The Impact of Seasonally Changing Feeding Habits on the Secondary Production and Accumulation of Mercury in a Filter-feeding Caddisfly.

by

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(ABSTRACT)

Food habits, net-spinning activity, energetics, and mercury accumulation in Hydropsyche morosa were examined over a one year period on the South River in central Virginia. Feeding nets were observed as early as April and were widespread by May. Nets were virtually absent from late November through March. Gut content analysis revealed seasonal patterns in the consumption of various food items. From April through October, when feeding nets were widespread, detritus formed the bulk of the diet in terms of both numbers of particles and volume occupied. From November through March however, the algal component dominated in terms of numbers of particles although the detritus component still occupied a greater volume. Ivlev's preference index was employed and indicated that the seasonal differences in the relative amount of the three food types were not simply a matter of changing seston concentrations, but rater suggested a shift from a filter-feeding mode of feeding in the summer months to grazing on diatoms in the winter.

H. morosa was bivoltine on the South River. The estimate of secondary production for the summer cohort was 3,246 mg AFDW/m^2/yr, while the estimate for the winter cohort was 2,145 mg AFDW/m^2/yr. The secondary production also was estimated for each season based on food habits to determine the impact of the observed seasonal switch in feeding habits on production and egestion rates. During the summer, the detritus component contributed most to production averaging about 50 percent. Animal and algal material contributed 30 and 20 percent, respectively. During the winter, algal material contributed most to the production, averaging just over 62 percent. Detritus also contributed during the winter averaging over 30 percent. Monthly rates of production and egestion were between 3 and 3.5 times faster during the summer.

The concentrations of total mercury in seston, periphyton, and in the body tissue of H. morosa were analyzed each month. Mercury concentrations were between four and six times higher in the seston than in the periphyton. The concentration of mercury in the body tissue of H. morosa ranged from 0.14 ppm in March to over 1.20 ppm in July. Differences in Mercury concentration in the insects between seasons were significant. Regression analysis revealed a significant relationship between Hg concentration in the insects and the relative amount of detritus found in the guts.

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INTRODUCTION

Considerable research has been devoted to understanding the distribution and bioaccumulation of mercury in aquatic systems. Much of this research effort has centered around fish and shellfish because of the direct association of these organisms with man. Until recently, few investigations have dealt with the bioaccumulation of mercury by aquatic insects except to explain mercury concentrations in fish.

Mercury is available for absorption by aquatic organisms both from the water and from ingestion of contaminated food. However, it appears that most of the mercury body burden accumulates through food chains (Lock 1975, Kudo and Mortimer 1979). Spatial and temporal variability in mercury concentration in fish have been explained by changes in diet (e.g. MacCrimmon et al. 1983). However, the relationships between diet and mercury accumulation have not been examined in aquatic insects.

Hydropsychid caddisflies have been classified as collector-filterers based on the way in which they use silk to spin feeding nets (Wiggins, 1978). These nets are oriented to the current in such a way as to capture organic material suspended in the water column. However, recent studies suggest seasonality in feeding habits. For example, Rhame and Stewart (1975) and Fuller and Mackay (1980) demonstrated a shift from filtering food in the warmer months to grazing algae from the substrate in the cooler months, for several species of Hydropsyche.

The present study examines some of the effects of such shifts in feeding habits using a common caddisfly, Hydropsyche morosa in a river contaminated with mercury. Hydropsyche morosa was chosen as the experimental organism because it was abundant and easily identified. The study site was a riffle area of the South River which is contaminated with mercury. The objectives of this study were three-fold: 1. To determine if H. morosa changes from a filter-feeding to a grazing mode of feeding as observed in other Hydropsyche (Rhame and Stewert 1975, Fuller and Mackay 1980). 2. To categorize and quantify the material ingested by H. morosa. 3. To determine the relationship between the mercury body burden of these insects and their feeding habits.

LITERATURE REVIEW

Feeding Habits

Studies concerning the feeding habits of Hydropsyche prior to 1939 are summarized in Balduf (1939). Of the nine species reviewed, one was found to be entirely predacious. Both plant and animal material was found in the guts of the other eight species. Lloyd (1915) pointed out that variability in gut contents was often a reflection of availability of food and not simply a matter of preference. In summary, Balduf characterized most groups of the order Trichoptera as "promiscuous feeders", i.e., feeding on a variety of foods, and that variation observed in food ingested could be strongly influenced by such factors as "season of the year, age of the larvae, and normal differences in the organic contents of several habitats".

I found little information concerning the feeding ecology of aquatic insects in the literature between 1940 and 1970. However, there appears to have been a renewed interest in functional relationships of aquatic insects in the early 1970's (Cummins 1973, and references therein). therein). Recent feeding studies have corroborated Balduf's suggestion that most species of hydropsychids are omnivorous (e.g. Wallace and Merrit 1980, Rhame and Stewert 1975, Fuller and Mackay 1980). Many recent studies have attempted to correlate food ingested to feeding net mesh size. For example some authors have suggested there is a change in food

type and an increase in mean particle size in the foregut with subsequent instars and mesh sizes (Wallace 1975, Malas and Wallace 1977, Cummins and Klug 1979). However, Alstad (1987) showed that hydropsychid caddisflies in Utah streams did not conform to the particle size model put forth by Wallace. Alstad showed instead that resource concentration rather than particle size, was the basis of community organization among filter-feeding Trichoptera.

Other investigations have shown a relationship between feeding strategies and the longitudinal distribution of hydropsychids from headwaters to mouth (Gordon and Wallace 1975, Wiggins and Mackay 1978, Ross and Wallace 1980). In general, it was shown that shifts in species composition of net- spinning caddisflies were a function of physical factors such as temperature, stream morphology, and sizes and types of available food. In addition, biotic factors such as the efficiency with which the insect community in stream segments further upstream process energy inputs may also effect the longitudinal distribution of hydropsychids (Ross and Wallace, 1980).

Seasonal variability in food habits of caddisfly larvae was first reported by Noyes (1914). She found that diatoms formed the bulk of the larval diet in fall and winter, while animal food predominated in spring and summer. Badcock (1949) found large numbers of the diatom, Cocconeis present in the guts of two species of Hydropsyche larvae. This diatom was rare in the plankton and subsequently Badcock concluded that some food material was brushed up from the bottom rather than netted. This repres-

ents the first report of an alternative (grazing) feeding mode in filter-feeding Trichoptera.

Net-spinning activity of caddisfly larvae has been observed to decrease with temperature in the lab (Phillipson and Moorhouse 1974) and in the field (Fremling 1960, Williams and Hynes 1973, Rhame and Stewert 1976, Wallace et. al. 1977, Fuller and Mackay 1980). However, it has been suggested that temperature alone is not responsible for decreased net-spinning in winter months. For example, Fuller and Mackay (1980) found increasing day lengths correlated better than increasing stream temperatures with the resumption of net production in spring.

Rhame and Stewart (1976) were the first to correlate the decreased net-spinning activity in Winter with a shift in diet. Preference studies showed that the shift from an animal and detrital based diet to an algal based diet was not a result of changes in seston composition. They concluded that H. simulans shifted from a passive filter-feeding mode in Summer, to an active grazing feeding mode in Winter. Fuller and Mackay (1980) obtained similar results for three species of Hydropsychidae in southern Ontario.

Secondary Production

Secondary production is equal to the amount of tissue elaboration or biomass produced by animal populations during some time interval (Ivlev, 1945). Production estimates are thought to be of considerable importance

because they combine both individual growth and population survivorship into a singe measurement (Benke, 1984). A number of factors have been shown to influence production by either directly or indirectly effecting one or both of these variables. These factors include temperature, nutrients, diet, flow rate and length of aquatic life (Downing and Riggler, 1984).

It is production that is important from the ecosystem standpoint because this biomass is available to higher trophic levels (Waters, 1977). Production studies involving filter- feeders are few, though most of these suggest that filter-feeders play a significant role in the productivity of fresh waters (e.g. Cudney and Wallace 1980, Parker and Voshell 1983, Ross and Wallace 1983). This is particularly true in the midreaches of shallow, stony-bottom streams characteristic of the southeastern United States, where filter-feeders are often the most conspicuous member of the macrobenthos community (Parker, 1981).

Estimates of secondary production for a single species of Hydropsyche range from 278 mgAFDW/m^2/yr in a small headwater stream in Massuchusetts (Neves, 1979) to 1.316 kgAFDW/m^2/yr below an impoundment on the North Anna River in Virginia (Parker and Voshell, 1983) [production values reported in units other than mgAFDW/m^2/yr have been transformed using conversion factors given in Waters (1977)]. In stony-bottomed, mid-reach (third and fourth order) streams, annual production estimates range from 86 mgAFDW/m^2/yr for H. sparna in the Tallulah River in Georgia, to about

14,000 mgAFDW/ m^2/yr in the nutrient enriched Horokiwi stream in New Zealand (Hopkins, 1976).

Trophic Basis of Production

Although the qualitative roles (types of food consumed) of aquatic insects have been studied since the early 1900's (Cummins 1973 and references therein), only recently have there been attempts to quantify these roles by determining the secondary production of individual species as well as entire functional groups. More recently still, attempts have been made to fine tune energy pathway models in benthic communities by determining the trophic basis of production. Wallace and Merrit (1980) suggested that production estimates, coupled with precise feeding habits and bioenergetic data could yield a better understanding of the functional roles of individual species in ecosystems. For example, this approach has been used to clarify the role of filter-feeding caddisflies in processing stream seston.

Integration of food habits with production data has yielded a number of conclusions regarding the role of filter-feeding caddisflies in streams. For example, net spinning Trichoptera appear to have little effect on the quantity of seston carried by streams (Haefner and Wallace 1981, Georgian and Wallace 1981, Ross and Wallace 1983). On the other hand, Ross and Wallace (1983) found that filter-feeders reduce the nutritional quality of seston transported by the streams. The explanation seems to be that while the seston ingested is composed of high quality

animal and algal material, as well as, the low quality detritus component, they egest the unassimilated portion of high quality food as detritus. Thus, it has been suggested that large populations of filter feeding insects are self-limiting by reducing the energy content of the seston available to populations further downstream (McCullough et al., 1979a).

Trophic basis of production analyses have also been used to determine the relative importance of various food types to the production of filter-feeding caddisflies at different points along the river continuum. For example, Ross and Wallace (1983) found that the relative contribution of animal material to the production of net-spinning caddisflies was very high in the headwater streams but decreased further downstream. Conversely, the relative importance of diatoms and filamentous algae to the production by these animals increased in a downstream direction.

Mercury Pollution in Aquatic Systems

In the early 1950's a previously unknown neurological disorder in fish, birds, and humans, was traced to mercury compounds released by a factory into Minimata Bay, Japan (Goldwater, 1971). Since that time studies of the toxic properties of mercury on stream biota and the distribution and bioaccumulation of mercury in aquatic ecosystems have proliferated.

Methylmercury has been shown to be the most toxic form of mercury to aquatic biota. However mercury is usually discharged as the much less toxic elemental mercury or Hg(II) chloride and hydroxide complexes

(Hildebrand et al. 1980). Transformations from inorganic to methylmercury are bacterially mediated, and often complex, and involving many steps.

Upon discharge into the aquatic system, much of the inorganic mercury adsorbs to suspended organics in the seston and settles out into sediments varying distances from the outfall (Jackson, 1986). Bacteria associated with sediments convert inorganic mercury to one of several forms of methylmercury. Zepp et al. (1974) showed that methylmercury ions that redissolve are again readily complexed to suspended organics in freshwater. Therefore, mercury is available to filter-feeders in both the inorganic and methylated forms. Jackson (1986) showed that the relative amount of each form of mercury available to aquatic organisms is site specific, depending on factors that effect bacterial action, such as the amount of nutrients and temperature. This may explain discrepancies in the relative amount of total mercury that is methylated in benthic organisms. For example, Hildebrand et al. (1980) found that between 29 and 57 percent of the total mercury found in hydropsychid caddisflies was in the methylated form depending on the site at which the sample was collected, while other studies looking at benthic invertebrates have found much less of the total mercury was in the methylated form (Jernelov, 1971).

Aquatic organisms have been found to absorb dissolved mercury from the water through gills or skin, and from food through the gut wall. Recent studies designed to elucidate the relative importance of these two mech-

anisms of mercury absorbtion in both fish and benthic invertebrates have concluded that mercury is mainly absorbed from food (Jernelov 1971, Lock 1975, Kudo and Mortimer 1979). Mercury has been shown to be persistent in storage organs and muscle tissue, and individuals of higher trophic levels generally have longer life spans. These observations along with the fact that most mercury is absorbed through the food chain, has led to the concept of biomagnification. Essentially this is the commonly observed phenomenon where the highest mercury concentrations are associated with individuals in higher trophic levels within a food chain (Potter et al. 1975).

Various factors have been shown to correlate with mercury concentration in fish including length, weight and age of the fish. Dietary changes also have been shown to be important. For example, MacCrimmon et al. (1982) found that increased rates of Hg uptake by lake trout after reaching six years in age was due to a change in diet from benthic invertebrates to the highly contaminated rainbow smelt, Osmerus mordax.

Hornung and Krungalz (1984) found that in general the distribution of mercury in benthic invertebrates follows the same pattern as the distribution of mercury in surficial sediments. However, this study was carried out in an estuary and looked only at molluscs and crabs. Jernelov (1971) found considerable variation between functional groups of benthic invertebrates and suggested that the mercury content of animals that feed on suspended material probably depends on the quantity of mercury rich particles in the intestines of the animals.

MATERIALS AND METHODS

Description of Study Area

The South River is a fourth order stream originating on the western slope of the Blue Ridge Mountains and flowing in a northerly direction to combine with the Middle and North Rivers to form the South Fork of the Shenandoah River. The South River drains an area of 373 square kilometers. The drainage basin is primarily limestone and shale and the riparian zone is diverse. The flood plain of the South River is used extensively for crops and livestock.

The city of Waynesboro, Virginia is the only industrialized area on the South River and is the point source of several pollutants including the effluent of an acetate fiber plant as well as the effluent from the municipal sewage treatment plant. From 1929 to 1950 the fiber plant used mercuric sulfate as a catalyst in a closed-loop system. In 1977, the E. I. DuPont de Nemours Company announced that there was apparently a leak in the system during that time as mercury deposits were found on their property. Subsequent sampling of fish and sediments downstream of the plant revealed excessive amounts of mercury.

Two study riffles were chosen on the South River on the basis of their ecological similarity as well as their location with respect to the acetate fiber plant in Waynesboro. One site was located at Oak Hill,

approximately 5.5 kilometers upstream of Waynesboro and was chosen solely for the purpose of determining background mercury levels in suspended particulates and stream biota. The other site was was located near Crimora, about 15.0 kilometers downstream of Waynesboro. The study riffles contained primarily large, cobble substrates, and at the downstream site lush growths of moss covered the rocks throughout the year. Parker and Voshell (1983) found similar growths of moss in the North Anna River and showed several species of Hydropsychidae found this moss suitable for retreat material (J. R. Voshell, personal communication).

Physical and Chemical Measurements

Water samples were collected each month and analyzed for nutrients (nitrates, total phosphates, and ortho-phosphates) using spectrophotometry as described by the EPA manual, Methods for Chemical Analysis of Water and Wastes (1984). Depth was measured with a meter stick and flow with a General Oceanics Torpedo flow meter attached to a D-frame kick net frame, at the site of each sample. Mean discharge data was obtained from a U.S. gauging station located in Chrimora, Virginia, approximately 1.5 kilometers downstream from the study riffle. Temperature was recorded continuously with a Ryan Model J thermograph and daily averages, maximum, and minimum temperatures were recorded. Degree days were also determined using a Tamaya digital planimeter by integrating the area under the curve from the thermograph tapes.

Benthic Sampling

A Hess Sampler was used to quantitatively sample benthic macroinvertebrates. The Hess sampled an area of 0.1 m^2 and had a net mesh size of 250 microns. Each month, from April 1986 to March 1987, six sample sites were randomly chosen at each site and all the invertebrates within the confines of the sampler, and down to about 15 cm into the substrate, were washed into the collecting net. Samples were transferred to Nalgene sample bottles and preserved in 10% formalin. Upon returning to the lab, all H. morosa were picked from the samples and sorted to instar. Total density and number of individuals in each instar were calculated.

Food Habits

Larvae of H. morosa and their associated nets and retreats were removed from rocks and preserved in 10 percent formalin. Upon returning to the lab, the feeding nets of fifth instar H. morosa were measured with an ocular micrometer. Average mesh size was determined by measuring 35 nets. Three measurements per net (total of 105 observations) were taken from near the center of the nets where stretching and disfigurations were rare. Presence or absence of feeding nets in the stream was recorded every two weeks.

Food habits were determined by gut analysis as described by Cummins (1973) with modifications outlined by Wallace (1975). In this method the

proventriculi were removed and their contents filtered onto grided millipore filter paper. Three food types were recognized: animal material, vascular plant and detritus, and algae. Particle number as well as volume of each food type was determined. Volume estimates were determined by measuring the area of each particle with a Whipple grid (Parker, 1981). The percentage of empty guts and numbers of algal genera were recorded each month as well.

