominalis	1	0	0	0	0	0
Ephemeroptera						
Baetidae						
Baetis sp. A	3	1	0	0	0	0
Baetis herodes	2	0	0	0	0	0
Baetis vagans	5	0	0	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 1)

Taxa	DEP CH1 (Hess)	CH2	CH3	SUR	SRK	KIC
Ephemerellidae						
Ephemerella bicolor	56	5	1	5	4	0
Ephemerella deficiens	34	5	1	0	2	1
Ephemerella rotunda	78	9	2	0	9	3
Ephemerella subvaria	2	0	0	0	2	0
Heptageniidae						
Epeorus dispar	18	0	1	2	0	0
Heptagenia sp. A	3	0	0	2	2	0
Stenacron heterotarsale	5	1	0	1	0	0
Stenonema ithica	13	1	0	4	2	1
Stenonema pulchellum	5	0	0	0	0	0
Stenonema rubrum	22	1	0	6	5	1
Stenonema vicarium	48	3	1	7	11	5
Leptophlebiidae						
Paraleptophlebia mollis	11	0	0	0	0	0
Potamanthidae						
Potamanthus myops	2	0	0	0	9	0
Siphlonuridae						
Isonychia bicolor	7	1	0	0	5	4
Megaloptera						
Corydalidae						
Nigronia fasciata	5	3	3	0	3	1
Odonata						
Coenagrionidae						
Agria translata	4	0	0	0	1	0
Gomphidae						
Gomphurus externus	0	0	0	0	1	0
Stylogomphus albistylus	0	0	0	1	0	0
Plecoptera						
Capniidae						
Allocapnia sp. A	2	0	0	0	0	0
Paracapnia sp. A	4	0	0	0	0	0
Paracapnia sp. B	1	1	0	1	0	0
Chloroperlidae						
Alloperla sp. A	5	0	0	0	0	0
Isoperlidae						
Isoperla sp. A	23	3	0	3	2	1

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 1)

Taxa	DEP					
	CH1 (Hess)	CH2	CH3	SUR	SRK	KIC
Leuctridae						
Leuctra sp. A	1	0	0	0	0	0
Nemouridae						
Nemoura sp. A	4	0	0	0	0	0
Perlidae						
Phasganophora capitata	1	0	0	0	0	0
Taeniopterygidae						
Brachyptera sp. A	2	0	0	0	0	0
Trichoptera						
Brachycentridae						
Micrasema rusticum	2	1	1	1	6	0
Glossosomatidae						
Glossosoma sp. A	0	0	2	2	2	0
Helicopsychidae						
Helicopsyche borealis	1	1	0	0	1	0
Hydropsychidae						
Cheumatopsyche minuscula	25	3	0	2	4	2
Cheumatopsyche spp.	16	2	1	3	3	0
Hydropsyche betteni	5	1	0	4	0	2
Hydropsyche bifida	10	1	0	3	2	0
Hydropsyche bronta	9	1	0	1	3	0
Hydropsyche hageni	1	0	1	3	0	0
Hydropsyche slossonae	5	2	1	0	1	0
Lepidostomatidae						
Lepidostoma sp. A	1	0	0	0	1	0
Limnephilidae						
Neophylax sp. A	1	2	0	1	2	1
Pyenopsyche sp. A	2	3	0	1	2	1
Philopotamidae						
Chimarra aterrima	0	0	1	0	0	0
Chimarra obscura	2	2	0	0	0	0
Chimarra socia	3	2	0	0	3	1
Psychomyiidae						
Neureclipsis crepuscularis	0	0	0	1	0	0
Polycentropus sp. A	1	0	0	0	0	0
Rhyacophilidae						
Rhyacophila sp. A	0	0	1	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
			(Sample site 1)			
MOLLUSCA						
GASTROPODA						
Basommatophora						
Ancylidae						
Ferrissia sp. A	0	0	0	0	1	0
Planorbidae						
Gyraulus sp. A	0	1	0	0	0	0
Mesogastropoda						
Pleuroceridae						
Mudalia carinata	7	12	8	13	56	11
PELECYPODA						
Heterodonta						
Sphaeriidae						
Sphaerium simile	0	0	0	0	2	0
NEMATODA	1	0	0	0	0	0
PLATYHELMINTHES						
TURBELLARIA						
Tricladida						
Planariidae						
Cura foremanii	1	0	1	0	0	0
			(Sample site 2)			
ANNELIDA						
OLIGOCHAETA						
Opisthopora						
Lumbricidae						
Eiseniella spp.	1	0	0	2	1	0
ARTHROPODA						
ARACHNIDA						
Acari						
Sperchonidae						
Sperchon sp. A	3	0	0	0	0	0
Torrenticolidae						
Torrenticola(rusetria)	5	0	0	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 2)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
CRUSTACEA						
Decapoda						
Astacidae						
Cambarus longulus	0	0	0	0	1	0
INSECTA						
Coleoptera						
Elmidae						
Dubiraphia quadrionotata	4	3	0	1	0	0
Limnius lativsculus	4	1	2	1	0	0
Optioservus trivitatus	46	14	7	24	17	14
Promorsia tardella	1	0	0	2	1	0
Stenelmis sandersoni	1	2	0	1	0	0
Hydraenidae						
Hydraena sp. A	0	0	0	0	1	0
Psephenidae						
Psephenus herichi	7	4	0	2	9	4
Diptera						
Chironomidae						
Cricotopus sp. B	1	0	0	0	0	0
Eukiefferiella sp. A	2	0	0	1	0	0
Microtendipes sp. A	0	2	0	0	1	0
Nanocladius sp. A	1	0	0	0	0	0
Polypedilum sp. A	1	0	0	0	0	0
Prodiamesa sp. A	1	0	0	0	0	0
Rheocricotopus sp. A	0	2	0	0	0	0
Thienemanniella sp. A	11	2	3	0	0	1
Tribelos sp. A	1	2	0	2	0	0
Tipulidae						
Hexatoma sp. A	0	1	0	0	0	0
Ephemeroptera						
Baetidae						
Baetis herodes	2	1	0	0	0	0
Ephemerellidae						
Ephemerella bicolor	36	4	0	2	2	1
Ephemerella deficiens	12	4	0	0	0	0
Ephemerella rotunda	8	0	0	0	2	0
Ephemerella subvaria	0	1	0	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 2)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Heptageniidae						
Epeorus dispar	7	0	0	0	0	0
Heptagenia sp. A	1	0	1	0	0	0
Stenacron frontale	2	0	0	1	0	0
Stenacron heterotarsale	8	1	0	0	0	0
Stenonema ithica	2	0	0	1	1	0
Stenonema pulchellum	2	0	0	0	0	0
Stenonema rubrum	8	1	0	0	2	0
Stenonema vicarium	32	7	0	4	10	6
Leptophlebiidae						
Paraleptophlebia mollis	1	0	0	0	0	0
Potamthidae						
Potamanthus myops	4	1	0	0	0	0
Siphlonuridae						
Isonychia bicolor	8	1	0	0	2	2
Lepidoptera						
Pyralididae						
Paragyractis sp. A	1	0	0	0	0	0
Megaloptera						
Corydalidae						
Nigronia fasciata	0	0	1	0	1	0
Odonata						
Coenagrionidae						
Agria translata	2	3	0	0	0	0
Gomphidae						
Ophiogomphus rupensulensis	1	0	0	0	0	0
Plecoptera						
Capniidae						
Paracapnia sp. A	1	0	0	0	0	0
Chloroperlidae						
Alloperla sp. A	3	0	0	1	1	0
Isoperlidae						
Isoperla sp. A	5	3	0	1	0	0
Leuctridae						
Leuctra sp. A	0	1	0	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 2)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Trichoptera						
Helicopsychidae						
Helicopsyche borealis	0	1	1	0	1	0
Hydropsychidae						
Cheumatopsyche minuscula	1	0	1	2	1	0
Cheumatopsyche spp.	13	9	0	0	0	1
Hydropsyche betteni	0	1	0	0	0	0
Hydropsyche bifida	1	0	0	0	0	0
Hydropsyche bronta	7	0	0	0	1	1
Hydropsyche slossonae	0	0	0	1	0	0
Limnephilidae						
Neophylax sp. A	0	0	0	0	0	1
Pycnopsyche sp. A	6	1	0	1	2	0
Philopotamidae						
Chimarra obscura	1	1	0	1	0	0
Chimarra socia	2	2	0	0	1	0
Psychomyiidae						
Polycentropus sp. A	0	1	0	0	0	0
MOLLUSCA						
GASTROPODA						
Basommatophora						
Planorbidae						
Gyraulus sp. A	0	1	0	0	0	0
Mesogastropoda						
Pleuroceridae						
Mudalia carinata	4	8	6	6	14	4

