



US Army Corps
of Engineers
Mississippi River
Commission

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LIFE HISTORY AND PRODUCTION OF DOMINANT LARVAL INSECTS ON STONE DIKES IN THE LOWER MISSISSIPPI RIVER

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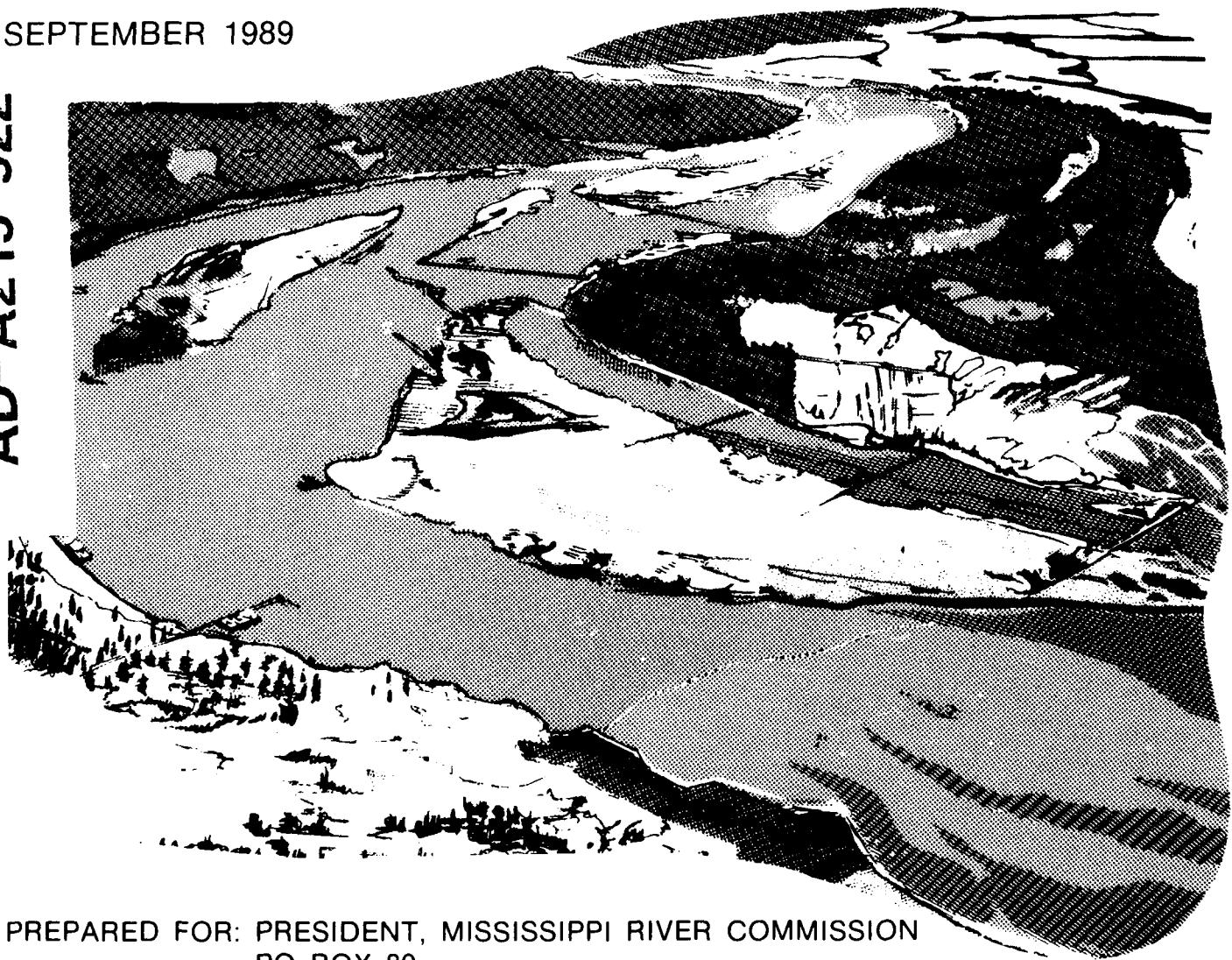
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LOWER MISSISSIPPI RIVER ENVIRONMENTAL PROGRAM
REPORT 18