The insects used for gut analysis were fifth instars obtained from the six Hess samples taken at random from the stream each month. Over 700 larval guts were examined over the twelve month period. I further modified the filter technique described by Cummins (1973), by lumping the contents of 35 to 100 guts each month in a beaker and filtering the mixture onto between six and ten filters, each of which represents a replicate for that particular month. Filters were cleared with immersion oil for 24 hours and subsequently mounted in glycerine on slides. Three grids out of a total of 32 were chosen at random for each slide (i.e. 9.4% of each slide). All particles contained within the boundries of the grids were characterized by type, counted, and measured. Monthly means and confidence limits were derived by averaging the results of all the slides. I was not able to assess the variability between individual insects within a riffle because I did not analyze each insect gut individually. However, by lumping the guts of many insects together in this way, I was able to get a better estimate of the feeding habits of the entire population in my study riffle.

Seston was analyzed each month from April 1986 through March 1987. Seston was collected by pouring a known amount of stream water (between 15 and 30 liters) through a stainless steel filter column fitted with removable stainless steel screens. Suction through the sieving apparatus was maintained at about 15 psi with a portable vacume pump (see Gurtz et al., 1980). The amount and the relative contribution of each of the three major food types were determined for each of the following size classes which corresponded to the sieve sizes of the filter apparatus: Medium large (ML), 234-864 um; small (S), 105-234 um; fine (F), 43-105 um; and very fine (VF), 25-43 um. The material that collected on each screen was washed into labeled nalgene containers and returned to the lab. Four replicates were taken each month. The material from three of the replicates were washed onto preashed and preweighed Gelman glass fiber filters (.45um). Filters were dried, weighed, ashed and reweighed to determine the average AFDM of each size class in the seston. The fourth replicate was washed onto gridded millipore filter paper. Qualatative estimates of the contribution of the three major food types to the seston was determined using this replicate by the same method used in gut analysis (see above).

Ivlev's Electivity Index (Ivlev, 1961) was calculated for each food category to determine potential preferences. Calculations are as follows:

$$E = (r1-p1)/(r1+p1)$$

where r1 = relative content of food type 1 in the gut (%)

p1 = relative content of food type 1 in the seston (%)

The E values range from -1 to +1. Positive values indicate preference, negative values indicate avoidance, and values close to 0 indicate the item is randomly ingested.

The General Linear Models procedure for analysis of variance was employed to statistically test for seasonal differences in gut contents and mean particle size.

Secondary Production

The removal-summation method for estimating secondary production was used because it calculates production for each sampling interval, thus providing an estimate of the contribution of each food item to the production for each month or season. However, the removal-summation method is only reliable when one can effectively differentiate between cohorts, and therefore great pains were taken to adequately separate cohorts. Size frequency histograms were constructed and used along with monthly density estimates to roughly define cohorts. Further refinement of cohorts was determined by analyzing mean instar weight data (see Results).

Monthly estimates of ash-free dry mass (AFDM) for each instar were based upon the preserved weights of several individuals of each instar.

In general, the effect of preservation on mean weight has been shown to be minimal for holometabolous insects (Howmiller 1972, Leuven et al. 1985). Larvae used in weighings were placed in a drying oven (55 C) for 24 hours and then transferred to a desiccator for an additional 24 hours. Oven-dried specimens were weighed on a Cahn 28 electrobalance to the nearest microgram to obtain dry mass and then ashed in a muffle furnace (500 C) for 1 hour and reweighed to obtain AFDM. Average weight of each instar was then multiplied by the relative abundance of that instar for that sampling date. These weighted instars were summed to obtain the weight of an average individual in the population for each sampling date.

Morin et al. (1988) described a method to correct for underestimation of densities associated with small larvae due to prolonged recruitment and poor sampling efficiency of small instars. In this method Allen curves are constructed after eliminating the data from the first sampling dates, when density is still rising. New initial densities are predicted by extrapolation from this line. This is essentially the same as using Allen curves to estimate the number of eggs that hatched (Southwood 1976).

Trophic Basis of Production

The relative contribution of each food category to the production for each season was determined using the technique developed by Benke and Wallace (1980). Following their analysis, I assumed assimilation efficiency values (AE) of 0.7 for animal matter, 0.3 for diatoms and other algae, and 0.1 for vascular plant material and detritus. The efficiency

of conversion of assimilated energy to production, or net production efficiency (NPE), was assumed to be 0.5. The percentage of each food category in the gut contents for a month or a season was multiplied by the appropriate AE and NPE to obtain the relative amount that each food category contributed to production. This relative amount was converted to a percentage and multiplied by the production estimated for that month or season to determine the actual production attributed to each food category. Consumption estimates were easily obtained by dividing the production attributed to each food type by the gross production efficiency (AE X NPE). The amount of each food type egested as detritus was also determined by multiplying the amount consumed by the egestion efficiency (1-AE).

Mercury Analysis

Total mercury concentration was measured in seston, periphyton, and the body tissue of *H. morosa* each month at both the upstream and downstream sites. Seston samples for mercury analysis were obtained by pumping several hundred gallons of stream water through a plankton net (mesh = 23 microns) and washing the filtrate into nalgene sample bottles. Upon returning to the lab samples were centrifuged for at least 10 minutes and the resulting seston pellet was frozen for later mercury analysis.

Data concerning mercury concentrations in attached algae were obtained by Larry Western, another graduate student in the Biology department, and used with his permission. Algae samples were scraped from rocks within

the study riffle and processed in the same way as the seston (i.e. centrifuged and the pellet frozen for later mercury analysis). Two to four samples were collected for most months.

Insects were collected with a ten-foot seine from several spots in the study riffles and frozen in the field with dry ice. Larvae were sorted to instar in the lab. Only fifth instars were used in an attempt to eliminate the effect of age on mercury concentrations. For the last six months of the study year, half of the insects were analyzed with the digestive tract removed, and the other half with their digestive tract in tact. Also, fifth instar H. morosa larvae were weighed with and without guts. By knowing the concentration of mercury in the insects with and without guts, and the relative weight of the gut, I was able to calculate the concentration of mercury in the gut as well as the percent of the total body burden that was associated with the guts and their contents.

The total mercury concentration of all samples were determined by the flameless atomic absorption method using a model 50-A Perkin-Elmer Mercury analyzer. Approximately 0.50 grams of each sample was digested and analyzed as described in Forrester, et al., (1972).

RESULTS

Physical and Chemical Measurements

The study riffles ranged between 10.0 and 40.0 cm in depth and the flow ranged between 0.5 and 2.0 m/sec. This segment of the South River was characterized by high dissolved oxygen (near saturation) and slightly elevated pH (between 7.5 and 8.0). Nitrate levels averaged 3.0 mg/l at the downstream site and 0.5 mg/l at the upstream site. Orthophosphate levels averaged 0.25 mg/l at the downstream site and 0.03 mg/l at the upstream site. Nutrient levels were significantly higher at the downstream site ($p<.05$). These differences in nutrient levels were probably due to the discharge of Waynesboro's municipal sewege treatment plant as well as inputs from agricultural sources.

Mean daily temperature ranged from 25.5 C on July 17, to near 0.00 C on January 28 (Figure 1). The total suspended particulate organic matter (POM), as well as the particulate organic matter available to H. morosa larvae (usable POM) for each month at the downstream site are shown in Figure 2. The usable POM is equivalent to all suspended material falling into the "fine" and "very fine" size classes (25-105 microns), and corresponded to the size range of particles found in the guts (see Figure 9). Total POM and usable POM exhibited similar patterns through time, and usable POM ranged from between 50.0 and 60.0 percent of the total POM. Both total and usable suspended POM reached maximum concentrations in

April at 0.92 and 0.55 mg/liter, respectively. POM concentrations fell abruptly in May and continued to decline slowly reaching the low for the year in October when total POM was 0.032 and usable POM was 0.025 mg/liter. Seston concentrations slowly increased through the remainder of the year (November-March).

The organic content of the seston at the downstream site ranged between 12 percent in July to nearly 40 percent in November (figure 3). Organic content of the seston was highest in the Fall of the year (August-December).

Feeding Habits

Feeding nets of H. morosa were observed as early as late April and were widespread by mid-May. Nearly every larva observed was associated with a feeding net from early June through late October. Nets were virtually absent from late November through March, although a few feeding nets were observed during the winter when water temperatures were abnormally high. For example, on December 12, 10.7% of the larvae observed were associated with feeding nets (n=75).

The average capture net mesh opening for fifth instar H. morosa was 172 by 102 microns for an area of 17,544 square microns. This is a small mesh opening relative to other species in the genus Hydropsyche (Table 1). However, some genera in the family Hydropsychidae exhibit much smaller dimensions such as Diplectrona which is commonly found in pools

and riffle margins and Macronema, which utilizes a unique retreat construction allowing them to spin very fine-meshed feeding nets while occupying relatively swift current velocities.

The detrital component of the diet was characterized by small amounts of identifiable vascular detritus (particularly in the fall of the year). However, most of the detritus was amorphous and of unidentifiable origin. The algal component of the diet consisted mainly of diatoms. Table 2 is a summary of the most common algal genera found in the guts and the months in which they were found. Navicula and Melosira were most abundant during the summer, and only rarely were other genera observed during the summer months. During the winter nearly all genera listed in Table 2 were present each month though their relative abundances fluctuated. The number of algal genera found in the gut contents each month are shown in Figure 4. Average numbers of genera in the guts during the winter (Nov.-March) ranged from six to ten, and between two and four genera during the summer months (April-Oct). There were significantly more genera of algae and diatoms in the guts during the winter months ($p<.0001$).

Animal particles observed in the guts of H. morosa consisted primarily of rotifers and scleritized insect parts (head capsules, anal claws, and mandibles). Small crustaceans were also present on rare occasions.

Gut analysis showed detritus to be the major component of the diet in terms of numbers of particles from April through October. Numbers of detritus particles found in the guts throughout this period represented

between 60 and 90 percent of the total number of particles consumed (Fig. 5). The proportion of detritus in the diet fell to between 21 and 28 percent of the total from November through March. Algae and diatoms were the dominant component of the diet, in terms of numbers of particles, between November and March, comprising between 70 and 80 percent of the total number of particles consumed (Fig. 5). However, from April through October the proportion of the diet comprised by the algal component fell sharply.

Therefore two seasons were recognized on the basis of gut contents. A summer season between April and October, when the majority of food particles found in the guts were detritus, and a winter season between November and March when the majority of food particles consumed were algae and diatoms. These two seasons also correlate with net-spinning behavior. Differences in the numbers of both detritus and algal particles were significant between seasons ($p<.0001$).

Animal particles were only present from June through October and never formed an appreciable amount of the total number of particles found in the gut. The greatest concentration of animal material in the gut was found in August at only 1.04 percent.

Area measurements were made on particles from the guts to determine the relative volume occupied by each food component. Detritus was determined to be the major constituent of the diet in terms of volume throughout the year (Figure 6). The estimates ranged from 75 to 93 per-

cent of the total through the Summer months, and between 55 and 61 percent through the Winter months. There was considerable variation in the volume occupied by detritus within some months (Figure 7). However, this variation was associated with those months when animal material was also found in the guts. Although the presence of animal particles were rare, when encountered on a slide their volume was considerable and thus displaced other particles. Therefore, on a slide containing a single rotifer the volume of detrital particles would be reduced considerably relative to the other six or seven slides where no animal particles were found. However, the variability between months within each season were not unreasonable, and when I tested for differences in the mean volume of detritus in the guts between winter (Nov.-March) and Summer (April-October), the differences were significant ($p=.0001$).

The relative volume occupied by the algal component ranged from 4.0 to 21.0 percent in the summer months, and from 34 to 45 percent in the winter months (Figure 6). As with the detrital component the algal component clearly shows seasonal trends (Figure 8). The observed seasonal differences in the volume of the algal component were statistically significant as well ($p<.0001$). Although the animal component did not represent a substantial portion of the diet in terms of particle number (Figure 5), a considerable fraction of the food volume found in the guts throughout much of the summer was animal material (Figure 6).

Average particle size found in the guts for each month are described in Figure 9. Average particle sizes ranged from about 500 to nearly 2300

square microns. There were no real differences in mean particle size throughout the winter. Mean particle size increased and particles were significantly larger during the summer ($p=.0059$). Variability in mean particle size found in the guts was substantially larger in the summer than in the winter (Table 3). The coefficient of variation in mean particle size for each month during the summer ranged from 26 to 141 percent, and from 9 to 65 percent during the winter. Variability between months during the summer months was nearly 40 percent and during the winter was about 25 percent. The percentage of empty guts was significantly higher in winter (Table 10). Seasonal differences were significant in all variables measured (Table 4).

Ivlev's preference index was employed to determine whether observed shifts in the composition of guts was the result of a direct change in the mode of feeding or simply a reflection of changing seston compositions. Table 5 compares the relative amount of each major food type found in the guts to the relative amount of each major food type comprising the seston for each month as well as the associated index values. Figure 11 is a graphical representation of Ivlev's index values throughout the year for each food type. Detritus appeared to be ingested at random throughout much of the summer as reflected by index values near zero. Larvae showed a strong preference for animal material for all months when present in the environment. Early in the summer (April and May) algal material appeared to be ingested at random while in late summer (June-October) there was apparently a slight preference for diatoms. However, this correlates with that period when animal material was present in the

environment and may be a reflection of the gut contents of rotifers. During the winter months (Nov- March) on the other hand there was a strong preference for diatoms and strong avoidance of detrital particles.

Life Cycle

H. morosa is bivoltine on the South River (Figure 12) with a summer generation that hatches in May, develops rapidly, and emerges as adults throughout August. The winter generation hatches in mid-September, rapidly obtains fifth instar and although growth continues through the winter, further development (i.e. molting, pupation and emergence to adults) ceases until late March when stream temperatures again begin to rise (Figure 1).

Figure 13 shows mean weights of fifth instar H. morosa larvae throughout the year. The large drop in weight between April and May suggests that at least some of the fifth instars present in May are from a new cohort. However, the mean weight continued to drop from May to June indicating that a percentage of the fifth instars in May are from both the winter and summer cohorts. To accurately separate cohorts, I regressed fifth instar weights for June-August and extrapolated back to obtain the weight of a fifth instar in May. I was then able to calculate the number of individuals from the winter cohort (April) weighing 6.33 mg necessary to increase the weight from the extrapolated weight (1.51 mg) to the observed weight (2.83 mg) of fifth instars in May. In this way I was able to make a more accurate split of the two cohorts.

Secondary Production

Allen curves constructed to correct for prolonged recruitment of early instars are illustrated in Figure 14. Density on the first sampling date was predicted by linear regression for both the summer and winter cohorts. It was these predicted values for the first sampling dates that were used in the production calculations.

The production calculations of both cohorts are shown in Table 6. The production of both cohorts (annual production) was estimated to be 5,391 mg AFDW/m^2/yr (3,246 mg from the summer cohort and 2,145 mg from the winter cohort). Cohort P/B ratios were low (less than 5) for both cohorts. The annual P/B ratio for the summer cohort was 5.72 while that of the winter cohort was 4.90, a difference of only 14 percent. The average standing stock (B) was 1,702 mg for the summer cohort and 657 mg for the winter cohort, a difference of nearly 61 percent.

The production attributed to fifth instars alone was also calculated for both cohorts because conclusions about the trophic basis of production (see below) are based on gut analysis of only fifth instars. The calculations for fifth instar production are shown in Table 7. The annual production of fifth instar H. morosa was 4,385 mg AFDW/m^2/yr, about 81% of the annual production of all instars. The summer cohort produced 2,716 mg/m^2/yr, nearly 84% of the production by all instars in the summer cohort. The production by fifth instars in the winter cohort was 1,669 mg/m^2/yr, nearly 80% of the production for all instars.

Trophic Basis of Production

Gut analyses indicated that the diet of H. morosa was detritus based in the summer (April-October) and algal based in the winter (Figure 5). Production associated with the summer diet (i.e. the sum of the weight lost column from April-October in table 6) was 4,034 mg/m^2/yr. The production associated with the winter diet (i.e. the sum of the weight lost column from November-March in table 6) was 1,357 mg /m^2/yr.

Volume estimates of each of the three major food types for each month and the averages for each season (as described by diet) are shown in Table 8. These data along with the seasonal production data described above were used to determine the production attributable to each food category for each season. The trophic basis of production calculated separately for each season using the method of Benke and Wallace (1980) is shown in Table 9.

Food habits and the contribution of each food type to the production during each season (as described by diet) are compared in Figure 16. The detritus component makes up the majority (by volume) of the food consumed for both seasons, and the majority of the production during the summer season comprising nearly half of the total production. Consumption of algal material increases from about 11.0 percent in the summer to nearly 40.0 percent in the winter, and the algal component is responsible for the bulk of the production during the winter making up about 62.0 percent of the total. Consumption of animal material was relatively small

throughout the entire year, averaging about 7.0 percent in the summer and only 2.0 percent in the winter. However, animal material did contribute significantly to the secondary production during the summer, comprising 30.0 percent of the total.

The amount of each food type consumed to account for the production varied greatly between seasons as one would expect (Table 10). During the seven months comprising the summer season, H. morosa consumed 48,910 mg AFDW/m^2 of food. During the five months of the winter season, only 14,186 mg/m^2 were consumed or about 29 percent of that consumed during the summer. Approximately 58 percent of the total (by volume) was detritus in the winter compared to over 80 percent in the summer. During the winter, nearly 40 percent of the food consumed was of algal origin compared to less than 12 percent during the summer.