(Sample site 3)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
ARTHROPODA						
ARACHNIDA						
Acari						
Hygrobatidae						
Hygrobates (hygrobates)	1	1	0	1	0	0
Sperchonidae						
Sperchon sp. A	8	0	0	1	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 3)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
CRUSTACEA						
Isopoda sp. A	1	0	0	0	0	0
INSECTA						
Coleoptera						
Elmidae						
Limnius lativsculus	1	0	0	0	0	0
Optioservus trivitatus	18	7	0	11	5	2
Promorsia tardella	2	2	0	1	0	1
Stenelmis sandersoni	0	1	0	0	0	0
Psephenidae						
Psephenus herichi	2	2	1	0	1	0
Diptera						
Chironomidae						
Cricotopus sp. A	0	1	0	0	0	0
Cricotopus sp. D	1	1	0	0	0	0
Eukiefferella sp. A	0	0	0	0	1	0
Rhagionidae						
Atherix variegata	1	0	0	0	0	0
Ephemeroptera						
Baetidae						
Baetis vagans	2	0	0	0	0	0
Caenidae						
Caenis sp. A	0	1	0	0	0	0
Ephemerellidae						
Ephemerella aestiva	0	0	0	0	1	0
Ephemerella bicolor	6	0	1	0	2	0
Ephemerella deficiens	5	3	0	0	0	0
Ephemerella rotunda	23	4	1	0	3	2
Ephemerella subvaria	1	0	0	0	0	0
Heptageniidae						
Epeorus dispar	11	1	0	0	0	0
Rhithrogena sp. A	1	0	0	0	0	0
Stenonema ithica	4	0	0	0	0	0
Stenonema pulchellum	2	0	0	1	0	0
Stenonema rubrum	12	0	0	1	0	1
Stenonema vicarium	33	4	1	1	1	1

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 3)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Potamanthidae						
Potamanthus myops	0	1	0	0	1	0
Siphlonuridae						
Isonychia bicolor	5	1	0	0	1	1
Plecoptera						
Capniidae						
Paracapnia sp. A	2	0	0	0	0	0
Isoperlidae						
Isoperla sp. A	7	2	0	0	0	1
Isoperla sp. B	1	0	0	0	0	0
Nemouridae						
Nemoura sp. A	1	0	0	0	0	0
Perlidae						
Acroneuria abnormis	1	0	0	0	2	0
Taeniopterygidae						
Brachyptera sp. A	4	1	0	0	0	0
Trichoptera						
Hydropsychidae						
Cheumatopsyche minuscula	5	0	1	0	0	0
Cheumatopsyche spp.	2	0	0	1	2	0
Hydropsyche betteni	0	0	0	0	2	0
Hydropsyche bifida	2	0	1	0	1	0
Hydropsyche bronta	6	2	0	0	2	6
Hydropsyche slossonae	2	1	0	0	0	0
Lepidostomatidae						
Lepidostoma sp. A	1	0	0	0	0	0
Limnephilidae						
Pycnopsyche sp. A	0	0	1	0	0	0
Philopotamidae						
Chimarra obscura	1	0	0	0	0	0
Chimarra socia	1	0	0	0	0	0
MOLLUSCA						
GASTROPODA						
Mesogastropoda						
Pleuroceridae						
Mudalia carinata	0	0	0	1	2	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