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✓ Macroinvertebrate samples were obtained monthly from stones on dikes in the Lower Mississippi River (river miles 510-515) near Vicksburg, Miss., from September to November 1987 and May to October 1988. The midge <i>Rheotanytarsus</i> sp. and the caddisfly <i>Hydropsyche orris</i> were the dominant epifaunal aquatic insects. Seasonal changes in relative abundance of instars indicated trivoltine and bivoltine life cycles for <i>Rheotanytarsus</i> sp. and <i>H. orris</i>, respectively. Developmental synchrony was high among individuals in both populations. Production-to-average standing crop (P/B) ratios were estimated for each generation of each population based on life cycle, density, and individual dry weight data. The spring, summer, and fall generations of <i>Rheotanytarsus</i> sp. had P/B ratios of 4.2, 4.3, and 3.0, respectively. The spring and late-summer generations of <i>H. orris</i> had P./B ratios of 4.1 (Continued)					
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and 4.0. These values closely match those in published studies for other midge and hydropsychid caddisfly populations.

Annual production of *Rheotanytarsus* sp. was 344.0 mg (dry weight)/m². This is the first production estimate for this midge. Annual production of the *H. orris* population was 10.1 g/m², a value that closely matches the average value of 12.6 g/m² based on nine published accounts of highly productive lotic hydropsychid populations on natural cobble riffles. Stone dikes are an important source of stable coarse-grained substrate in the Lower Mississippi River and support high production of rheophilic epifaunal species such as *Rheotanytarsus* sp. and *H. orris*. *Rheotanytarsus* sp. and *H. orris* are important components of the epifaunal community in the Lower Mississippi River.

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PREFACE

The Lower Mississippi River Environmental Program (LMREP) is being conducted by the Mississippi River Commission (MRC), US Army Corps of Engineers. It is a comprehensive program of environmental studies of the leveed floodplain of the Lower Mississippi River. The objectives of the LMREP are to develop an inventory of environmental resources for the study area and to develop environmental design considerations for channel training and levee features of the main stem Mississippi River and Tributaries Project.

One component of the LMREP is the Dike System Investigation. This report contains results of a study describing the density, life history, and production of two dominant larval insects (*Hydropsyche orris*, a caddisfly, and *Rheotanytarsus* sp., a midge) that inhabit stone dikes in the Lower Mississippi River, near Vicksburg, Miss. Data were collected between river miles 510 and 515 during the periods September to November 1987 and May to October 1988.

These studies were conducted by personnel of the Aquatic Habitat Group (AHG), Environmental Laboratory, US Army Engineer Waterways Experiment Station, Vicksburg, Miss. This report was prepared by Dr. Barry S. Payne, Mr. C. Rex Bingham, and Dr. Andrew C. Miller, AHG.

The investigation was managed by the Planning Division of the MRC and was sponsored by the Engineering Division, US Army Engineer Division, Lower Mississippi Valley. Mr. Stephen P. Cobb, MRC, was the program manager for the LMREP. The investigation was conducted under the direction of the President of the Mississippi River Commission, BG Thomas A. Sands, EN.

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LOWER MISSISSIPPI RIVER ENVIRONMENTAL PROGRAM

Life History and Production of Dominant Larval Insects on Stone Dikes in the Lower Mississippi River

PART I: INTRODUCTION

Background

The Mississippi River

The Mississippi River is the fourth largest drainage basin the world (1,245,000 square miles), exceeded in size by the watersheds of the Amazon, Congo, and Nile rivers. The Lower Mississippi River (LMR) originates with the confluence of the Ohio and Middle Mississippi rivers at Cairo, Ill. Between its origin and the Gulf of Mexico, it traverses a distance of approximately 975 river miles (RM) (Zimpfer et al. 1988). Historically, flooding on this river has been a major deterrent to development.

The Mississippi River Commission (MRC) was established by Congress in 1879 to carry out flood control and navigation measures for the Lower Mississippi River that would be financed by the Federal Government. The MRC is responsible for carrying out the Mississippi River and Tributaries (MR&T) Project, which is a comprehensive plan for flood control and navigation works on the main stem of the river and major tributaries. The purpose of this plan is to construct channel improvements on the LMR, including levee and dike systems, bank protection measures, and other improvements (Baker et al. 1988).

Lower Mississippi River Environmental Program (LMREP)

The LMREP is being conducted by the MRC. The objectives of this program are to develop baseline environmental resource data on the river and associated leveed floodplain and to formulate environmental design considerations for channel training works (dikes and revetments) and the main stem levee system. The LMREP consists of five work units: levee borrow pit investigations; dike system investigations; revetment investigations; habitat inventories; and development of the Computerized Environmental Resources Data System, a geographic information system containing environmental data. The study described

in this report is part of the dike system investigations. For more information on the LMREP, see Baker et al. (1988).