The amount of food material egested as detritus during the summer totaled 40,842 mg/m^2 compared to 11,472 mg/m^2 during the winter (table 10). During both seasons the majority of material egested was of detrital origin (88% and 65% respectively). It is clear that H. morosa processes a larger amount of food material during the seven months of the summer season, when feeding nets were present.

Monthly rates of utilization of food material were also calculated for each season (table 11). The overall consumption rate was nearly 3.5 times faster in the summer (6988 mg/m^2 /mo) than in the winter (2,027 mg/m^2/mo). The rate of tissue elaboration, or production, was nearly three times

faster in the summer (576 mg/m^2/mo) than in the winter (193 mg/m^2/mo). Finally, the egestion rate was over 3.5 times faster in the summer with H. morosa egestion 5,834 mg/m^2/mo of food material as detritus and only 1,638 mg/m^2/mo during the winter.

Mercury Analysis

In September of 1986 a variety of insect orders as well as minnows and crayfish were analyzed for total mercury. Table 12 summarizes the results. The mean mercury concentration in the muscle tissue of minnows was the highest for all the groups measured with a mean of .586 ppm. The mean mercury concentration for Hydropsyche sp larvae was .463 ppm., while the lowest Hg concentration measured was in the predator Corydulus cornutus which had a mean Hg concentration of 0.27 ppm.

The total mercury concentration was measured in seston, periphyton and in the body tissue of H. morosa and the results summarized in table 13. Mean mercury concentrations in seston ranged from a low of 14.15 ppm in April, to a high of 20.61 ppm in August. Differences in the mercury concentrations were not significant between months or between seasons.

The mercury concentration in periphyton samples were highly variable ranging from 0.76 ppm in August to 3.21 ppm in May. No seasonal patterns were evident and differences in mercury concentrations between months and seasons were not significant, owing to a large extent to the large amount of variability associated between replicates within a month.

The concentration of mercury in the body of H. morosa was highest in July (mean of 1.23 ppm), and lowest in March (mean of .141 ppm). However enough insects were not collected in August for analyses. The concentration of mercury in the insects was significantly higher in the summer ($p=.035$).

Total mercury concentrations in seston and attached algae are shown in Figure 17. Mean Hg levels in seston were from 5 to 27 times greater than in the periphyton. Between 80 and 95 percent of the volume of the seston was detritus and it was therefore of interest to look at the relationship between volume of detritus consumed and the amount of mercury accumulated in the insects.

The percentage of detritus in the guts and the mean mercury concentration in the body each month are shown in Figure 18. The trends are remarkably similar with high mercury concentration and percent detritus in the gut during the summer months and both declining rapidly in November and remaining low throughout the winter months. However, there is some digression in this pattern between January and March. During this period the relative volume of detritus in the diet remained essentially the same while the mercury concentration in the insects continued to decline. Regression Analysis was performed with total mercury concentration in the body as the dependent variable and the percentage of detritus in the foregut as the independent variable (figure 19). The relationship between detritus consumed and mercury accumulated was significant ($p=.0004$ and $r^2=0.76$).

From October through March, total mercury in the insects was measured both with the digestive tract intact, and with the digestive tract removed. In this way I was able to get a picture of the distribution of mercury within the insect. Unfortunately I did not have the insight to begin analyzing insects in this way until October, and as a result, October is the only month when the insects were filtering their food that was analyzed in this way. Insects were also weighed with and without digestive tracts and it was determined that the digestive tract represented between 4.0 and 10.0 percent of the total body weight. Knowing the relative weight of the digestive tract (mean=7%), the Hg concentration in intact insects, and the Hg concentration of insects with the digestive tract removed (body tissue), it was a simple matter to calculate the Hg concentration in the gut alone. Also, the percentage of the total body burden of Hg that was associated with the gut and its contents was easily calculated. These data are presented in table 14.

The mercury concentration in the whole animal decreased sharply between October and November, and continued to decline through the remainder of the year. The same pattern was observed in the mercury concentration in the gut alone. Mercury concentrations were very high in the gut in October (7.71 ppm), dropped sharply in November (3.53 ppm), and continued to decline reaching a low of .367 ppm in March.

The pattern of mercury accumulation in the body tissue (minus-gut) was somewhat different in that the peak in Hg concentration was not reached

until December at .399 ppm, with a subsequent decline through the remaining three months reaching a low in March of .124 ppm.

Nearly 71 percent of the total body burden of mercury was associated with the guts and its contents in October. The relative amount of mercury associated with the guts declined to less than 50 percent in November, and continued to decline although more slowly through March, where less than 20 percent of the total body burden of mercury was associated with the gut and its contents. This is essentially the same as saying that although the total amount of mercury in the insects declines throughout the winter, a larger percentage was associated with body tissues (minus gut) as the winter progressed.

DISCUSSION

Feeding Habits

It is clear from the data that H. morosa exhibited a behavioral shift in feeding habits. Direct evidence for the shift came from examination and quantification of foregut contents (Figures 5 and 6). There were significant seasonal differences in the relative abundance and volume of food types found in the foregut. For example, during the Summer months (April-October), when feeding nets were widespread, the relative abundance and volume of algal material was significantly lower than in the Winter (November-March), when feeding nets were virtually absent. Comparison of the relative proportion of each food type found in the guts to the relative proportion of each food type in the seston (Figure 11) showed observed changes in the quality of food consumed to be the result of a functional shift in feeding habits and not a function of food availability in the seston. These data are consistent with other feeding studies of filter-feeding caddisflies (Rhame and Stewert 1975, Fuller and Mackay 1980), and support the hypothesis that net-spinning caddisflies cease maintaining feeding nets in the Winter and switch to grazing. There was other evidence supporting this hypothesis as well. For example there was an increase in the number of algal genera found in the guts during the colder months when feeding nets were absent (Figure 4). One would expect the number of algal genera consumed during the time when insects were filter-feeding to be associated with the number of algal genera which

were dying and sloughing off into the water column, and thus becoming a portion of the seston component. On the other hand, one would expect the number of algal genera consumed during grazing to be better reflected by the number of algal genera present in the stream. Therefore it is not surprising that a significantly greater number of algal genera were found in the guts of H. morosa in the Winter when they were grazing, since there would obviously be more algal genera present in the stream at a given time than would be dying and entering the water column at a given time.

A shift in feeding habits would also likely be reflected in the mean particle size consumed. Based on the assumption that these insects were filtering their food in the Summer and grazing in the Winter, I assumed that the mean particle size found in the gut in the summer would be limited by the mesh of their feeding net, thus particles would tend to be larger and show less variability than in the Winter, when these insects were actively grazing their food. However, this was not the case as seen in Figure 9. Although mean particle size was larger in the summer, most of the variability in mean particle size was observed in the Summer (Table 3) due to the consumption of very large animal particles as well as the consumption of very small algae particles. Throughout the Winter when diatoms represented the majority of food particles consumed and animal material was rare, the variability around the mean particle size was small (Table 3), probably due to limits in particle size imposed on the animal by mouth part morphology.

Net Spinning Activity

Feeding nets were widespread in the South river from early May through mid-November. Net spinning activity correlated well with temperature (Figure 1), as the number of feeding nets observed in the stream dropped dramatically with a concomitant drop in average daily stream temperatures. For example, between November 9 and November 14, the average daily temperature dropped from 13 C to 5.5 C. Also, on October 30 feeding nets were widespread, yet by November 26 they were virtually absent. Likewise, net-spinning activity increased with the rising limb of the thermograph in early spring. It appears that there may be a threshold of about 10 C, below which net-spinning activity begins to decrease. These results are consistent with other studies concerning the relationship of temperature to net-spinning activity in caddisfly larvae (e.g. Fremling 1960, Williams and Hynes 1973, Rhame and Stewert 1975).

Other factors have also been shown to affect net-spinning activity in hydropsychid caddisflies. For example, Fuller and Mackay (1980) found that manipulating temperature or flow rate affected the number of larvae that spun feeding nets in laboratory streams, and that preferences for both were species- specific. Fuller and Mackay (1980) also found that the resumption of net-spinning in spring correlated well with the concentration of epilithic material present in the seston. However, in the South River both seston concentration (figure 2) and the percent organic matter in the seston (figure 3) were rising at the time when the larvae

ceased net-spinning activity. Therefore, it is unlikely that H. morosa larvae use seston quality or quantity to cue net-spinning activity.

It is interesting that the cessation of net-spinning activity coincides with that period when H. morosa larvae are in a period of developmental diapause (figure 12). I suggest that it is possible that the suppression of developmental hormones may simultaneously suppress the physiological systems responsible for spinning silk. Thus, declining stream temperatures would indirectly limit silk production. However, larval diapause in hydropsychid caddisflies has not been studied to any great degree and the above statements are only speculations based entirely on crude correlations between presence or absence of feeding nets, temperature, and instar frequency histograms.

Secondary Production

Hydropsyche morosa was bivoltine on the South River exhibiting a pattern of development similar to that found by Mackay (1984) in the lower Humber river. It is interesting that while the winter cohort continues to grow, development is delayed until March (Figure 12) when stream temperatures again begin to rise (Figure 1). It is not surprising then that larvae from the winter cohort reached a greater weight at maturity than did larvae from the summer cohort (Figure 13). This appears to be the rule in hydropsychid caddisflies (Parker and Voshell 1983, Mackay 1983), and this absence of larval development may suggest larval diapause during the winter. If indeed this is true diapause, a token stimulus such as

an increase in day length, would be necessary to reset the hormonal physiology necessary for larvae to resume development (Tauber and Tauber, 1981).

The annual production for Hydropsyche morosa was 5391 mg AFDW/m^2/yr. This falls well within the range of production estimates previously reported for single species of Hydropsyche. Over sixty percent of the annual production was attributed to the summer cohort (table 6). The annual P/B is directly related to individual growth and is roughly equivalent to the biomass turnover rate (Benke, 1984). The annual P/B ratio for the summer cohort was only about 14 percent higher than for the winter cohort. Conversely, the mean standing stock was over 61 percent higher in the summer cohort suggesting that most of the difference observed in production estimates between the two cohorts was not the result of a greater growth rate, but due to higher densities observed in the summer cohort. The shapes of the survivorship curves for both cohorts are similar but initial densities are much higher in the summer cohort and therefore remain higher throughout their growing season. One possible explanation for this would be that adults from the winter cohort are more fecund. Fifth instars from the winter cohort reached considerably larger weights than did fifth instars from the summer cohort (Figure 13). Fecundity of hemimatabolous insects have been shown to be a function of body size (e.g. Clifford, 1970). It may be that fecundity is a function of body size in H. morosa as well.

Trophic Basis of Production

In order to explain the importance of a shift from filtering to grazing food it was necessary to estimate the relative volume of each of the major food types consumed each month (Martin and Mackay, 1981). Again, there was a significant increase in the relative volume of algal material found in the guts from summer to winter (Figure 8). Conversely, there was a significant decrease in the relative volume of the detrital component found in the guts from summer to winter (Figure 7). Using this information along with the literature derived assimilation efficiencies and production efficiencies, it was possible to determine the functional role of *H. morosa* and how it changes with the seasons.

A great deal of work has been devoted to determining the functional role of net-spinning caddisflies, but it has primarily centered around site-specific variation, differences in the role of a species from one site to the next (e.g. Parker and Voshell 1983, Ross and Wallace 1983), and species-specific variation, differences in the role of a number of species at a particular site (e.g. Benke and Wallace 1980, Cudney and Wallace 1980). However, with the knowledge of fundamental changes in feeding habits from Summer to Winter in many species of net-spinning caddisflies (Rhame and Stewert 1975, Fuller and Mackay 1980, and this study), it is interesting to compare the functional role of a single species within a site, between seasons.

The summer cohort of this bivoltine population is present from May through August (figure 12) and are therefore relying exclusively on filter-feeding to obtain their food. The winter cohort is present from September through April and so filter their food in September and October, brush food material up from the bottom (what I have been calling "grazing") from November through March, and again resume filter-feeding in April when stream temperatures increase.

Clearly there are considerable changes in the relative importance of the major food types to the production of H. morosa as the seasons change. During the summer months the detrital component was responsible for the majority of production, while both the animal and algal component contributed significantly as well (figure 16). During the winter however, the algal component was responsible for over 60 percent of the production, with detritus contributing significantly also. The animal component was not a major food source during the winter and only a minimal amount of the production was associated with animal food.

H. morosa processes more food material (table 10) and at a faster rate (table 11) during the summer when they are filtering their food. Much of the food material ingested during this time is detritus (nearly 82%). Assuming that H. morosa does not consume a significant proportion of the total seston passing over them (Haefner and Wallace 1981, Ross and Wallace 1983), then it is unlikely that H. morosa lowers the food quality of the seston to individuals further downstream. Although other studies have found otherwise (e.g. McCullough et al. 1979a, Parker and Voshell 1983),

the species represented in those studies were much more predacious. The volume of the animal component ingested is small throughout the year (figure 6) suggesting that H. morosa is not much of a predator. However, caution should be exercised when interpreting these results because individuals used in gut analysis were generally collected in the afternoon, when insect drift densities are characteristically low (Waters 1961, Bournaud and Thibault 1973). In other words, had the samples been collected at dusk, it is possible that a larger volume of animal material may have been present in both seston and in larval guts. Therefore, the importance of animal food to the production of this species may have been underestimated during the summer season.

During the winter, H. morosa brushes its food up from the stream bottom, and removes little or no food material from seston. At the same time H. morosa egests 1,638 mg AFDW/m^2/month (table 11) which presumably becomes part of the seston. Therefore, given the large densities often observed in populations of hydropsychids, and the characteristically low flows of most streams in mid winter, it is likely that H. morosa does add significantly to the quantity of seston in transport and thus available to other collector populations further downstream during the winter months.

Benke and Wallace (1980) discussed the potential error associated with using literature derived assimilation efficiencies in this type of analysis. They concluded that while error certainly exists, it should not exceed the error associated with production estimates in general. However, the studies from which these assimilation values were taken were

laboratory studies where individuals of a given species were fed completely different food types from one trial to the next. One recent study using aquatic snails suggested that some aquatic invertebrates can compensate for low food quality by increasing the efficiency in which they assimilate (Rollo and Hawryluk, 1988). Therefore it should be recognized that while this type of analysis characteristically uses literature derived assimilation efficiencies, there is some question as to their validity.

Feeding Habits and Mercury Accumulation

The third objective of the study was to determine whether changes in feeding habits would affect the accumulation of mercury in the insects. The assumption is that these insects acquire mercury through the ingestion of contaminated food.

Hydropsyche sp larvae accumulated high concentrations of mercury relative to other groups in the benthic community (table 12). Hildebrandt et al (1971) found Hydropsyche larvae to have the highest concentration of mercury of all groups of the insect community in the Holsten river. High mercury concentrations along with the high densities of these insects observed in the stream throughout the year, suggest that they may be important sources of mercury to higher trophic levels. It is interesting to note that Corydalus cornutus, a predacious insect, had the lowest Hg concentration of all groups measured. This is inconsistent with the concept of biomagnification (Williams and Weiss, 1972), which states that

the concentration of mercury in the body tissues increase with successive trophic levels.

The mercury concentration in the seston was found to be five to twenty seven times greater than in the periphyton throughout the year (table 13). High concentrations of mercury in suspended solids is typical in contaminated streams (Baldi and Bargagli 1984, Langston and Zhou 1986) because mercury dissolved in the water has a high affinity for suspended organics. Therefore it was expected that H. morosa larvae would accumulate more mercury in the summer, when they were filtering seston for food. As expected, H. morosa larvae had significantly higher concentrations of mercury during those months when they were filtering their food (table 13). Also, the concentration of mercury in the gut was between three and thirty one times greater than in the body tissue (table 14). These data suggest that mercury was acquired through the consumption of contaminated food. This is consistent with earlier findings. For example, Jernelov (1971) suggested that the mercury content of both sediment feeders and seston feeders depended on the quantity of Hg rich particles in the intestines of the animals.

No less than 81 percent of the total volume of the seston was composed of detrital particles in any month. Given the relatively low concentrations of Hg observed in the algae and the relatively small volume of animal material in the seston, it is reasonable to assume that the high Hg concentrations in the seston were associated with the detritus component. Therefore, I suggest that the amount of mercury that accumulated

in the insects was limited by changes in the relative volume of detritus consumed by the insects.

The trends observed for mercury concentration in the insects and the relative volume of detritus in the guts are remarkably similar (figure 18). Furthermore, correlation analysis of mercury concentration in the insects on the relative volume of detritus in the guts revealed that 76 % of the variability in mercury concentration in the insects throughout the year, was explained by the relative volume of detritus in the guts (figure 19).

Much of the remaining variability in the relationship was associated with the late winter when the relative volume of detritus consumed remained unchanged, while the mercury concentration in the insects continued to decline (figure 18). It is likely that this is a reflection of an decrease in the relative fullness of the insect guts. The percentage of empty guts was significantly higher in the winter (Nov-March) than in the summer (Apr-Oct), and there were more empty guts in March than in February (figure 10). However, I did not measure the relative fullness of those guts that were not empty and subsequently I was unable to make any kind of correlation.