	(Sample site 4)					
	DEP					
Taxa	CH1 (Hess)	CH2	CH3	SUR	SRK	KIC
ANNELIDA						
OLIGOCHAETA						
Opisthopora						
Lumbricidae						
Eiseniella spp.	0	0	0	0	1	0
ARTHROPODA						
ARACHNIDA						
Acari						
Sperchonidae						
Sperchon sp. A	9	1	0	0	0	0
CRUSTACEA						
Isopoda sp. A	0	0	1	0	0	0
INSECTA						
Coleoptera						
Elmidae						
Dubiraphia quadrionotata	3	0	0	0	0	0
Limnius latiusculus	3	1	3	0	0	0
Optioservus trivitatus	69	21	12	15	8	9
Promoresia tardella	19	14	8	5	0	0
Stenelmis sandersoni	2	3	1	3	0	0
Histeridae sp. A	1	0	0	0	0	0
Psephenidae						
Ectoparia nervosa	4	1	1	1	0	0
Psephenus herichi	29	22	5	3	5	0
Diptera						
Ceratopogonidae						
Atrichopogon sp. A	1	0	0	0	0	0
Chironomidae						
Cardiocladius obscura	0	0	0	1	0	0
Cricotopus sp. B	1	0	0	0	0	0
Eukiefferiella sp. A	11	1	0	1	0	0
Micropsectra sp. A	1	0	0	0	0	0
Microtendipes sp. A	3	1	2	2	1	1
Nanocladius sp. A	2	0	0	0	0	0
Orthocladius sp. A	1	0	0	0	0	0
Prodiamesa sp. A	0	0	0	0	1	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 4)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Pseudochironomus sp. A	0	1	0	0	0	0
Rheocricotopus sp. A	3	1	0	0	0	0
Rheocricotopus sp. B	5	0	0	0	0	0
Tanytarsus sp. A	1	0	0	0	0	0
Tanytarsus sp. B	2	1	0	0	0	0
Thienemanniella sp. A	7	2	0	1	0	1
Rhagionidae						
Atherix variegata	2	0	0	0	1	0
Tipulidae						
Antocha sp. A	1	0	0	0	0	0
Hexatoma sp. B	0	1	0	0	0	0
Ephemeroptera						
Baetidae						
Baetis herodes	3	0	0	0	0	0
Baetis vagans	4	0	0	1	0	0
Caenidae						
Caenis sp. A	1	1	0	0	0	0
Ephemerellidae						
Ephemerella aestiva	4	1	0	1	0	0
Ephemerella bicolor	67	11	2	5	5	0
Ephemerella deficiens	50	2	0	3	1	1
Ephemerella rotunda	49	4	0	2	2	2
Ephemerella subvaria	2	0	0	1	0	0
Heptageniidae						
Epeorus dispar	17	0	0	7	0	1
Stenacron heterotarsale	5	0	0	0	0	0
Stenacron frontale	1	0	0	0	0	0
Stenonema anexium	1	0	0	0	0	0
Stenonema ithica	5	0	0	0	1	0
Stenonema pulchellum	3	0	0	1	0	0
Stenonema rubrum	41	0	0	2	1	0
Stenonema vicarium	77	4	1	5	33	25
Leptophlebiidae						
Paraleptophlebia mollis	1	0	0	0	1	0
Potamanthidae						
Potamanthus myops	9	5	2	1	3	2

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 4)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Siphlonuridae						
Isonychia bicolor	18	1	1	2	5	3
Hemiptera						
Gerridae						
Metrobates hesperius	0	0	0	2	0	0
Lepidoptera						
Pyralididae						
Paragyractis sp. A	0	0	1	0	0	0
Megaloptera						
Corydalidae						
Nigronia fasciata	0	0	0	1	0	0
Odonata						
Coenagrionidae						
Agria translata	4	0	0	0	2	0
Gomphidae						
Dromogomphus spinosus	0	0	0	0	1	0
Gomphus descriptus	1	0	0	0	0	0
Hagenius brevistylus	0	0	1	0	0	0
Stylogomphus albistylus	1	0	0	0	0	0
Macromiidae						
Macromia alleghaniensis	0	0	0	0	1	0
Plecoptera						
Capniidae						
Allocapnia sp. A	1	0	0	0	0	0
Paracapnia sp. A	3	0	0	1	0	0
Chloroperlidae						
Alloperla sp. A	4	0	1	0	1	0
Isoperlidae						
Isoperla sp. A	12	1	2	1	2	0
Nemouridae						
Nemoura sp. A	1	0	0	0	0	1
Perlidae						
Acroneura abnormis	0	1	0	0	1	0
Taeniopterygidae						
Brachyptera sp. A	1	0	0	0	0	0
Taeniopteryx sp. A	0	1	0	0	0	0

Appendix Table I. Species list and number of individuals collected per sample site above Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and Kicknet sampling methods (continued).

(Sample site 4)

Taxa	DEP CH1 (Hess)	DEP CH2	DEP CH3	SUR	SRK	KIC
Trichoptera						
Brachycentridae						
Micrasema rusticum	3	2	0	0	0	1
Glossosomatidae						
Protoptila sp. A	0	0	1	0	0	0
Helicopsychidae						
Helicopsyche borealis	4	2	2	1	0	0
Hydropsychidae						
Cheumatopsyche minuscula	17	2	4	0	3	0
Cheumatopsyche spp.	14	2	1	4	1	2
Hydropsyche sp. A	0	0	1	0	0	0
Hydropsyche betteni	0	0	1	2	0	0
Hydropsyche bifida	0	0	0	6	3	0
Hydropsyche bronta	5	5	1	3	0	1
Hydropsyche hageni	3	1	1	0	0	0
Hydropsyche slossonae	2	1	0	0	1	0
Hydroptilidae						
Ochrotricha spinosa	2	0	0	0	0	0
Limnephilidae						
Neophylax sp. A	1	1	0	1	1	0
Pycnopsyche sp. A	4	2	0	1	0	2
Philopotamidae						
Chimarra aterrima	0	0	0	1	0	0
Chimarra obscura	2	1	1	1	0	0
Chimarra socia	4	2	1	2	0	0
Psychomyiidae						
Neurelipsis crepuscularis	1	0	0	0	0	0
Polycentropus sp. A	0	0	0	1	0	0
MOLLUSCA						
GASTROPODA						
Mesogastropoda						
Bythiniidae						
Pomatiopsis sp. A	1	0	0	0	0	0
Pleuroceridae						
Mudalia carinata	3	2	2	2	2	1
NEMATODA	1	0	0	0	0	0

Appendix Table II. Species list and total number of individuals collected for 16 benthic samples taken below Covington on the Jackson River, Virginia, with Depletion, Modified Hess, Surber, and 2 Kicknet sampling methods.[a]

Taxa	DEP[b]	HESS	SUR	SRK	KICK
ANNELIDA					
HIRUDINEA					
Arhynchobdellida					
Erpobdellidae					
Erpobdella punctata	8	4	3	3	0
OLIGOCHAETA					
Opisthopora					
Lumbricidae					
Eiseniella spp.	1	0	0	0	0
Plesiopora					
Tubificidae					
Bothrioneurum veidovskyanum	15	10	2	0	0
Limnodrilus sp. A	3	1	1	0	0
Prosopora					
Lumbriculidae					
Lumbriculus varigatus	497	392	95	235	149
ARTHROPODA					
ARACHNIDA					
Acari					
Sperchonidae					
Sperchonopsis verrucosa	1	1	0	0	0
Torrenticolidae					
Torrenticola sp. A	0	0	0	1	0
CRUSTACEA					
Amphipoda					
Talitridae					
Hyalella azteca	0	0	0	1	0
Isopoda					
Asellidae					
Asellus militaris	284	191	115	128	62
INSECTA					
Coleoptera					
Dryopidae					
Helichus lithophylis	2	0	0	0	0
Elmidae					
Dubiraphia vittata	44	29	13	23	9
Macronychus galabratus	2	1	0	0	0
Microcylloepus pusillus	81	55	11	20	1
Optioservus trivitatus	147	120	42	45	21
Promoresia tardella	13	8	2	3	0
Stenelmis crenata	41	29	6	8	1
Stenelmis concinna	1	0	0	0	0
Stenelmis lateralis	89	58	10	16	5

Appendix Table II. Species list and total number of individuals collected for 16 benthic samples taken below Covington on the Jackson River, Virginia, with Depletion, Modified Hess, and 2 Kicknet sampling methods[a] (continued).