Habitat value of stone dikes

Stone dikes, constructed by the US Army Corps of Engineers to maintain the authorized navigation channel and to reduce dredging requirements, are an important component of the channel improvement feature of the MR&T Project on the LMR. Dike structures are constructed to contract the width and increase the depth of the navigation channel at low flows, to reduce divided-flow conditions, and to adjust channel alignment and increase channel stability. These structures are constructed of riprap and protrude into the river obliquely or at right angles to the shore.

Stone dikes have been identified as prominent and important aquatic habitats in the LMR (Bingham 1982, Wright 1982, Beckett et al. 1983, Conner et al. 1983, Pennington et al. 1983, Cobb et al. 1984, Cobb and Magoun 1985), and provide diverse microhabitats for aquatic biota (Mathis et al. 1982). Rheophilic (flow-loving) organisms such as filter-feeding caddisflies and midges inhabit stone surfaces exposed to swift currents. Despite the diversity of microhabitats associated with dikes, the highest density populations are on stone surfaces exposed to high-velocity water (Mathis et al. 1982). Lentic species inhabit quiescent water in interstices among and under stones.

Stone dikes in the LMR provide a large quantity of hard substrate for the production of macroinvertebrate epifauna. These channel training structures are found in the LMR from close to Cairo, Ill. (RM 951), to immediately upriver of the town of Old River (RM 320). As of September 1988, 221 miles (of 339 authorized miles) of dikes had been constructed, and 44.5 miles of dikes were scheduled to be elevated or otherwise modified. While the amount of stone surface area made available by the dikes is unknown, it appears to constitute a significant quantity of substrate for epifauna in addition to that naturally occurring in the submersed snags and brush.

Mathis et al. (1982) concluded that stone dikes in the LMR were valuable aquatic habitats. This assessment was based on the dense and diverse macroinvertebrate fauna found on the stone surfaces of dikes. Assessments of community parameters such as species richness and diversity generally provide an indication of stability and structural complexity. High population densities usually indicate adequate nutrition and appropriate water quality.

Productivity of dominant taxa (i.e., the quantity of animal biomass produced per unit area per unit time) can be assessed by consideration of density (individuals per unit area), biomass (weight per individual), and life history (growth rates and generations per year) (e.g., Russell-Hunter 1970). Productivity estimates provide a useful measure of habitat value important to higher trophic levels, including recreational and commercial fishes (e.g., Krueger and Waters 1983), and allow direct comparison of the value of dikes relative to naturally occurring lotic substrates, such as cobble riffles, that support a similar fauna (e.g., Parker and Voshell 1983). Prior to completing this study, direct measures of productivity have not been made for macroinvertebrates on stone dikes.

Purpose and Scope

The purpose of this study was to document the life history and production of dominant larval insects (the caddisfly *Hydropsyche orris* and the midge *Rheotanytarsus* sp.) on stone dikes in the LMR. Both species are abundant on coarse-grained substrate exposed to swift currents (e.g., Benke et al. 1984) and are dominant macroinvertebrates on dikes in the LMR (e.g., Mathis et al. 1982).

PART II: STUDY AREA AND METHODS

Study Area

Samples for macroinvertebrates were obtained from the two upstream dikes in both the Leota and Lower Cracraft dike systems (Figure 1). The Leota dikes were on the left descending bank immediately downriver of Kentucky Bend Revetment at RM 515 in Washington County, Mississippi. The Lower Cracraft dikes were in Chicot County, Arkansas, on the right descending bank near RM 510.

Field Sampling

Regular (approximately monthly) sampling was conducted from September to November 1987 and May to October 1988. Sampling always occurred on a falling or steady low river stage (Figure 2) to ensure that collected stones had been recently submersed. Sustained low water caused by the drought of the summer and fall of 1988 greatly facilitated this sampling program. On each sampling date, three to five 10-kg stones were obtained from high-velocity water (i.e., about 1 m/sec) near the tip of each dike. Stones (with attached macroinvertebrates) were individually placed in labeled plastic bags and returned to the laboratory at Vicksburg, Miss.

Laboratory Analysis

A random subsample that typically included three of the five stones taken from each dike was selected for analysis. All material was brushed from each stone, sieved through a 0.25-mm screen, and preserved in 10% buffered formalin. All macroinvertebrates (other than bryozoans and sponges) were identified. Each stone was then covered with aluminum foil. Foil weight was converted to surface area based on the weight-to-surface area ratio of the foil. These surface area measurements enabled a determination of macroinvertebrate density (individuals/m²).