Both the mercury concentration in the whole insect and in the digestive tract decline from October through March (table 14). One would expect such a decline in mercury concentration as the relative volume of the highly contaminated detritus component becomes less and less important

to the diet. However, the accumulation of Hg in the body tissue exhibits a different pattern, in that the peak in Hg concentration is not reached until December, then declines through the remainder of the winter (table 14). The observed delay in this peak is not a simple function of time as the winter cohort reaches fifth instar in October, and, although they continue to grow there is no apparent developement until emergence in April (figure 12). Therefore, if accumulation of Hg in the body tissue was a simple function of time, one would expect these fifth instar larvae to accumulate more and more Hg into their tissues until their emergence. This was not the case however as mercury concentrations dropped from January through March.

A more plausible explanation for the observed pattern relates to the absorpsion-depuration dynamics. The rate at which mercury is absorbed into the body from the gut may be controlled by the concentration of mercury in the gut (i.e. a donor controlled model). For example, it may be that for October, November, and December, the concentration of Hg in the gut is high enough that the rate of absorpsion of Hg from the gut into the body tissue is greater than the rate of depuration of Hg out of the body. Likewise, for January, February, and March, the concentration of mercury in the gut may have been at such low levels that it was depurated from the body faster than it was absorbed from the gut. These data suggest that absorpsion and depuration rates are at equilibrium when the concentration of mercury in the gut is about 2.0 ppm. Anything above 2.0 ppm, and the larvae accumulate mercury into the body tissues; anything less than 2.0 ppm., and there is a net loss of mercury from the body.

Lock (1975) found a similar balance between Hg absorpsion and depuration in Daphnia and trout and suggested that the equilibrium value was directly related to the Hg concentration in either the food or water.

The relative amount of the total body burden of mercury associated with the gut and its contents declines from October through March as well (table 14). This can be explained in two ways. The most likely explanation is that the concentration of mercury in the gut drops off rapidly as the diet becomes more and more algal based. Conversely, depuration of mercury occurs at a much slower rate. Therefore, a larger percentage of the total body burden would be associated with the body tissue in the winter.

Another possible explanation has to do with the differences in the efficiency between which Hydropsyche larvae assimilate detritus and algae. As discussed earlier, the assimilation efficiency for algae and diatoms is about 30 percent. In contrast the assimilation efficiency for detritus is about 10 percent. It may be that since algae is assimilated more efficiently than detritus, then the mercury associated with the algae might be assimilated more efficiently as well.

CONCLUSIONS

In summary, it is clear that Hydropsyche morosa exhibited a seasonal shift in feeding patterns between summer and winter. It is doubtful that this species has a very serious impact on seston quality because only a small amount of the food ingested during the summer when they are filtering seston is of the high quality animal food. On the other hand, it appears that this species may actually increase the amount of seston in transport during the Winter when larvae are consuming attached algae and benthic POM and egesting detritus, which likely becomes suspended in the water column and transported downstream.

Concomitant with this shift in feeding habits from summer to winter is a decline in the total mercury concentrations observed in the insects. Most of this mercury is associated with the guts and its contents indicating that most of the mercury is taken in from the consumption of contaminated food. Only a small percentage of mercury is actually absorbed into the body tissue, and the rate of absorpsion appears to depend on the concentration of mercury in the gut. It is clear that a large amount of mercury is associated with suspended organics in the South river and is therefore available to filter-feeders. Even though there were no monthly or seasonal differences in the mercury concentration of the seston, there was significantly less mercury in the bodies of Hydropsyche morosa during the winter. My data suggests that the observed change in feeding habits from summer to winter was primarily responsible for this phenomenon.

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FIGURES

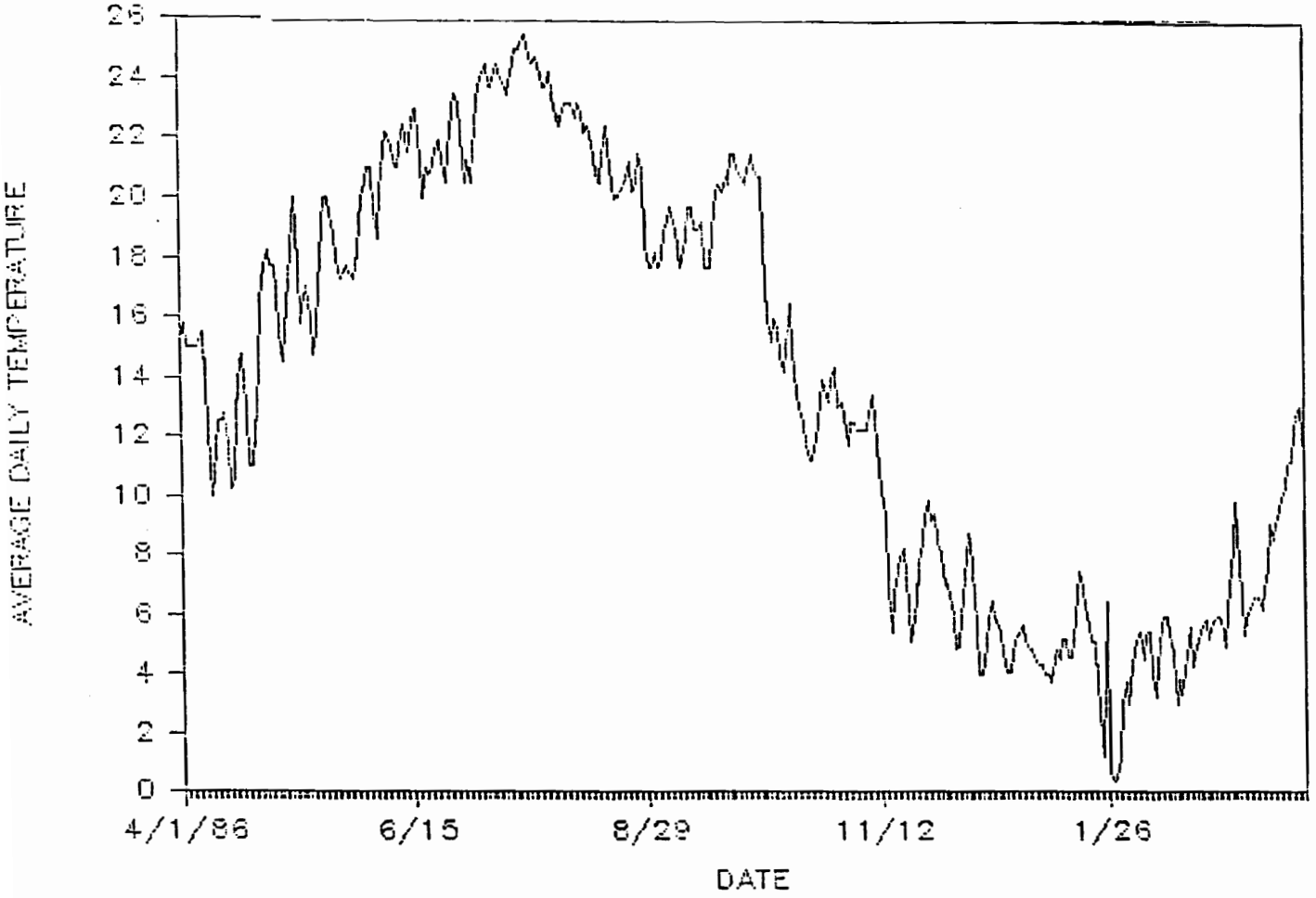

Fig. 1. Average daily water temperature from April 1986 - March 1987.

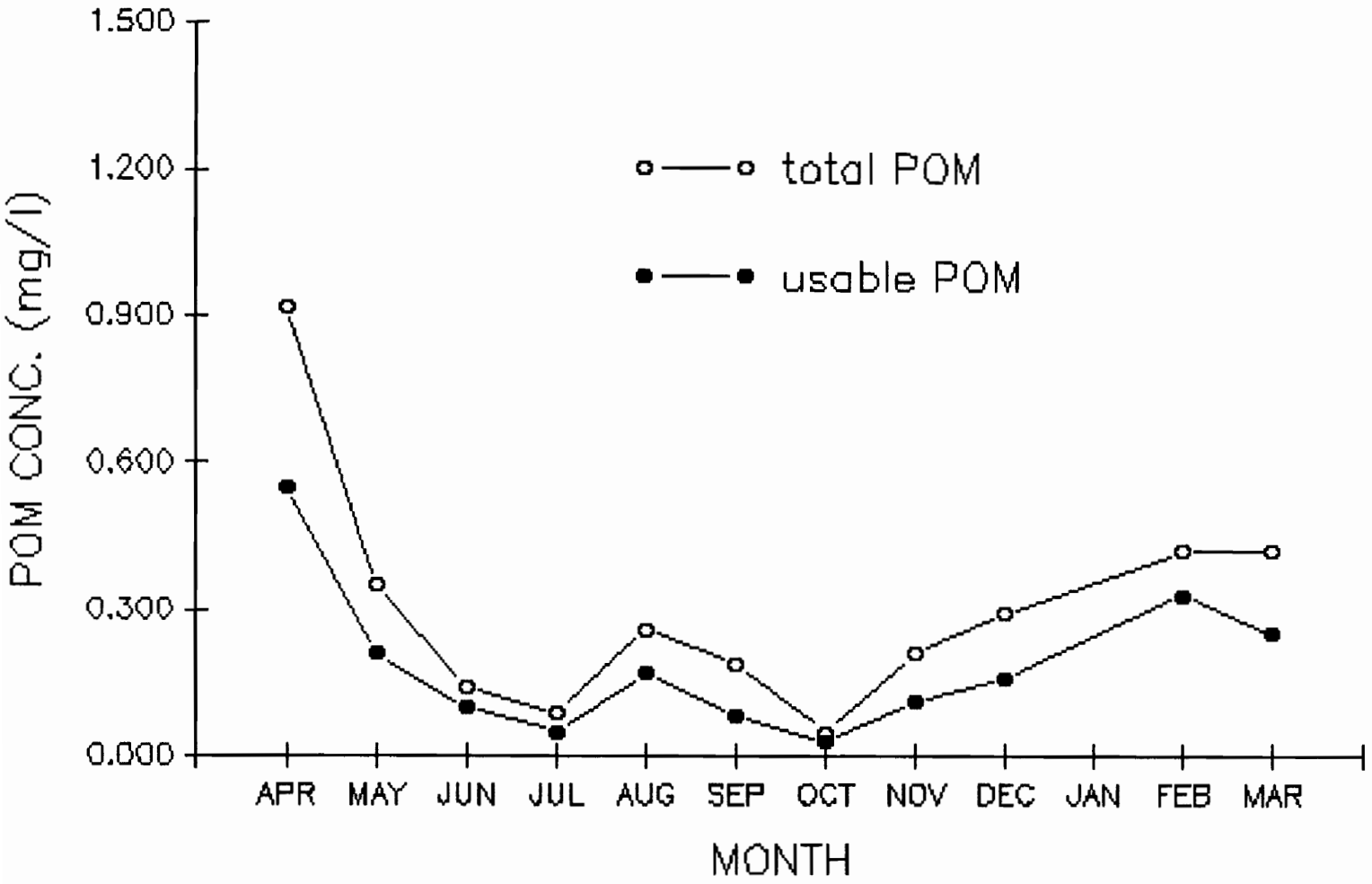

Fig. 2. Total and usable POM in the seston.

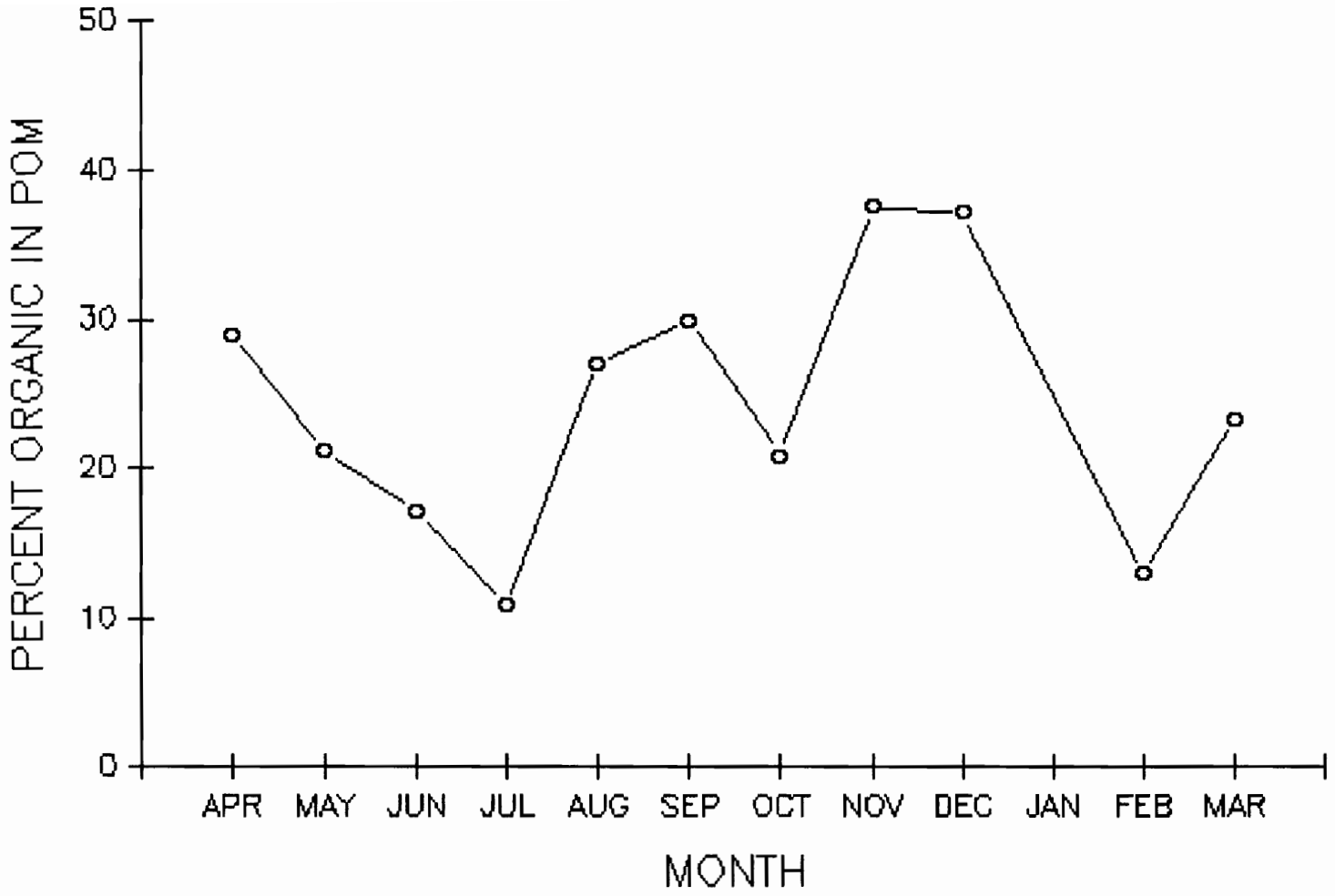

Fig. 3. Percent organic matter in the seston.

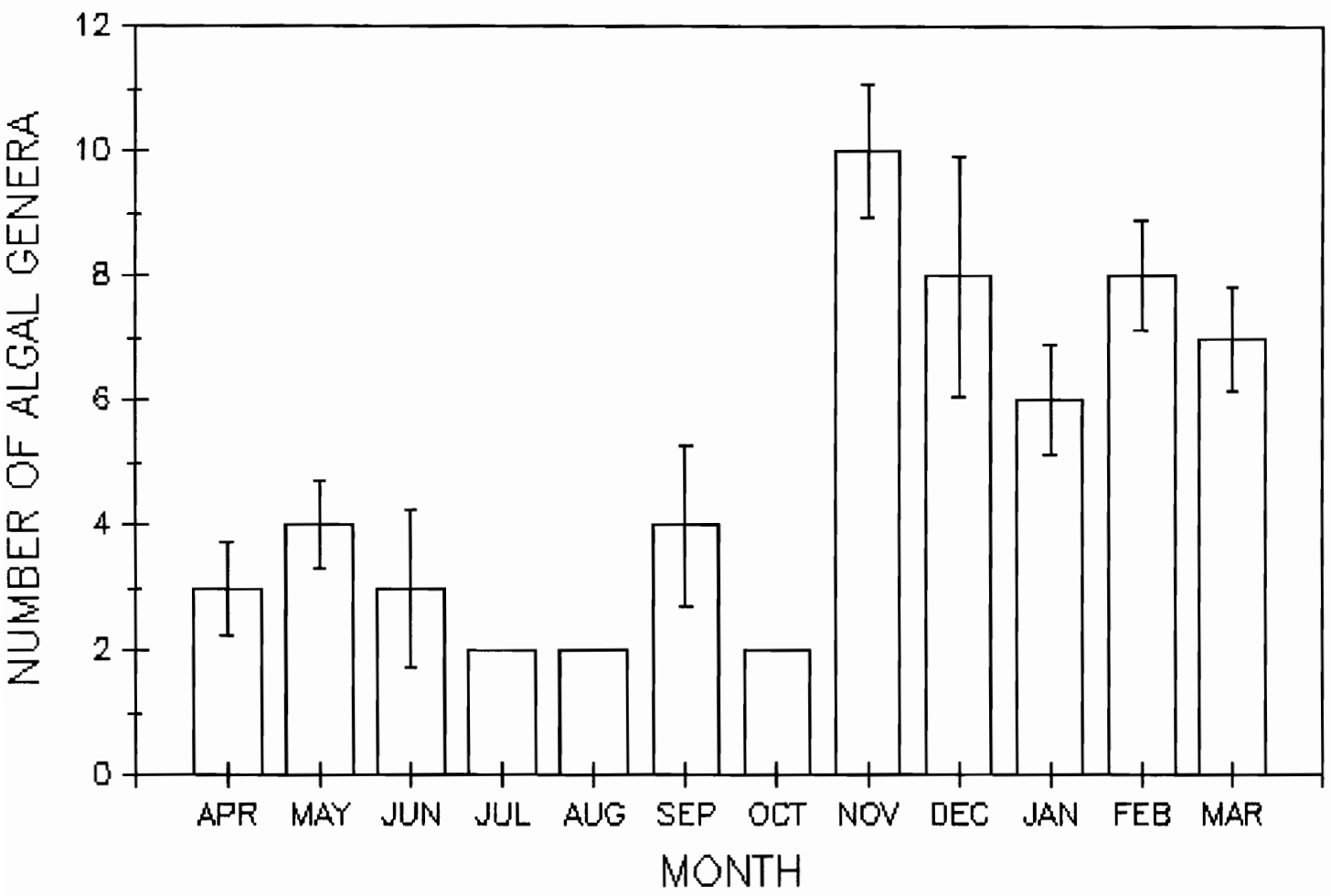

Fig. 4. Number of algal genera found in guts.
Means +/− 1 standard deviation.