Taxa	DEP[b]	HESS	SUR	SRK	KICK
Hydrophilidae					
Berosus sp. A	82	64	13	24	7
Limnichidae					
Lutrochus laticeps	1	0	0	0	0
Psephenidae					
Ectoparia nervosa	2	2	0	1	0
Psephenus herichi	71	47	15	23	9
Diptera					
Ceratopogonidae					
Dasyhelia sp. A	1	1	1	1	0
Palpomyia sp. A	1	1	0	0	0
Chironomidae					
Cardiocladius obscura	713	393	104	126	72
Chironomus sp. B	49	38	7	4	1
Cricotopus sp. A	5	3	0	2	0
Cricotopus sp. C	13	7	1	1	0
Cricotopus sp. D	4	4	7	0	0
Cricotopus sp. E	102	68	14	39	13
Cryptochironomus sp. B	18	17	1	2	0
Endochironomus sp. A	1	1	0	0	0
Guttipelopia sp. A	1834	1496	260	220	102
Micropsectra sp. A	1	1	0	0	0
Microtendipes sp. B	0	0	2	0	0
Nanocladius sp. A	1	0	0	0	0
Polypedilum sp. A	2	2	0	0	0
Procladius sp. A	1	1	1	0	0
Psectrocladius sp. A	4	1	2	0	0
Pseudochironomus sp. A	1	1	0	0	0
Rheocricotopus sp. A	58	37	2	14	0
Rheocricotopus sp. B	26	23	2	3	0
Tanytarsus sp. B	8	7	0	0	0
Empididae					
Hemerodromia spp.	248	189	43	32	15
Simuliidae					
Simulum vittatum	5	2	0	0	0
Tipulidae					
Antocha spp.	4	1	1	3	0
Ephemeroptera					
Baetidae					
Baetis sp. B	1	1	0	0	0
Heterocloeon curisosum	6	1	0	2	0

Appendix Table II. Species list and total number of individuals collected for 16 benthic samples taken below Covington on the Jackson River, Virginia, with Depletion, Modified Hess, and 2 Kicknet sampling methods[a] (continued).

Taxa	DEP[b]	HESS	SUR	SRK	KICK
Caenidae					
Caenis spp.	3	1	0	0	0
Ephemerellidae					
Ephemerella bicolor	54	48	5	5	2
Heptageniidae					
Epeorus dispar	0	0	0	1	0
Stenonema rubrum	1	1	0	0	0
Stenonema vicarium	5	2	0	0	0
Siphlonuridae					
Isonychia bicolor	2	1	0	0	0
Hemiptera					
Veliidae					
Rhagovelia obesa	1	1	1	0	0
Megaloptera					
Corydalidae					
Corydalus cornutus	313	226	69	134	44
Sialidae					
Sialis sp. A	3	2	0	1	1
Odonata					
Coenagrionidae					
Agria translata	2	1	0	1	0
Gomphidae					
Dromogomphus spinosus	1	0	0	0	0
Gomphurus externus	1	0	0	0	0
Ophiogomphus rupensulensis	1	0	0	0	0
Stylogomphus albistylus	3	1	0	0	0
Macromiidae					
Macromia alleghaniensis	0	0	0	0	2
Plecoptera					
Capniidae					
Paracapnia sp. A	0	0	1	0	0
Perlidae					
Acroneuria abnormis	46	34	7	8	4
Trichoptera					
Hydropsychidae					
Cheumatopsyche spp.	1	1	0	0	0
Hydropsyche betteni	122	74	21	52	39
Hydropsyche hageni	49	33	10	25	2
Hydropsyche sp. A	50	34	8	5	1
Philopotamidae					
Chimarra aterima	0	0	0	1	0

Appendix Table II. Species list and total number of individuals collected for 16 benthic samples taken below Covington on the Jackson River, Virginia, with Depletion, Modified Hess, and 2 Kicknet sampling methods[a] (continued).

Taxa	DEP[b]	HESS	SUR	SRK	KICK
MOLLUSCA					
GASTROPODA					
Basommatophora					
Ancylidae					
Ferrissia spp.	211	144	47	68	29
Physidae					
Physa gyrina	63	41	14	21	6
Planorbidae					
Gyraulus sp. A	87	55	24	32	13
Mesogastropoda					
Pleuroceridae					
Mudalia carinata	2	0	1	1	0
PELECYPODIA					
Heterodonata					
Sphaeriidae					
Sphaerium simile	8	6	0	2	0
NEMATODA	17	12	1	2	0
NEMATOMORPHA					
NEMATOMORPHA					
Gordiida					
Gordiidae					
Gordius sp. A	1	1	0	0	0

[a]With sample areas totaling 5.33, 5.33, 1.49, and 2.97 sq m, respectively.
[b]Removal estimates.

Appendix Table III. Species list, catch data, and population and catchability estimates from a CDS sample collected above the Gathright dam construction site on the Jackson River, Virginia.

Taxa	Catch 1	Catch 2	Catch 3	$\hat{N}$	$\hat{P}$
ARTHROPODA					
ARACHNIDA					
Acari					
Hygrobatidae					
Hygrobates (hygrobates)	11	2	0	13	0.867
Lebertiidae					
Lebertia (pilolibertia)	4	1	0	5	0.833
Sperchonidae					
Sperchononpsis verrucosa	1	0	0	1	1.000
CRUSTACEA					
Decapoda					
Astacidae					
Cambarus longulus	3	0	0	3	1.000
INSECTA					
Coleoptera					
Elmidae					
Dubiraphia quadrinotata	2	0	0	2	1.000
Gonielmis dietrichi	7	2	0	9	0.818
Optioservus trivitatus	26	7	3	36	0.735
Optioservus (larvae)	132	110	93	740	0.181
Promorsia tardella	4	4	1	9	0.600
Stenelmis crenata	12	0	1	13	0.867
Stenelmis (larvae)	16	19	6	53	0.380
Psephenidae					
Ectoparia nervosa	1	0	0	1	1.000
Psephenus herichi	26	9	6	43	0.603
Diptera					
Chironomidae					
Cricotopus sp. D	2	0	0	2	1.000
Epoieocladious sp. A	0	0	1	1	0.333
Gutipelopia sp. A	28	4	0	32	0.889
Micropsectra sp. A	23	0	2	25	0.862
Microtendipes sp. A	0	0	1	1	0.333
Nanocladius sp. B	1	0	0	1	1.000
Prodiamesa sp. A	1	0	0	1	1.000
Tanytarsus sp. A	183	14	0	197	0.934
Tribelos sp. A	0	0	1	1	0.333
Empididae					
Hemerodromia	2	0	0	2	1.000
Rhagionidae					
Atherix variegata	1	1	0	2	0.667

Appendix Table III. Species list, catch data, and population and catchability estimates from a CDS sample collected above the Gathright dam construction site on the Jackson River, Virginia (continued).