The size/age structure of the two dominant insects (*H. orris* and *Rheotanytarsus* sp.) was determined for each sampling period. A random subsample of approximately 200 midges and 200 caddisflies, obtained by pooling samples from one to three stones, was used to make these assessments. The

interocular distance of *H. orris* was measured to the nearest 0.02 mm using a dissection microscope equipped with an ocular micrometer. Midges were mounted on glass slides, using methods described by Beckett and Lewis (1982), and identified. The labial plate width of each *Rheotanytarsus* sp. (the dominant midge) was measured to the nearest 6.25 μm using an ocular micrometer in a compound microscope. Dry weight (DW, overnight oven-drying at 70° C) determinations were made for batches of individuals from each instar of *H. orris* and *Rheotanytarsus* sp.

Standing Crop and Production Estimates

Average standing crop of *H. orris* and *Rheotanytarsus* sp. was estimated for each instar of each generation. Mean density of each instar per generation (individuals/m²) was estimated by first dividing the sum of monthly density estimates by the number of months in the larval lifespan of that generation. This estimate was then adjusted using a ratio of P_e to P_a (defined below) (Hamilton 1969) because the time spent by larvae in each instar is not equal. The term P_e represents the proportion of larval life spent in each instar if all instars were of equal duration (i.e., 0.20 for five instars and 0.25 for four instars). The term P_a is the actual proportion of larval life spent in each instar. This adjusted mean density was multiplied by the mean individual DW ($\mu\text{g}/\text{individual}$) to estimate average standing crop ($\mu\text{g}/\text{m}^2$) of each instar per generation. Instar-specific standing crops were summed to estimate the average standing crop of the population during each generation.

Production of each generation was computed using Hamilton's (1969) modification of the size-frequency method of Hynes and Coleman (1968). This approach involved first estimating the mean density of individuals per instar, followed by estimation of reductions in density between successive instars. To estimate the mean density of individuals that developed into each instar using the size-frequency method, the P_e/P_a -adjusted mean density per instar used in standing crop estimates must be multiplied by the number of instars. (The mathematical foundation of this "times loss" factor is described in detail by Hamilton 1969 and Menzie 1981.) Each reduction in density between successive instars (individuals/m²) was multiplied by the average individual

size at loss ($\mu\text{g}/\text{individual}$) to estimate production per instar (cumulative $\mu\text{g}/\text{m}^2$ produced during the duration of that instar).

Size at loss between successive instars was estimated as the geometric mean of individual DW of the successive stages. The biomass of final instars lost to pupation was estimated as the mean individual biomass plus one standard deviation based on observed variance in the size of final instars. Summation of instar production provided an estimate of total production of each generation (cumulative $\mu\text{g}/\text{m}^2$ produced by the generation); summation of production of each generation per year provided an estimate of annual production of the population (cumulative $\mu\text{g}/\text{m}^2$ produced by all generations in a year).

PART III: RESULTS

Community Composition

The epifaunal macroinvertebrate community on the Lower Cracraft and Leota dikes consisted of aquatic insects (mayflies, caddisflies, and stoneflies), crustaceans, molluscs, aquatic worms, and hydrozoans. More than 50 taxa were identified, although the majority of these comprised less than 5 percent of the total assemblage (Table 1). Four species made up approximately 95 percent of the macroinvertebrates (Table 1). Dominant aquatic insects included the caddisfly (Arthropoda:Insecta:Trichoptera) *H. orris* and the midge (Arthropoda:Insecta:Diptera) *Rheotanytarsus* sp. The dominant crustacean was the amphipod (Arthropoda:Crustacea:Amphipoda) *Corophium lacustre*. All three of these invertebrates build and live in tubes that are built from sand grains and detritus. The other abundant species was the free-living flatworm (Platyhelminthes:Tricladida) *Dugesia tigrina*.

Hydropsyche orris typically comprised over 95 percent (by number) of the caddisfly community. *Rheotanytarsus* sp. numerically dominated the midges; on the average this taxon represented 72 percent of the larval chironomids. *Polypedilum convictum* was the second most abundant midge, but, on average, was one fifth as abundant as *Rheotanytarsus* sp. *Corophium lacustre* overwhelmingly dominated the only other amphipod crustacean found on the dikes, a nontubicolous *Gammarus* of which only a few were collected. *Dugesia tigrina* was the only flatworm obtained.