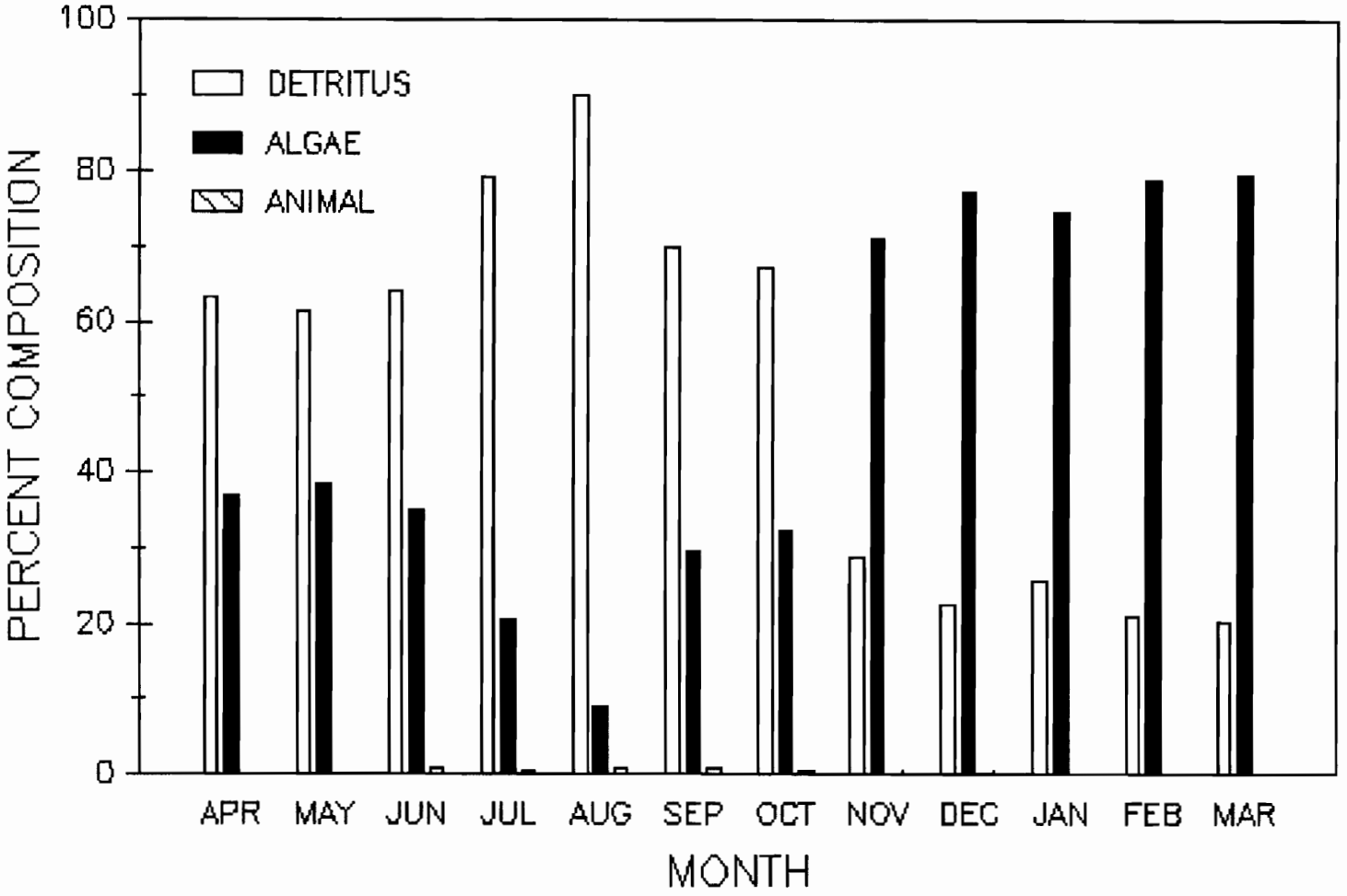

Fig. 5. Relative number of particles of ea. food type in guts.

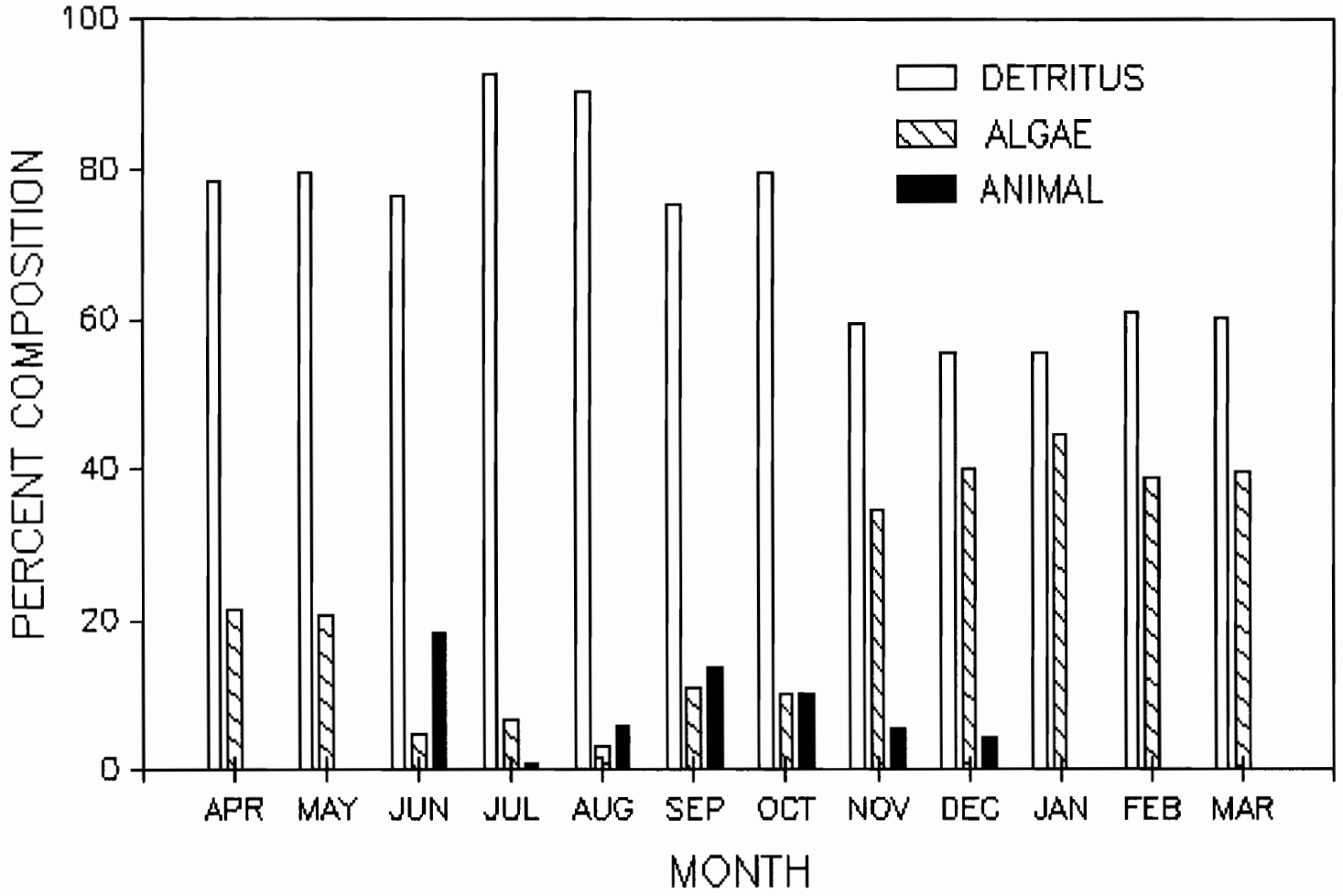

Fig. 6. Rel. volume of ea. food type in guts.

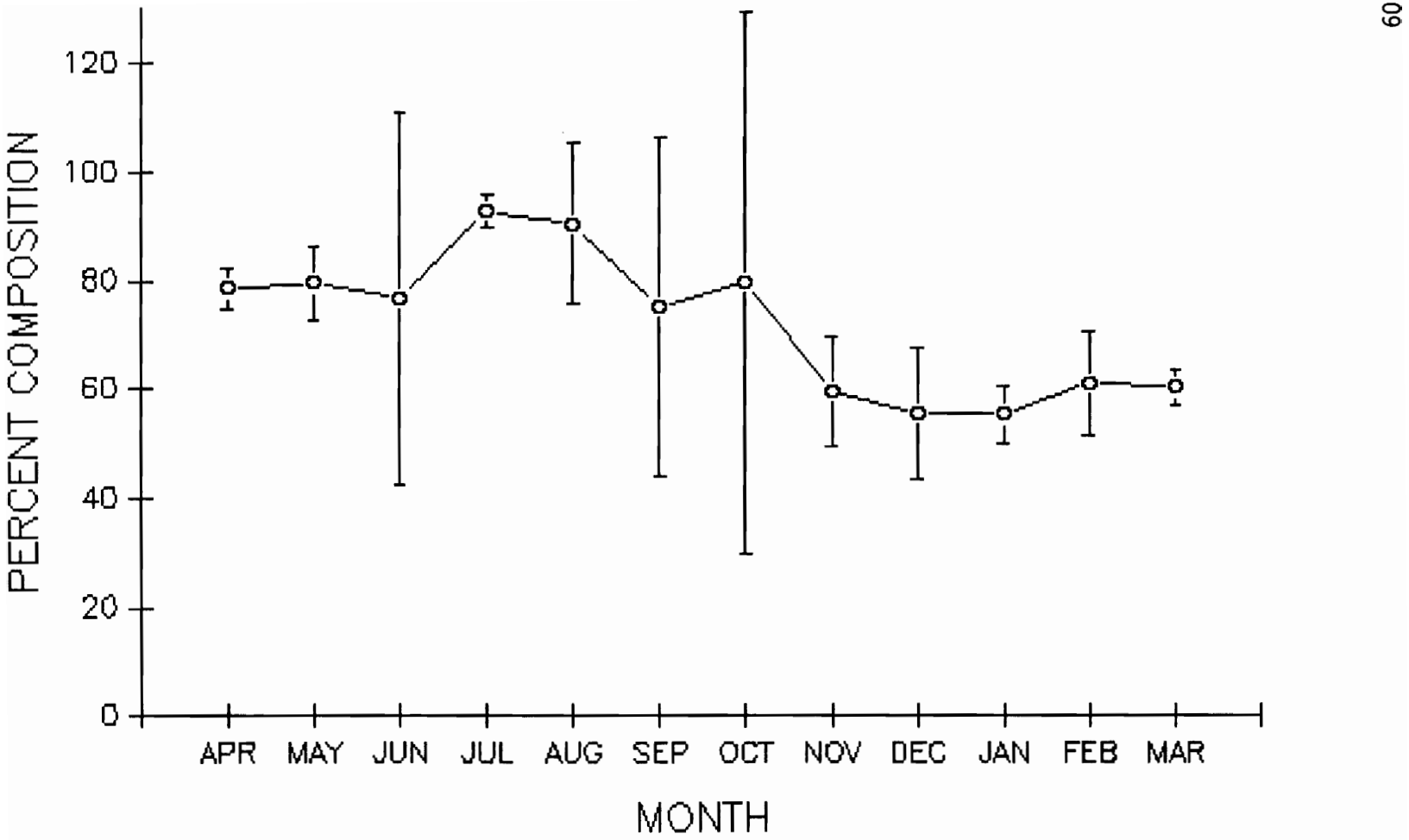

Fig. 7. Relative volume of detritus in guts.
Means +/− 95% C.L.

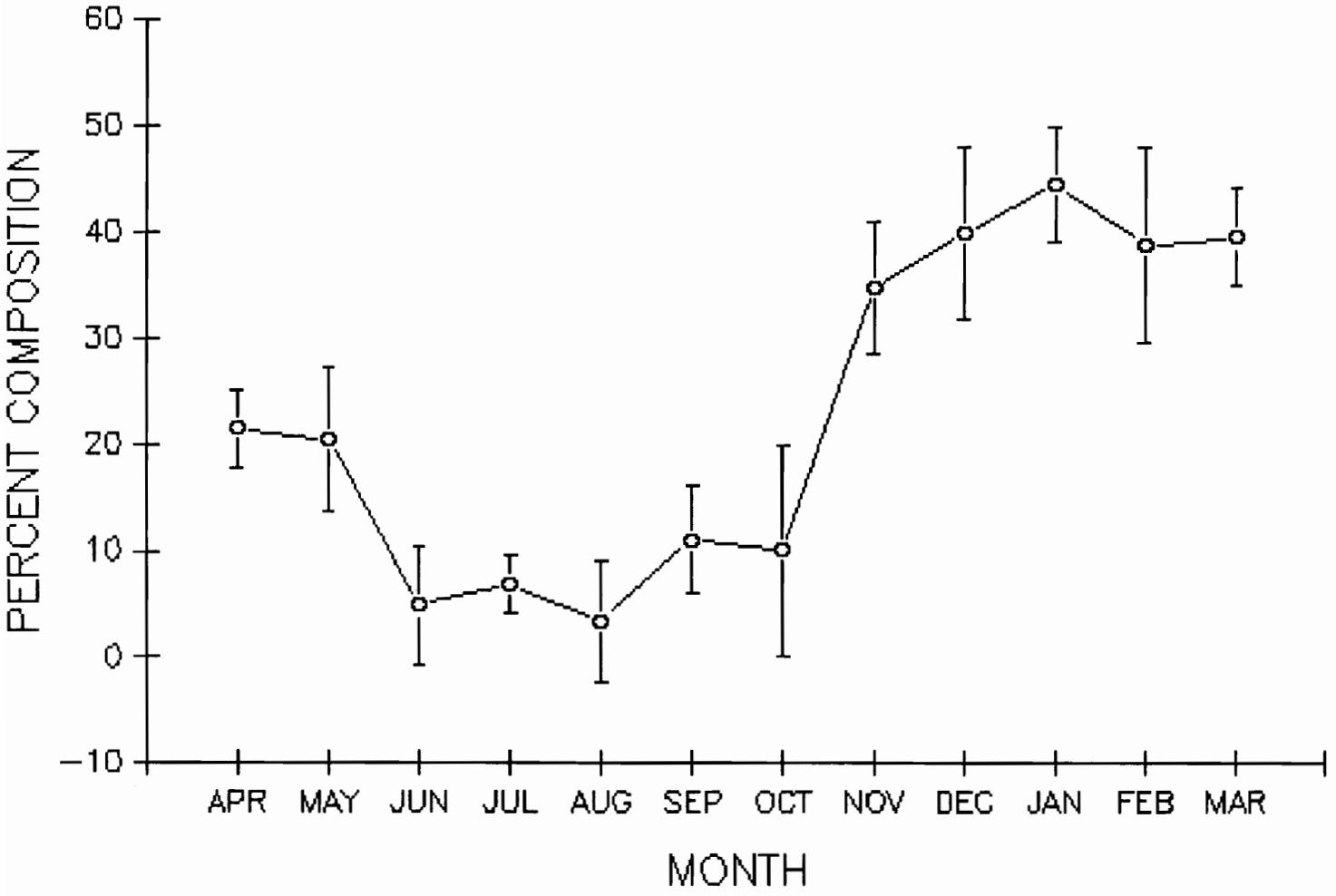

Fig. 8. Relative volume of algae in guts.
Means +/- 95% C.L.