Taxa	Catch 1	Catch 2	Catch 3	$\hat{N}$	$\hat{P}$
Tipulidae					
Antocha spp.	2	4	0	6	0.600
Eriocera spp.	0	1	0	1	0.500
Ephemeroptera					
Baetidae					
Pseudocloen myrsum	0	1	0	1	0.500
Caenidae					
Caenis sp. B	7	5	2	15	0.538
Ephemeridae					
Ephemera simulans	0	0	1	1	0.333
Heptageniidae					
Heptagenia aphrodite	0	1	0	1	0.500
Stenonema vicarium	0	1	0	1	0.500
Lepidoptera					
Pyralididae					
Paragyractis spp.	2	4	0	6	0.600
Megaloptera					
Corydalidae					
Nigronia fasciata	2	0	0	2	1.000
Plecoptera					
Leuctridae					
Leuctra spp.	3	4	0	7	0.636
Trichoptera					
Brachycentridae					
Brachycentrus notabulus	17	14	8	51	0.371
Helicopsychidae					
Helicopsyche borealis	2	4	1	7	0.538
Hydropsychidae					
Cheumatopsyche spp.	4	0	0	4	1.000
Hydropsyche bifida	3	1	1	5	0.625
Hydroptilidae					
Hydroptila sp. B	7	5	2	15	0.538
Limnephilidae					
Neophylax spp.	3	2	2	7	0.538
Pycnopsyche spp.	12	7	2	23	0.559
Philopotamidae					
Chimarra socia	1	0	0	1	1.000
Psychomyiidae					
Polycentropus sp. C	1	0	0	1	1.000
Rhyacophilidae					
Rhyacophila sp. B	0	2	0	2	0.500

Appendix Table III. Species list, catch data, and population and catchability estimates from a CDS sample collected above the Gathright dam construction site on the Jackson River, Virginia (continued).

Taxa	Catch 1	Catch 2	Catch 3	$\hat{N}$	$\hat{P}$
MOLLUSCA					
GASTROPODA					
Basommatophora					
Ancylidae					
Ferrissia spp.	1	0	0	1	1.000
Mesogastropoda					
Pleuroceridae					
Mudalia carinata	19	17	12	75	0.282

Appendix Table IV. Species list, catch data, and population and catchability estimates from a CDS sample collected below the Gathright dam construction site on the Jackson River, Virginia.

Taxa	Catch 1	Catch 2	Catch 3	N	P
ARTHROPODA					
CRUSTACEA					
Amphipoda					
Talitridae					
Hyalella azteca	1	0	0	1	1.000
Decapoda					
Astacidae					
Cambarus longulus	2	0	0	2	1.000
Isopoda					
Asellidae					
Asellus militaris	1	0	0	1	1.000
INSECTA					
Coleoptera					
Elmidae					
Optioservus trivitatus	2	0	0	2	1.000
Stenelmis sandersoni	0	1	1	2	0.400
Psephenidae					
Psephenus herichi	8	3	1	12	0.706
Diptera					
Chironomidae					
Microtendipes sp. A	5	0	0	5	1.000
Polypedilum sp. A	11	0	1	12	0.857
Rhagionidae					
Atherix variegata	4	0	0	4	1.000
Tipulidae					
Antocha spp.	1	0	0	1	1.000
Tipula abdominalis	1	0	0	1	1.000
Ephemeroptera					
Baetidae					
Baetis levitens	2	0	0	2	1.000
Pseudocloeon carolina	0	2	0	2	0.500
Caenidae					
Caenis sp. B	1	1	0	2	0.667
Ephemerellidae					
Ephemerella deficiens	3	2	2	7	0.538
Ephemeridae					
Ephemera simulans	1	0	0	1	1.000
Heptageniidae					
Epeorus rubidus	0	2	0	2	0.500
Stenonema vicarium	0	0	1	1	0.333

Appendix Table IV. Species list, catch data, and population and catchability estimates from a CDS sample collected below the Gathright dam construction site on the Jackson River, Virginia (continued).

Taxa	Catch 1	2	3	N	P
Megaloptera					
Corydalidae					
<u>Corydalus cornutus</u>	0	1	0	1	0.500
Odonata					
Gomphidae					
<u>Gomphus descriptus</u>	1	0	0	1	1.000
<u>Stylogomphus albistylus</u>	2	0	0	2	1.000
Plecoptera					
Perlidae					
<u>Acroneuria abnormis</u>	0	1	0	1	0.500
Trichoptera					
Hydropsychidae					
<u>Cheumatopsyche</u> spp.	0	0	1	1	0.333
<u>Hydropsyche bifida</u>	2	0	1	3	0.600
Philopotamidae					
<u>Chimarra obscura</u>	0	0	1	1	0.333
<u>Chimarra socia</u>	0	0	1	1	0.333
MOLLUSCA					
GASTROPODA					
Mesogastropoda					
Pleuroceridae					
<u>Mudalia carinata</u>	34	41	27	235	0.171
PELECYPODA					
Heterodonta					
Sphaeriidae					
<u>Sphaerium simile</u>	1	0	0	1	1.000

APPENDIX B

Diversity Data

Appendix Table I. Number of benthic species collected above and below Covington, Virginia, in Depletion, Modified Hess, Surber, and Kicknet samples.

Sample number*	Depletion	Modified Hess	Surber	SR Kicknet	Kicknet
1	85	75	31	43	17
2	55	45	20	21	10
3	40	35	9	15	8
4	77	67	37	27	15
5	29	25	16	21	11
6	20	19	10	13	4
7	29	22	11	12	4
8	23	21	15	15	5
9	28	23	15	19	13
10	32	28	17	19	11
11	28	27	17	19	12
12	30	24	13	15	4
13	34	31	22	18	13
14	33	32	16	22	8
15	31	28	14	24	12
16	25	21	10	14	8
17	28	25	16	18	7
18	26	19	11	13	8
19	26	18	8	10	2
20	19	15	7	13	3

*Samples 1-4 taken above Covington, 5-20 taken below Covington.