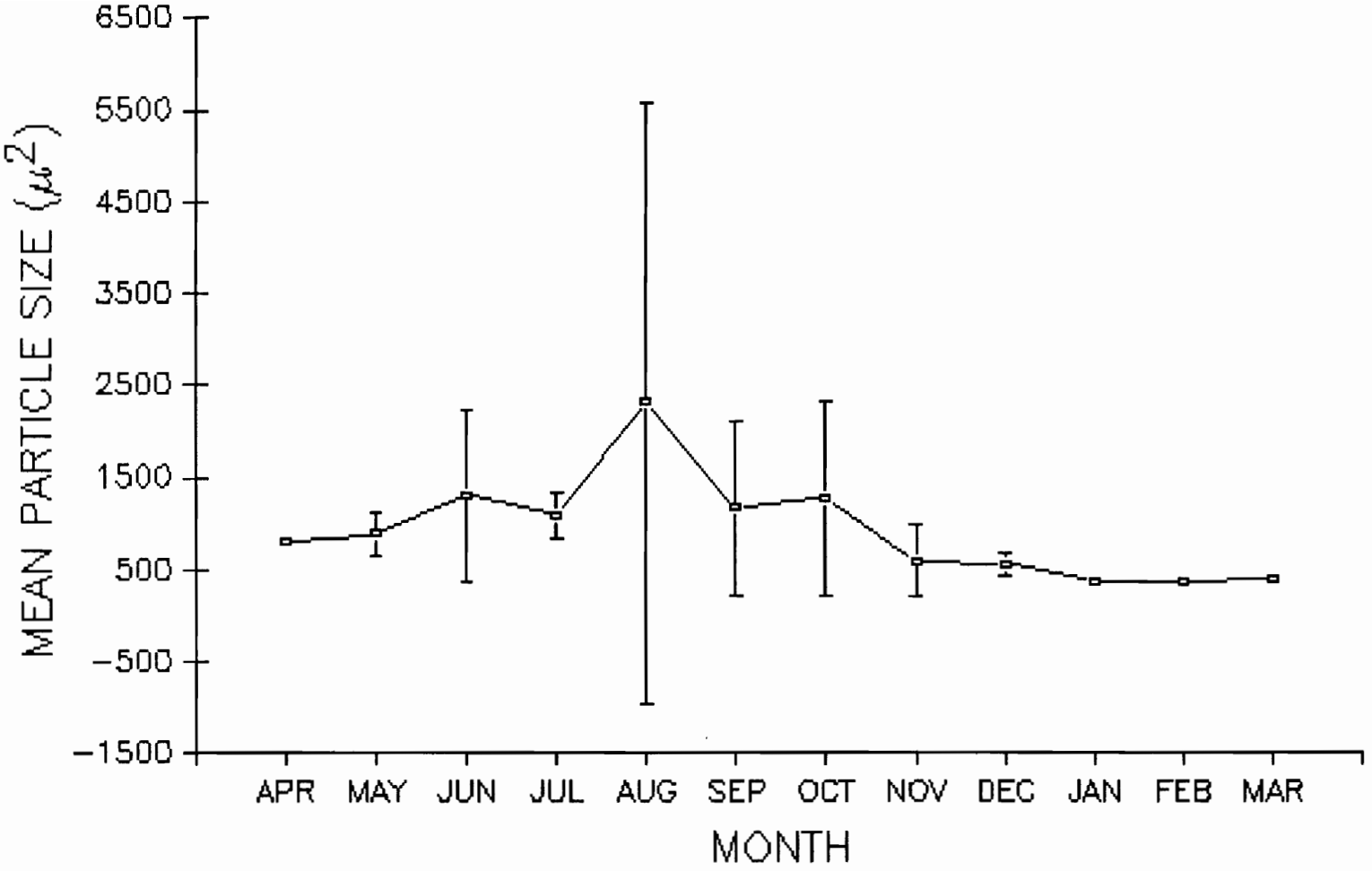

Fig. 9. Mean size of food particles.
Means +/− 95% C.L.

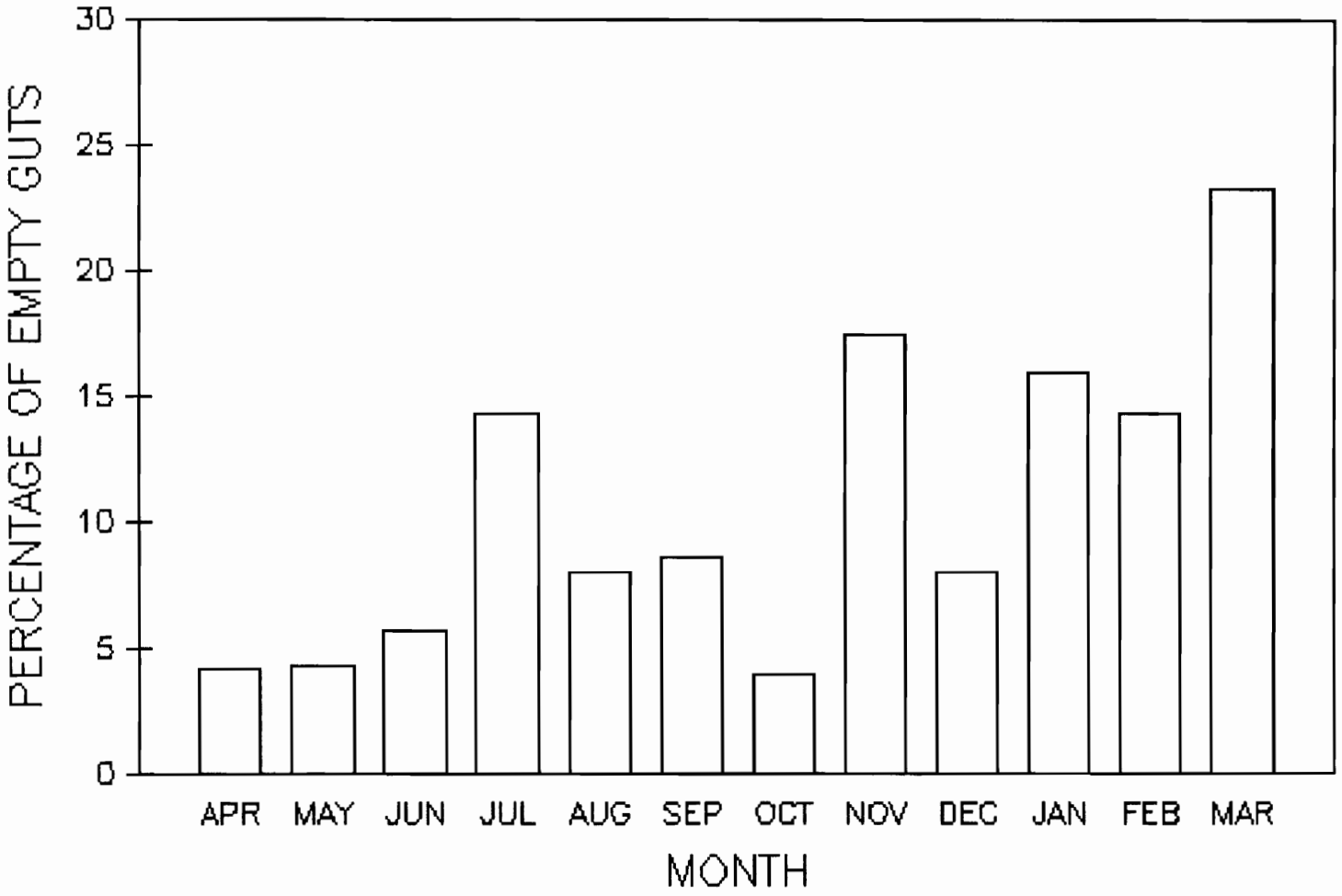

Fig. 10. Percentage of total guts analyzed that were empty

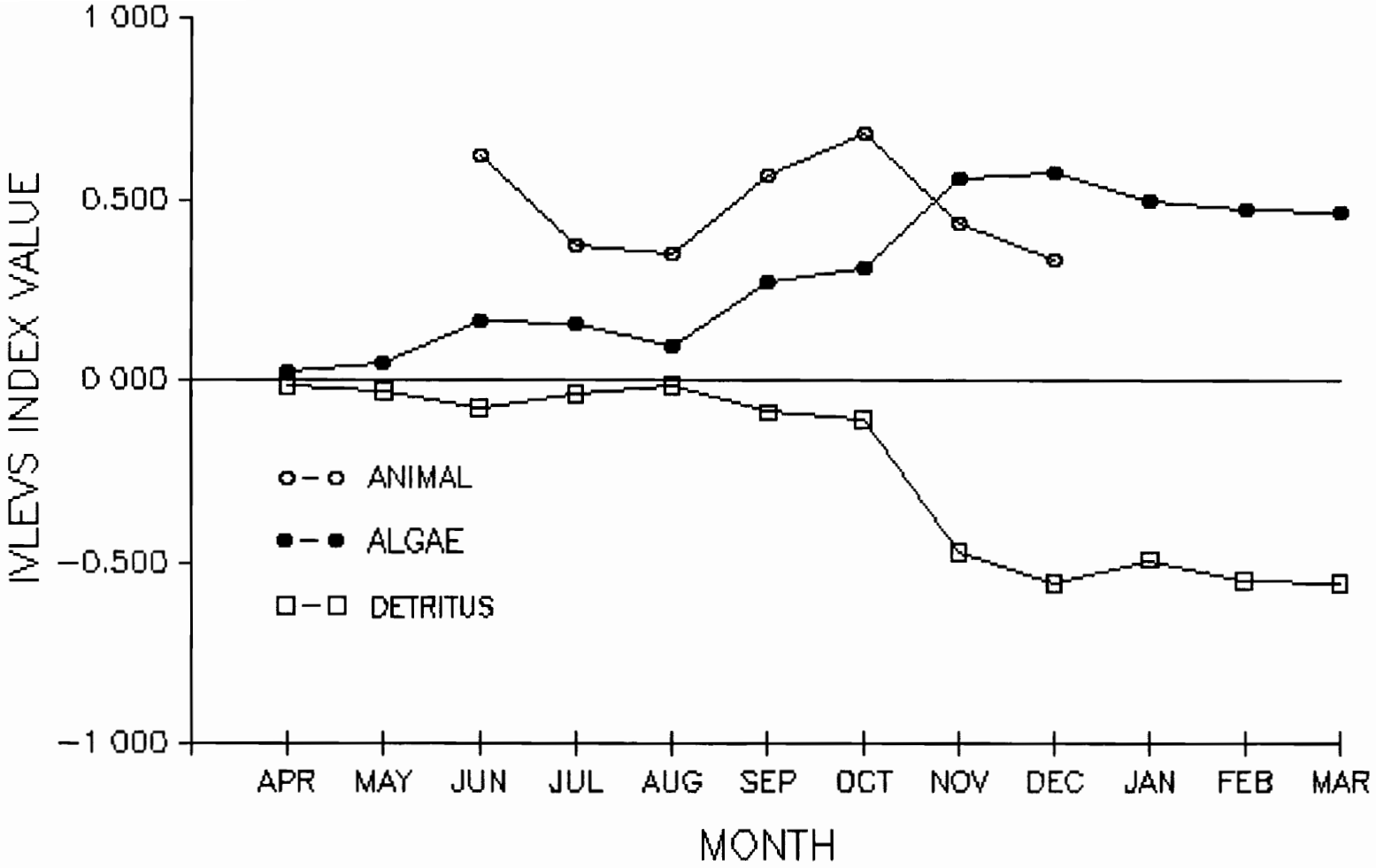

Fig. 11. Ivlevs preference index.

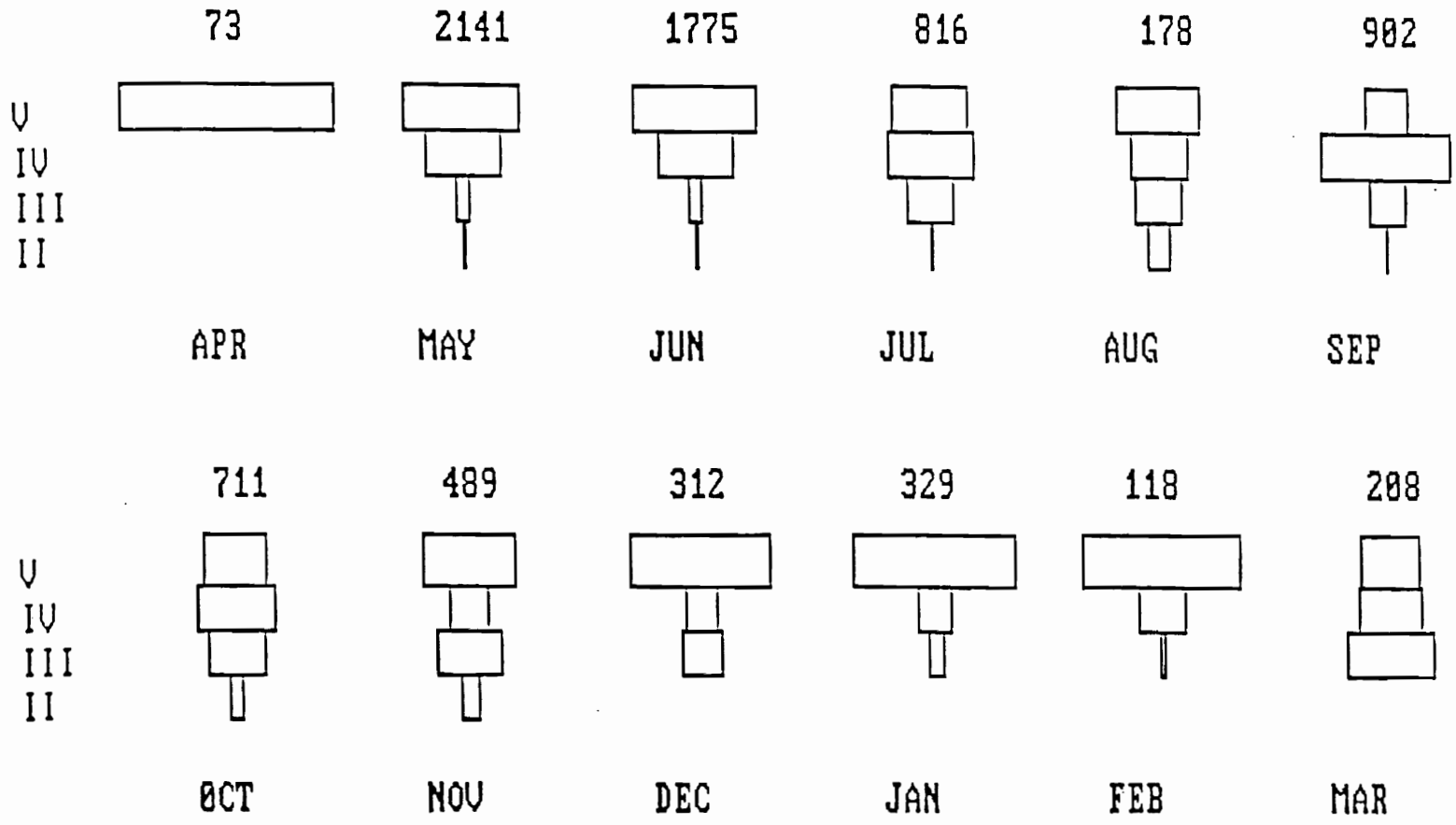

Fig. 12. Instar Frequency Distribution of H. morosa larvae on the South River, Virginia.

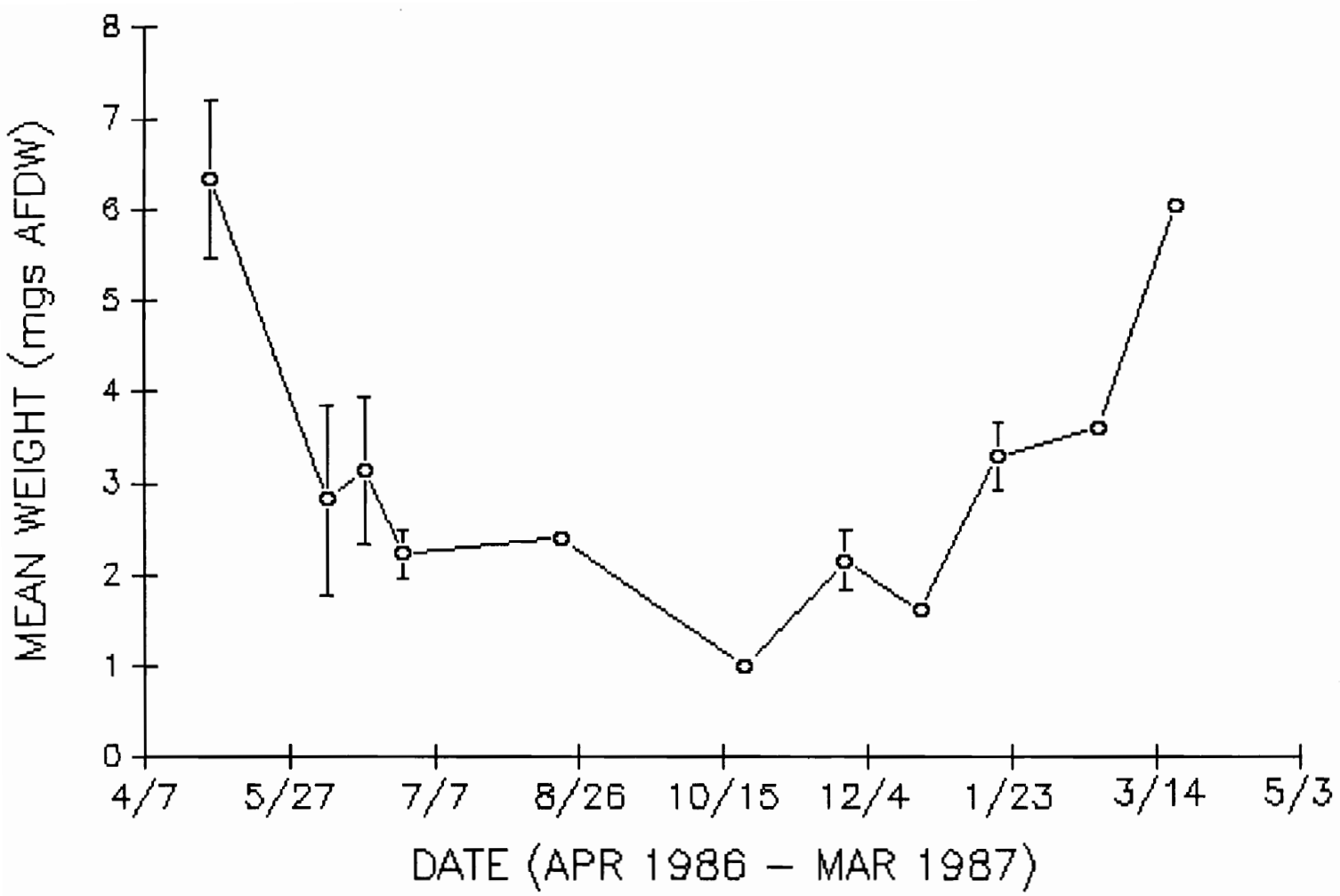

Fig. 13. Average weight of fifth instar.
Means +/– 95% C. L.