Appendix Table II. Evenness diversity (1-r) for benthic collections taken above and below Covington, Virginia, with Depletion, Modified Hess, Surber, and Kicknet samplers.

Sample number*	Depletion	Modified Hess	Surber	SR Kicknet	Kicknet
1	0.7332	0.7370	0.8102	0.6405	0.6852
2	0.7419	0.7499	0.4838	0.6201	0.6111
3	0.7413	0.7431	0.0000	0.7982	0.4430
4	0.7294	0.7320	0.7849	0.5644	0.4522
5	0.6168	0.5545	0.5845	0.6680	0.7154
6	0.5317	0.4684	0.5311	0.7384	0.8602
7	0.3435	0.3071	0.2120	0.1542	0.0000
8	0.4523	0.4551	0.3461	0.3259	0.2663
9	0.5135	0.6526	0.7233	0.8256	0.6283
10	0.6729	0.6976	0.7203	0.5882	0.4998
11	0.6255	0.6101	0.7922	0.7792	0.6249
12	0.5345	0.4217	0.4189	0.6732	0.6309
13	0.6239	0.7031	0.6797	0.7920	0.7450
14	0.7122	0.7045	0.6231	0.7608	0.7132
15	0.5505	0.5350	0.4067	0.8025	0.5434
16	0.5065	0.4793	0.5807	0.3890	0.3866
17	0.8080	0.8144	0.7200	0.6718	0.3966
18	0.6677	0.6280	0.6501	0.7729	0.6680
19	0.4677	0.4859	0.7965	0.4816	0.0000
20	0.4865	0.4747	0.6454	0.4636	0.2473

*Samples 1-4 taken above Covington, 5-20 below Covington.

APPENDIX C

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia.

Taxa	Catchability: Adults	Catchability: Larvae large-small	Catchability: Pupae
ANNELIDA			
HIRUDINEA			
Arhynchobdellida			
Erpobdellidae			
Erpobdella	--	0.615	--
OLIGOCHAETA			
Opisthopora			
Lumbricidae			
Eiseniella	--	0.220	--
Plesiopora			
Enchytraeidae			
Enchytraeus	--	0.561	--
Naididae			
Naidium	--	0.450	--
Nais	--	0.823	--
Pristina	--	0.741	--
Slavina	--	0.811	--
Stylaria	--	0.796	--
Tubificidae			
Branchiura	--	0.735	--
Bothrioneurum	--	0.714	--
Limnodrilus	--	0.534	--
Prosopora			
Branchiobdellidae			
Cambarincola	--	0.814	--
Lumbriculidae			
Lumbriculus	--	0.752	--
ARTHROPODA			
ARACHNIDA			
Acari	--	0.691	--
Araneida	--	0.860*	--
CRUSTACEA			
Amphipoda			
Grammaridae			
Crangonyx	--	0.667*	--
Talitridae			
Hyalella	--	0.750*	--
Cladocera	--	0.953	--
Copepoda	--	0.914	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability		
	Adults	Larvae large-small	Pupae
Decapoda			
Astacidae			
Cambarus	--	0.877	--
Orconectes	--	0.795	--
Palaemonidae			
Palaemonectes	--	0.750*	--
Isopoda			
Asellidae			
Asellus	--	0.653	--
Lirceus	--	0.831	--
Ostracoda	--	0.500*	--
INSECTA			
Coleoptera			
Dryopidae			
Helichus	--	0.656	--
Dyticidae			
Deronectes	--	0.550*	--
Laccophilus	--	0.650*	--
Elmidae			
Ancyronyx	0.842*	--	--
Dubiraphia	0.755	0.438	--
Gonielmis	0.714	0.411	--
Limnius	0.763	0.312	--
Macronychus	0.750	0.438	--
Microcylloepus	0.684	0.382	--
Optioservus	0.734	0.230	--
Promorsia	0.750*	0.372	--
Stenelmis	0.660	0.380	--
Gyrinidae			
Dineutus	--	0.768	--
Hydrophilidae			
Berosus	--	0.680	--
Cymbiodyta	--	0.750*	--
Enochrus	--	0.667	--
Hydrobius	--	0.535	--
Paracymus	--	0.750*	--
Psephenidae			
Ectoparia	--	0.750	--
Psephenus	--	0.548	--
Ptilodactylidae			
Anchytarsus	--	0.678	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability Adults	Catchability Larvae large-small	Catchability Pupae
Collembola			
Isotomidae			
Isotoma	--	0.882	--
Isotomurus	--	0.667*	--
Poduridae			
Hypogastrura	--	0.750*	--
Sminthuridae			
Sminthurides	--	0.875	--
Diptera			
Anthomyiidae			
Limnophora	--	0.500*	--
Blepharoceridae			
Blepharocera	--	0.424	0.504
Cecidomyiidae	--	0.310	
Ceratopogonidae	--	0.666	
Chironomidae	--	--	0.740
(Chironominae, Chironomini)			
Chironomus	--	0.782	--
Cryptochironomus	--	0.753	--
Demicryptochironomus	--	0.485	--
Dicrotendipes	--	0.512	--
Microtendipes	--	0.465	--
Paratendipes	--	0.960	--
Polypedilum	--	0.925	--
Pseudochironomus	--	0.402	--
Stenochironomus	--	0.500*	--
Stictochironomus	--	0.650	--
Tribelos	--	0.725	--
(Chironominae, Tanytarsini)			
Cladontanytarsus	--	0.923	--
Micropsectra	--	0.932	--
Rheotanytarsus	--	0.623	--
Stempellina	--	0.667*	--
Tanytarsus	--	0.881	--
(Orthocladiinae)			
Brillia	--	0.550	--
Cardiocladius	--	0.489	--
Corynoneura	--	0.940	--
Cricotopus	--	0.636	--
Eukiefferiella	--	0.857	--
Metriocnemus	--	0.813	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability Adults	Larvae large-small	Pupae
Nanocladius	--	0.724	--
Orthocladius	--	0.643	--
Psectrocladius	--	0.890	--
Rheocricotopus	--	0.886	--
Thienemanniella	--	0.775	--
(Tanypodinae)	--		
Ablabesyia	--	0.927	--
Conchapelopia	--	0.767	--
Guttipelopia	--	0.801	--
Larsia	--	0.556	--
Procladius	--	0.930*	--
Culicidae			
Chaoborus	--	0.921	--
Empididae	--	0.742	0.842
Rhagionidae			
Atherix	--	0.525	--
Simuliidae			
Prosimulum	--	0.805*	--
Simulum	--	0.736	--
Tabanidae			
Crysops	--	0.808*	--
Tabanus	--	0.748	--
Tanyderidae			
Protoplasa	--	0.550*	--
Tipulidae			
Antocha	--	0.190	--
Eriocera	--	0.461	--
Hexatoma	--	0.602	--
(Polymedia, Ormosia)	--	0.674	--
Pseudolimnophila	--	0.728*	--
Tipula	--	0.833	--
Ephemeroptera			
Baetidae			
Baetis	--	0.925	--
Centroptilum	--	0.910	--
Heterocloeon	--	0.878	--
Neocloeon	--	0.902	--
Pseudocloeon	--	0.942	--
Baetiscidae			
Baetisca	--	0.582	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability Adults	Larvae large-small	Pupae
Caenidae			
Brachycercus	--	0.641*	--
Caenis	--	0.687	--
Ephemerellidae			
Ephemerella	--	0.880	--
Ephemeridae			
Ephemera	--	0.467	--
Hexagenia	--	0.479	--
Heptageniidae			
Cinygmula	--	0.888	--
Epeorus	--	0.748	--
Heptagenia	--	0.687	--
Rhithrogena	--	0.887	--
Stenacron	--	0.961	--
Stenonema	--	0.915	--
Leptophlebiidae			
Habrophlebia	--	0.674	--
Habrophlebiodes	--	0.485	--
Leptophlebia	--	0.792	--
Paraleptophlebia	--	0.941	--
Polymitarcidae			
Ephoron	--	0.385	--
Potamanthidae			
Potamanthus	--	0.686	--
Siphlonuridae			
Isonychia	--	0.865	--
Tricorythiridae			
Tricorythodes	--	0.578	--
Hemiptera			
Corixidae			
Sigara	--	0.852*	--
Gerridae			
Gerris	--	0.855	--
Metrobates	--	0.768	--
Veliidae			
Rhagovelia	--	0.688*	--
Lepidoptera			
Pyralididae			
Nymphula	--	0.667*	--
Paragyractis	--	0.500	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability Adults	Catchability Larvae large-small	Catchability Pupae
Megaloptera			
Corydalidae			
Corydalus	--	0.683-0.884	--
Nigronia	--	0.512-0.878	--
Sialidae			
Sialis	--	0.611	--
Odonata			
Aeshnidae			
Basiaeschna	--	0.667*	--
Boyeria	--	0.518*	--
Nasiaeschna	--	0.333*	--
Agrionidae			
Hetaerina	--	0.667*	--
Coenagrionidae			
Agria	--	0.762	--
Chromagrion	--	0.667*	--
Cordulegastridae			
Cordulegaster	--	0.438*	--
Corduliidae			
Helocordulia	--	0.682*	--
Gomphidae			
Dromogomphus	--	0.492	--
Erpetogomphus	--	0.548	--
Gomphurus	--	0.333*	--
Gomphus	--	0.532	--
Hagenius	--	0.505	--
Hylogomphus	--	0.333*	--
Lanthus	--	0.684	--
Ophiogomphus	--	0.533-0.822	--
Progomphus	--	0.471-0.730	--
Stylogomphus	--	0.528-0.921	--
Macromiidae			
Didymops	--	0.667*	--
Macromia	--	0.638	--
Orthoptera			
Tridactylidae			
Tridactylus	--	0.667*	--
Plecoptera			
Capniidae			
Allocapnia	--	0.683	--
Paracapnia	--	0.922*	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability: Adults	Catchability: Larvae large-small	Catchability: Pupae
Chloroperlidae			
Alloperla	--	0.867	--
Hastoperla	--	0.721	--
Paraperla	--	0.872*	--
Isoperlidae			
Isoperla	--	0.820	--
Leuctridae			
Leuctra	--	0.875	--
Nemouridae			
Amphinemura	--	0.902	--
Nemoura	--	0.856	--
Peltoperlidae			
Peltoperla	--	0.764	--
Perlidae			
Acroneuria	--	0.575	--
Neoperla	--	0.525	--
Paragnetina	--	0.633*	--
Perlesta	--	0.592	--
Phasganophora	--	0.683	--
Perlodidae			
Isogenus	--	0.767	--
Taeniopterygidae			
Brachyptera	--	0.910	--
Taeniopteryx	--	0.878	--
Trichoptera			
Brachycentridae			
Brachycentrus	--	0.371	--
Micrasema	--	0.483	--
Calamoceratidae			
Ganonema	--	0.667*	--
Glossosomatidae			
Glossosoma	--	0.323	--
Protoptila	--	0.333*	--
Helicopsychidae			
Helicopsyche	--	0.443	--
Hydropsychidae			
Cheumatopsyche	--	0.779	--
Diplectrona	--	0.752	--
Hydropsyche	--	0.641	--
Macronema	--	0.687	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability Adults	Catchability Larvae large-small	Catchability Pupae
Hydroptilidae			
Agraylea	--	0.458*	--
Hydroptila	--	0.310	--
Leucotrichia	--	0.435	--
Orthotrichia	--	0.420	--
Lepidostomatidae			
Lepidostomatidae	--	0.781	--
Leptoceridae			
Athripsodes	--	0.412	--
Mystacides	--	0.333*	--
Oecetis	--	0.380	--
Limnephilidae			
Drusinus	--	0.661*	--
Neophylax	--	0.645	--
Pycnopsyche	--	0.606	--
Philopotamidae			
Chimarra	--	0.656	--
Psychomyiidae			
Neureclipsis	--	0.667*	--
Polycentropus	--	0.712	--
Psychomyia	--	0.686	--
Rhyacophilidae			
Rhyacophila	--	0.434	--
Sericostomatidae			
Sericostoma	--	0.421	--
MOLLUSCA			
GASTROPODA			
Basommatophora			
Ancylidae			
Ferrissia	--	0.380	--
Lymnaeidae			
Fossaria	--	0.492	--
Physidae			
Physa	--	0.786	--
Planorbidae			
Gyraulus	--	0.668	--
Helisoma	--	0.512*	--
Mesogastropoda			
Pleuroceridae			
Mudalia	--	0.228-0.687	--

Appendix Table I. Average probabilities of capture from CDS samples for selected taxa collected from the upper James and Roanoke River drainages, Virginia (continued).

Taxa	Catchability Adults	Catchability Larvae large-small	Catchability Pupae
PELECYPODA			
Eulamellibranchia			
Unionidae			
Eliptio	--	0.635	--
Ligumia	--	0.500*	--
Heterodonta			
Sphaeriidae			
Sphaerium	--	0.625	--
NEMATODA	--	0.552	--
NEMERTEA	--	0.648	--
PLATYHELMINTHES	--	0.844	--

*Estimates based on less than 20 specimens.