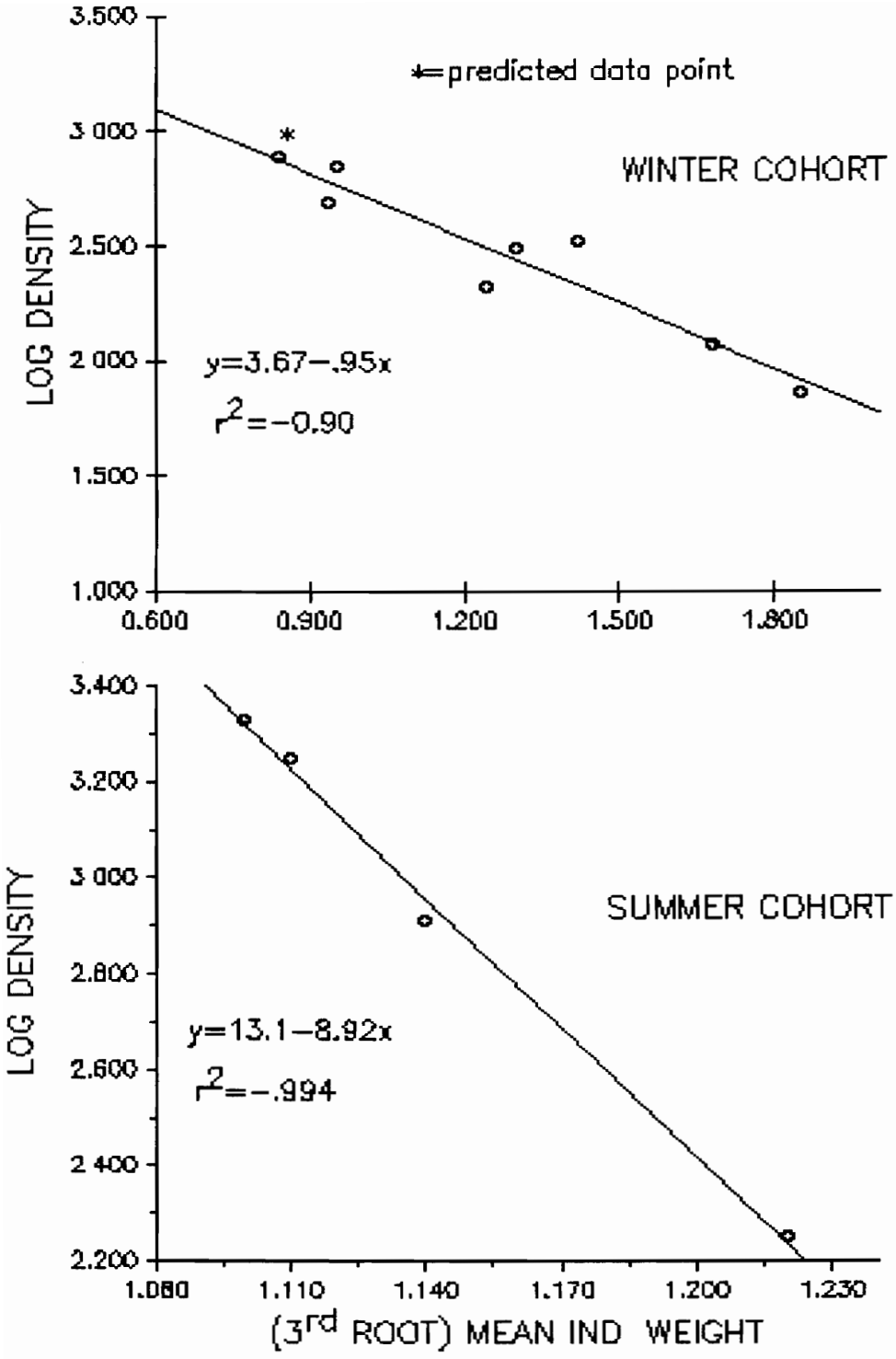

Fig. 14 Allen curves for both cohorts

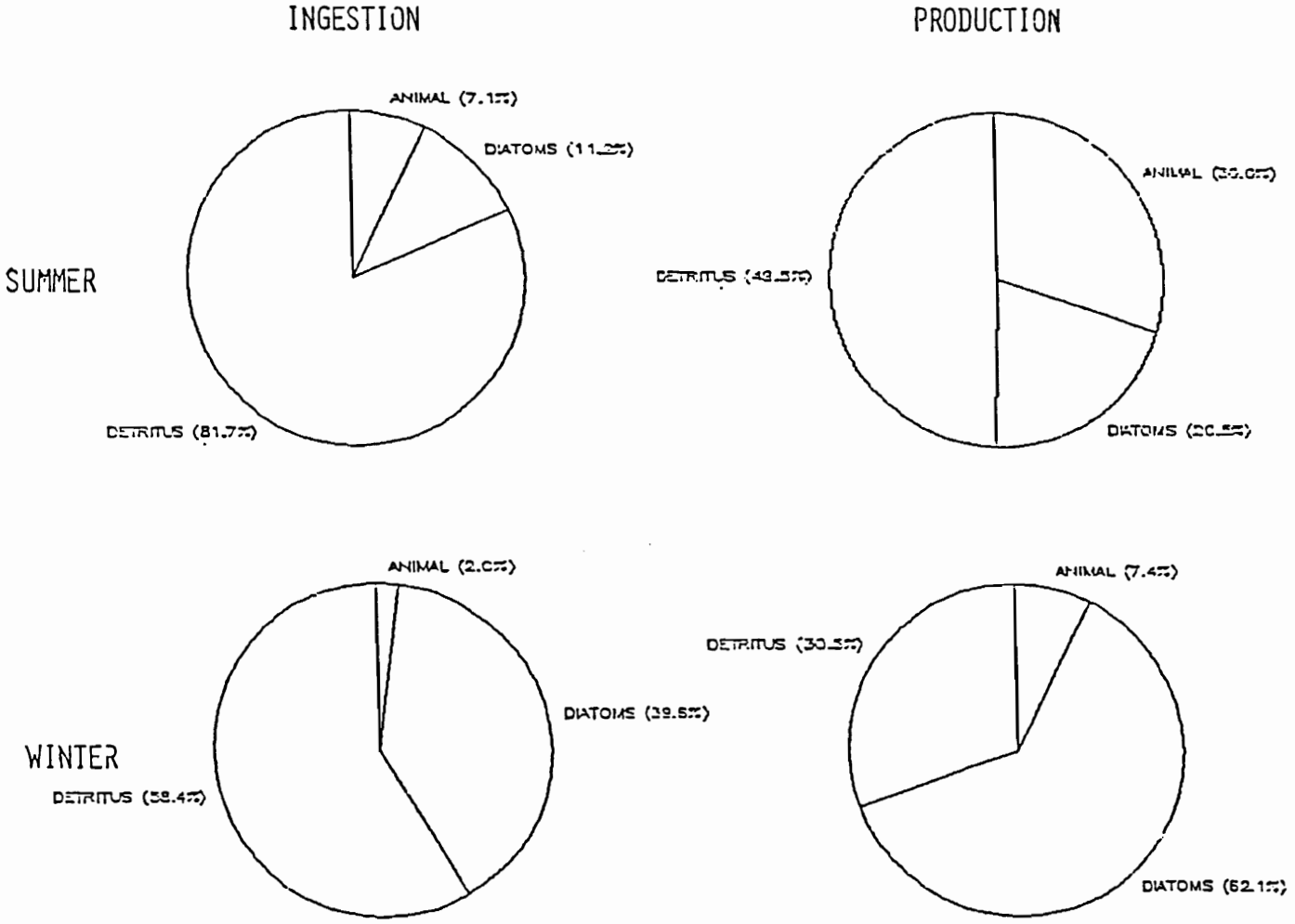

Fig. 15. Comparison of food habits and the relative contribution of each food type to the production of H. morosa.

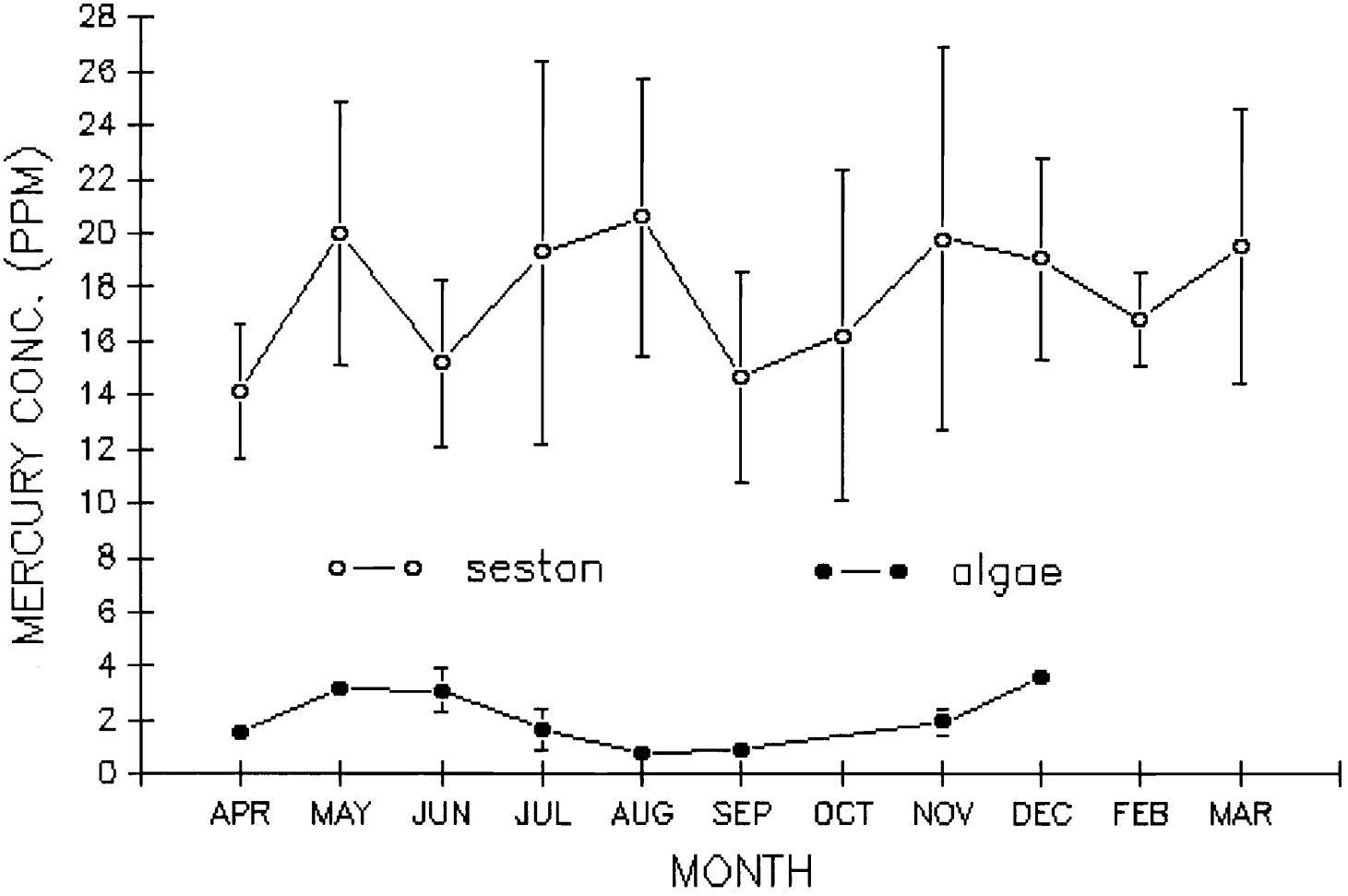

Fig. 16. Mercury concentration in seston and attached algae.
Means +/− 1 S.D.

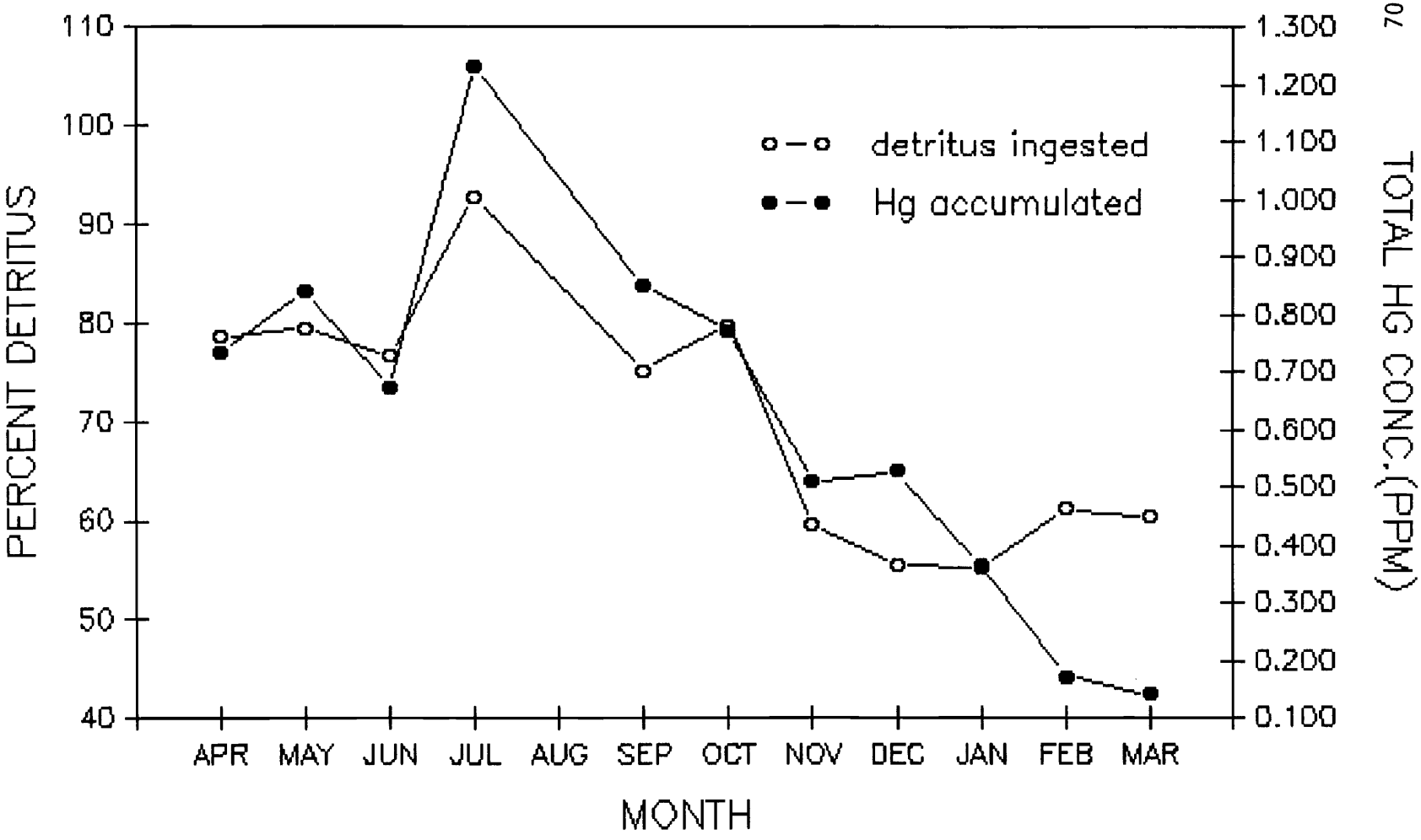

Fig. 17. Detritus ingested and Hg accumulated by larvae.

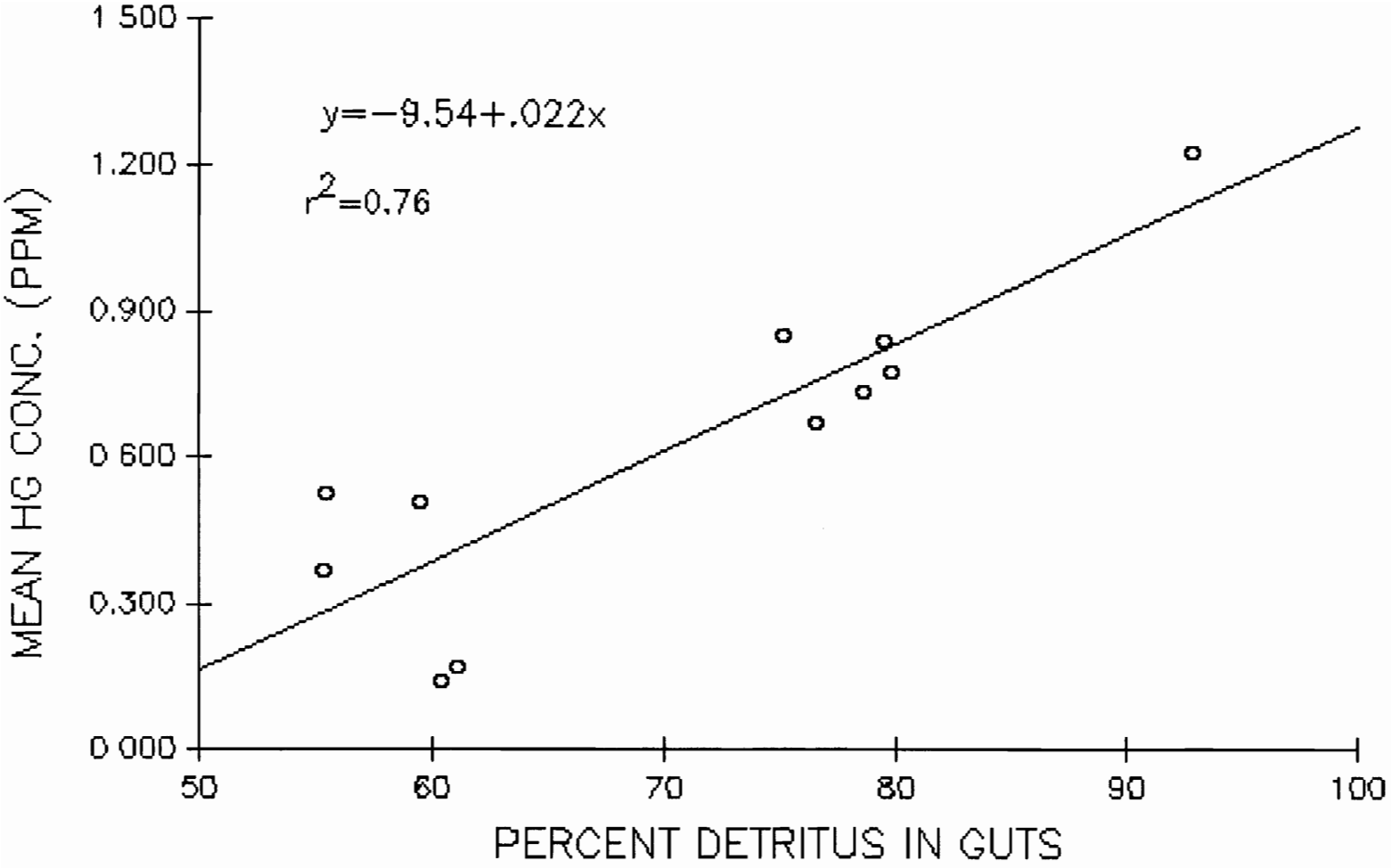

Fig. 18. Regression analysis of Hg in the insects on the percent detritus found in the guts.

Table 1. Comparison of the individual net mesh dimensions of several mature Hydropsychidae larvae.

Species	Location	References	(μ) Dimensions	Area of net mesh (μ^2)
Hydropsyche orris	Eastern N. Am.	Wallace, unpubl.	63 x 137	8,631
H. angustipennis	Europe	Kaiser, 1965	112 x 205	22,960
H. incommoda	Eastern N. Am.	Wallace, unpubl.	150 x 260	39,000
H. pellucidula	Europe	Kaiser, 1965	241 x 368	88,688
H. sparna	Eastern N. Am.	Williams & Hynes, 1973	190 x 300	57,000
H. morosa	Eastern N. Am.	This study	102 x 172	17,544
Arctopsyche irrorata	Eastern N. Am.	Wallace, 1975	403 x 534	215,202
Macronema zebratum	Eastern N. Am.	Wallace, unpubl.	5 x 40	200
Diplectroma modesta	Eastern N. Am.	Wallace, unpubl.	188 x 243	45,684

* Taken in Part from Wallace (1975)

Table 2. Presence or absence of algal genera found in the guts of *H. morosa*

Genera	April	May	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	Mar
Melosira	X	X	X	X	X	X	X	X	X	X	X	X
Navicula	X	X	X	X	X	X	X	X	X	X	X	X
Rhicosphenia	X	X				X		X	X	X	X	X
Cymbella		X	X								X	X
Diatoma								X	X	X	X	
Filamentous Green						X		X	X			X
Surriella								X				
Cocooneis								X		X	X	X
Fragillaria								X	X			
Nitzschia								X		X	X	X
*Cyclotella								X	X			
Pinnularia									X		X	

* Only Planktonic Diatom Found in Guts

Table 3. Mean size and coefficient of variation for particles found in the guts of *H. morosa* for each month and season.

	Date	Mean Particle Size	N	Standard Deviation	Coefficient of Variation (%)
	April 21	790.05	18	305.00	38.60
	May 31	888.09	105	233.03	26.23
	June 26	1310.32	50	931.29	71.09
Summer	July 29	1088.29	53	242.05	22.24
	August 20	2310.73	40	3272.39	141.62
	Sept. 18	1166.40	50	944.18	80.93
	October 22	1267.25	75	1056.35	83.36
		1260.16	391	500.67	39.73
	Nov. 26	596.66	60	384.96	64.5
	Dec. 22	557.4	75	133.20	23.90
Winter	Jan. 18	375.70	75	46.79	12.45
	Feb. 22	360.67	63	35.23	9.77
	Mar. 20	388.35	45	40.56	10.44
		455.76	318	112.00	24.57

Table 4. Summary of gut analysis variables.

Variable	Summer	Winter	Significance ($p \leq$)
Feeding Nets	Present	Absent	NA
Number of Detritus Particles	63-90%	20-29%	.0001
Volume of Detritus Particles	75-93%	55-61%	.0001
Number of Algal Genera	2-4	6-10	.0001
Mean Particle Size	730-2310	360-600	.0059

Table 5. Comparison of the relative amount of each food type found in the gut to the relative amount of each food type in the seston.

		% OF EACH FOOD COMPONENT IN THE DIET (by number)			% OF EACH FOOD COMPONENT (IN THE ENVIRONMENT (Seston by number)			Ivlev's Preference Index		
	Month	% Detritus	% Algae	% Animal	% Detritus	% Algae	% Animal	Det.	Algae	Animal
	April	63.11	36.89	* 0	64.90	35.10	* 0	-.01	.03	---
	May	61.48	38.52	* 0	64.00	36.00	* 0	-.03	.05	---
Summer	June	64.21	34.94	.85	74.55	25.25	0.20	-.08	.17	.62
(Filtering)	July	79.06	20.5	.44	84.90	14.90	0.20	-.04	.15	.38
	August	89.92	9.04	1.04	92.0	7.50	0.50	-.01	.09	.35
	September	69.79	29.48	.73	83.0	16.80	0.20	-.09	.27	.57
	October	67.24	32.23	.53	83.0	16.90	0.10	-.10	.31	.68
	Seasonal	70.69	28.80	0.72	78.05	21.77	0.30	-.05	.15	.52
	Mean ±1 S.D.	±10.30	±10.56	±0.24	±10.59	10.73	0.19	.04	.11	.15
	November	28.89	70.93	.18	80.0	19.93	0.07	-.47	.56	.44
Winter	December	22.55	77.39	.06	79.0	20.97	0.03	-.56	.57	.33
(Grazing)	January	25.60	74.40	* 0	75.0	25.0	* 0	-.49	.50	---
	February	21.02	78.98	* 0	72.0	28.0	* 0	-.55	.48	---
	March	20.22	79.78	* 0	71.0	29.0	* 0	-.56	.47	---
	Seasonal	23.66	76.30	.12	75.40	24.58	.05	-.53	.52	.38
	Mean ±1 S.D.	3.58	3.64	.08	4.04	4.06	.03	.04	.05	.08

* Not used in calculations

Table 6. Annual Production of *H. morosa* using removal-summation method.

	DATE	No./m^2	x ind. wt. mg.	Standing Stock (mg/m^2)	Numbers lost	Weight at loss (mg)	Weight lost (mg)	
	May	2141	1.33	2847.5				
	0				366	1.345	492.3	
Summer Generation	June	1775	1.36	2414.0				
					959	1.430	1371.4	Cohort P/B = 1.91
	July	816	1.50	1224.0				
					638	1.660	1059.1	Annual P/B = 5.72
	August	178	1.82	324.0				
					178	1.820	324.0	
				B=1702.4 mg			P=3246.5 mg/m^2	
	Sept 17	902	0.60	541.2				
					191	0.73	139.4	
	Oct 22	711	0.86	611.5				
					222	0.84	186.5	
Winter Generation	Nov 26	489	0.82	401.0				
					177	1.52	269.0	
	Dec 22	312	2.22	692.6				
					-17	2.55	-43.4	Cohort P/B = 3.26
	Jan 18	329	2.88	947.5				
					211	3.82	806.0	Annual P/B = 4.90
	Feb 21	118	4.76	561.7				
					-90	4.88	-439.2	
	Mar 20	208	5.00	1040.0				
					135	5.66	764.8	
	Apr 21	73	6.33	462.1				
					73	6.33	462.1	
				B = 657.2 mg			P = 2145.2 mg/m^2	

Total Annual Production = 5391.7 mg/m^2/yr

Table 7. Annual Production of *H. morosa* (5th instars only).

	DATE	No./m^2	x ind. wt. mg.	Standing Stock (mg/m^2)	Numbers lost	Weight at loss (mg)	Weight lost (mg)
Summer Generation	May	1148	1.56	1790.9			
					115	1.83	210.4
	June	1033	2.10	2169.3			
					740	2.25	1665.0
	July	293	2.40	703.2			
					221	2.78	613.3
	August	72	3.15	226.8			
					72	3.15	226.8
				B=1222.3 mg			P=2715.5 mg/m^2
Winter Generation	Sept 17	507	1.01	512.1			
					297	1.585	470.7
	Oct 22	210	2.16	453.6			
					-2	1.885	-3.8
	Nov 26	212	1.61	341.3			
					5	2.450	12.2
	Dec 22	207	3.29	681.0			
					-46	3.455	-158.9
	Jan 18	253	3.62	915.9			
					165	4.835	797.8
	Feb 21	88	6.05	532.4			
					30	6.080	182.4
	Mar 20	58	6.11	354.4			
					-15	6.220	-93.3
	Apr 21	73	6.33	462.1			
					73	6.330	462.1
				B = 531.6 mg			P = 1669.2 mg/m^2

Total Annual Production = 4384.7 mg/m^2/yr

Table 8. Relative volume of each food type found in the guts of *H. morosa*.

	Summer (Filtering) Volume				Winter (Grazing)		
Date	% Detritus	% Algae	% Animal	Date	% Detritus	% Algae	% Animal
April	78.55	21.45	0.00	Nov	59.55	34.77	5.68
May	79.53	20.48	0.00	Dec	55.44	40.06	4.50
June	76.62	4.88	18.50	January	55.36	44.64	0.00
July	92.85	6.87	1.00	February	61.11	38.89	0.00
August	90.52	3.88	6.10	March	60.38	39.62	0.00
Sept	75.17	11.08	13.75				
October	79.77	10.07	10.16				
Seasonal Mean	81.66	11.24	7.07		58.37	39.60	2.04
± 1 S.D.	6.94	7.13	7.33		2.76	3.52	2.82

Table 9. Trophic basis of production calculated for each season.

	Food type in foregut (%)		Assimilation Efficency (AE)		Net Prod. Efficiency (NPE)		Relative Amount to Production	Production Attributed to food type (%)	Production Attributed to food type (mg AFDW x $m^{-2} x yr^{-1}$)		Gross Produc. Efficiency (AE x NPE)		Amount of food type consumed (mg AFDW x $m^{-2} x yr^{-1}$)	Amount egested as detritus (mg AFDW x $m^{-2} x yr^{-1}$)	
Animal	7.07	x	.7	x	.5	=	2.47	30.0	1210	÷	.35	=	3457	1037	
Algae	11.24	x	.3	x	.5	=	1.69	20.5	827	÷	.15	=	5513	3859	Summer P=4034
Detritus	81.66	x	.1	x	.5	=	4.08	49.5	1997	÷	.05	=	39940	35946	(from Table 5)
Total (Annual)									4034				48910	40842	
Animal	2.04	x	.7	x	.5	=	.71	7.4	100	÷	.35	=	286	86	
Algae	39.60	x	.3	x	.5	=	5.94	62.1	843	÷	.15	=	5620	3934	Winter P=1357
Detritus	58.37	x	.1	x	.5	=	2.92	30.5	414	÷	.05	=	8280	7452	(from Table 5)
Total (Annual)									1357				14186	11472	

Table 10. Amount of energy produced, consumed and egested during each season.

	Food Type	Production ($mg \cdot m^{-2} \cdot sn^{-1}$)	Consumption ($mg \cdot m^{-2} \cdot sn^{-1}$)	Egestion ($mg \cdot m^{-2} \cdot sn^{-1}$)
Summer (Apr.-Oct.)	Animal	1,210	3,457	1,037
	Algae	827	5,513	3,859
	Detritus	1,997	39,940	35,946
	TOTAL	4,034	48,910	40,842
Winter (Nov.-Mar.)	Animal	100	286	86
	Algae	843	5,620	3,934
	Detritus	414	8,280	7,452
	TOTAL	1,357	14,186	11,472

Table 11. Energy processing rates calculated for each season.

	Consumption (mg x m^{-2} x m^{-1})				Production (mg x m^{-2} x mo^{-1})				Egestion (mg x m^{-2} x mo^{-1})			
	Animal	Algal	Detritus	Total	Animal	Algal	Detritus	Total	Animal	Algal	Detritus	Total
SUMMER	494	788	5706	6988	173	118	285	576	148	551	5135	5834
(%)	(7.1)	(11.3)	(81.6)		(30)	(20.5)	(49.5)		(2.5)	(9.4)	(88.1)	
WINTER	41	803	1183	2027	14	120	59	193	12	562	1064	1638
(%)	(2.0)	(39.6)	(58.4)		(7.2)	(62.2)	(30.6)		(.7)	(34.3)	(65.0)	

Table 12. Mean Mercury concentrations of different taxa in the South River.

Taxon	Tissue Type	Mercury Conc. (ppm)
Hydropsyche	whole animal	.463
Corydalus	whole animal	.271
Ephemeroptera	whole animal	.327
Crayfish	tail	.430
Minnows	muscle	.586

Table 13. Comparison of mean Mercury Concentration between insects, seston, and periphyton.

		MEAN MERCURY CONC. (PPM)			
		INSECT		ENVIRONMENT	
	Month	Whole Insect	Insect Gut	Seston	Periphyton
	April	.732	NA	14.15	1.52
	May	.841	NA	19.99	3.21
SUMMER	June	.673	NA	15.20	3.10
(fitering)	July	1.23	NA	19.30	1.70
	August	NA	NA	20.61	0.762
	Sept	.862	NA	14.66	0.920
	Oct	.773	.251	16.24	NA
	Nov	.510	.283	19.84	1.94
WINTER	Dec	.527	.399	19.09	3.62
(Grazing)	Jan	.368	.286	NA	NA
	Feb	.173	.147	16.85	NA
	March	.141	.124	19.55	NA

Table 14. Distribution of Mercury within the insect body.

	Mercury Conc. (ppm)			
Date	Whole Animal	Animal Gut	Gut Alone	% Mercury in Gut
October	.773	.251	7.71	70.99
November	.510	.283	3.53	48.40
December	.527	.399	2.23	29.64
January	.368	.286	1.46	27.61
February	.173	.147	.518	20.72
March	.141	.124	.367	18.40

CURRICULUM VITAE

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Professional Employment

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Helped design and coordinate a four year production study to determine the chronic effects of mercury pollution.
Coordinated two biomonitoring projects.
Coordinated annual fish collections for mercury analysis.
Collected periphyton and macroinvertebrates monthly for mercury analysis.
Performed bioassays.
Identified and processed samples of aquatic invertebrates.

1986-present — Graduate Teaching Assistant, Biology Department, VPI&SU
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1985-86 — Research Technician, Department of Biology, VPI&SU, Blacksburg, Virginia.
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Manuscripts in Review

Snyder, C.D., Willis, L.D., and A.C. Hendricks. Life History and Production of *Ephoron leukon* (Ephemeroptera: Polymitarcidae) on the South River, Virginia. Journal of the North American Benthological Society (submitted).

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Professional Societies

North American Benthological Society Ecological Society of America

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