APPENDIX D

Appendix Table I. Main calling program and subroutines of DPLETE.

```
      REAL D(20,200),RO(20),E(200),H(20),SR(200)
      INTEGER KR(20),C(3),ST,SP
      DO 2 I=1,20
      H(I)=0.
      DO 1 J=1,200
    1 D(I,J)=0.
    2 CONTINUE
      READ,RN,NS
    3 READ,ST,SP,C
      IF(ST.EQ.-1) GOTO 4
      CALL MAXA(C,RN,EST)
      D(ST,SP)=EST
      GOTO 3
    4 DO 8 ST=1,NS
      PRINT 5,ST
    5 FORMAT('1',10X,'STATION',1X,I2//1X,'(ESTIMATES BY THE METHOD OF
     #CARLE 1976)'/10X,'SPECIES',5X,'ESTIMATE'/)
      DO 7 SP=1,200
      IF(D(ST,SP).EQ.0.) GOTO 7
      PRINT 6,SP,D(ST,SP)
    6 FORMAT(/11X,I3,8X,F7.1)
    7 CONTINUE
    8 CONTINUE
      PRINT 9,(I,I=1,NS)
    9 FORMAT('1',45X,'EVENNESS DIVERSITY(1-REDUNDANCY)'/1X,'ITRS',45X,
     #'NUMBER OF SAMPLES POOLED'/1X,20(5X,I2))
      IX=13133
      DO 15 IT=1,50
      DO 14 J=1,10
      DO 10 I=1,NS
      CALL RANDU(IX,IY,R)
      IX=IY
   10 RO(I)=R
      CALL RANK(RO,NS,KR)
      DO 11 I=1,200
      SR(I)=0.
   11 E(I)=0.
      DO 13 I=1,NS
      S=0.
      ST=KR(I)
      DO 12 SP=1,200
      IF(D(ST,SP).GT.0.) SR(SP)=1.
      S=S+SR(SP)
   12 E(SP)=E(SP)+D(ST,SP)
      CALL RINDEX(E,S,A)
   13 H(I)=H(I)+A
   14 CONTINUE
   15 PRINT 16,IT*10,(H(I)/IT*.1,I=1,NS)
   16 FORMAT(/1X,I3,20(1X,F5.3))
      STOP
      END
```

Subroutine MAXA, an algorithm for determining depletion estimates from the method of Carle and Strub (1976).

```
      SUBROUTINE MAXA(C,R,E)
      INTEGER C(3)
      T=0.
      X=0.
      K=R
      DO 1 I=1,K
      T=T+FLOAT(C(I))
    1 X=X+FLOAT(C(I))*FLOAT(K-I)
      E=T-1.
    2 E=E+1.
      F=(E+1.)/(E+1.-T)
      G=R*E-X
      H=G-T
      DO 3 I+1,K
    3 F=F*(H+FLOAT(I))/(G+FLOAT(I+1))
      IF(F.GT.1.) GOTO 2
      RETURN
      END
```

Subroutine CI, an optional algorithm (not called in main program presented), for determining the normal approximation to 95% confidence intervals for removal estimates.

```
      SUBROUTINE CI(C,RN,EST,BL,UL)
      INTEGER C(3)
      T=0.
      X=0.
      K=RN
      DO 1 I=1,K
      T=T+FLOAT(C(I))
    1 X=X+FLOAT(C(I))*FLOAT(K-I)
      P=T/(RN*EST-X)
      Q=1.-P
      QC=Q**RN
      SE=SQRT((EST*QC*(1.-QC))/((1-QC)**2-(RN*P)**2*(Q**(RN-1.))))
      BL=EST-SE*1.96
      UL=EST+SE*1.96
      IF(BL.LT.T) BL=T
      RETURN
      END
```

Subroutine RANDU, a standard IBM algorithm for obtaining random numbers.

```
      SUBROUTINE RANDU (IX,IY,R)
      IY=IX*65539
      IF(IY)1,2,2
    1 IY=IY+2147483647+1
    2 R=IY
      R=R*.4656613E-9
      RETURN
      END
```

Subroutine RANK, an algorithm for ranking (NS)integers.

```
      SUBROUTINE RANK (RD,NS,KR)
      REAL RD(20)
      INTEGER KR(20)
      DO 2 I=5,NS
      HO=-1E 75
      DO 1 J=5,NS
      IF (RD(J).LE.HO) GOTO1
      HO=RD(J)
      KR(I)=J
    1 CONTINUE
    2 RD(KR(I))=-RD(KR(I))
      RETURN
      END
```

Subroutine RINDEX, an algorithm for calculating 1-r evenness diversity incorporating the built-in IBM, ALGAMA function for the calculation of the logs of factorials.

```
      SUBROUTINE RINDEX(E,R,S)
      REAL E(200)
      INTEGER SP
      F=0.
      G=0.
      R=0.
      DO 1 SP=1,200
      F=F+ALGAMA(E(SP)+1.)
    1 G=G+E(SP)
      IF(G.EQ.0.) GOTO 2
      B=ALGAMA(G-S+2.)
      R=(F-B)/(S*ALGAMA(G/S+1.)-B)
    2 RETURN
      END
```

BIOGRAPHICAL SKETCH

Frank Louis Carle was born October 29, 1949. He graduated from Watchung Hills Regional High School, New Jersey, in June, 1968. Mr. Carle received his B.S. from the University of Vermont and began graduate work at Virginia Polytechnic Institute and State University in 1972. He was married to Carol Jane Greenwood in January, 1973.

Frank Louis Carle

AN EVALUATION OF THE

REMOVAL METHOD FOR ESTIMATING

BENTHIC POPULATIONS AND DIVERSITY

by

Frank Louis Carle

ABSTRACT

A Circular Depletion Sampler (the CDS) was constructed in order to collect removal data for estimating benthic sample populations and species catchability. The removal sampling method was compared to Modified Hess, Surber, and Kicknet sampling methods, and gave consistently higher and less variable estimates than other methods. Taxa showing the lowest catchabilities included the case-building Trichoptera, the Mollusca, and the Annelida. The highest catchabilities were shown by the smaller Chironomidae and the nonburrowing Ephemeroptera. Taxa with high catchability generally showed high emigrability for Surber and Kicknet methods, particularly the aquatic Insecta. The determination of species richness and evenness diversity was significantly biased by low catchabilities or emigration or both with Modified Hess, Surber, and Kicknet sampling methods. Removal samples have a higher probability of representing rare species, and as expected, pooled removal collections accumulated species at a higher rate than the pooled collections of other methods. The dominance diversity of pooled CDS collections became stable more rapidly than those of other methods, and gave higher resolution between benthic communities of different structure. DPLETE, a computer program for making removal population estimates by the method of Carle and Strub (1976) and making dominance diversity estimates based on information theory is presented, and is suitable for use in any study where removal data has been collected.