During this study the highest densities of the dominant macroinvertebrates were in the summer and early fall of 1988 (Table 2). Typically, total macroinvertebrate density was low in late fall and spring (and presumably over winter) and high throughout summer and early fall. *Hydropsyche orris* and *Rheotanytarsus* sp. attained their highest density in June 1988. Densities for both of these invertebrates were considerably less during the previous fall and early spring (September 1987 to May 1988). Between July and November 1988, densities for these two invertebrates were about 10 to 25 percent of the June 1988 values. Densities of *C. lacustre* and *D. tigrina* were considerably lower in the first study year (September 1987-May 1988) than during the second year (June 1988-November 1988). The highest density of *C. lacustre* was measured in August and September of 1988 ($20,987 \pm 7,080$ and $38,937$

$\pm 9,165$ individuals/m² ($\pm$ standard error). These values were substantially greater than density determined for September 1987 (90 ± 34 individuals/m²) or October 1987 ($1,781 \pm 431$ individuals/m²). Density of the *D. tigrina* population peaked in July 1988 and was consistently high from July through October of that year. However, like *C. lacustre*, high density of *D. tigrina* was not observed in the fall of 1987.

Although it was not the intent of this study to investigate causes of interyear macroinvertebrate density differences, it is likely that these species were collected in 1988 because of the extreme low river stage brought about by the drought. These two invertebrates are common inhabitants of the benthos and are probably relatively more common at lower depths than the previously discussed aquatic insects.

In 1988, the peak density of both *H. orris* and *Rheotanytarsus* sp. was observed near the end of a 2-month-long decline in river stage. Maximum densities of both *C. lacustre* and *D. tigrina* corresponded to the sustained and exceptionally low river stage (<10 ft on the Greenville gage, Figure 2) caused by the prolonged 1988 drought throughout the Mississippi River basin.

Population Dynamics of *H. orris* and *Rheotanytarsus* sp.

The only notable interdiike difference in density of *H. orris* and *Rheotanytarsus* sp. was observed at river stages below 12.3 ft. At these low stages, the small submersed portion of the downstream dike in the Leota dike system was exposed only to slackwater (current velocity of less than 0.1 m/sec) instead of the typically swift current (>0.5 m/sec). The other three dikes remained exposed to swift currents. Density of *H. orris* and *Rheotanytarsus* sp. was markedly lower on the dike in slackwater than on the other three dikes, reflecting emigration from slackwater by both taxa (Figure 3). Because river stage was less than 3.75 m on the majority of sampling dates (Figure 2), stones were not subsequently collected from the unrepresentative downstream dike in the Leota field.

Analysis of the size demography of the *H. orris* population provided clear evidence of five instars in the larval molt sequence (Figure 4). The average (range indicated in parentheses) interocular distances (IO, in millimetres) per instar were 0.15 (0.12-0.18) for instar I, 0.26 (0.18-0.30) for instar II, 0.44 (0.30-0.52) for instar III, 0.67 (0.52-0.82) for instar IV, and 0.94

(0.82-1.10) for instar V. Dry weight (in milligrams) was regressed on IO, yielding the following equation:

$$\text{Log DW} = 2.773 (\text{Log IO}) + 0.231; r^2 = 0.97; p < 0.001$$

The instantaneous growth index (G) of *H. orris* was determined. This is a unitless measure estimated by dividing the DW of the average-sized fifth instar larva by the DW of the average-sized first instar (Waters 1987, and references within). Estimates of G equaled 159.

Demographic analysis of the *Rheotanytarsus* sp. population clearly revealed four instars in the larval molt sequence of this relatively small midge (Figure 5). The average (range indicated in parentheses) labial plate widths (LPW, in microns) of each instar were 22.0 (17.5-27.5) for instar I, 30.0 (27.5-35.0) for instar II, 41.7 (35.0-52.5) for instar III, and 61.2 (52.5-67.5) for instar IV. Regressions of DW (in micrograms) on LPW yielded the following equation:

$$\text{Log DW} = 3.638 (\text{Log LPW}) - 5.178; r^2 = 0.97; p < 0.001$$

Estimates of G of *Rheotanytarsus* sp. equaled 41.

The life cycles of both *H. orris* and *Rheotanytarsus* sp. were determined by analyzing seasonal shifts in the relative abundance of instars comprising the larval populations (Figures 6 and 7). Periods of adult emergence followed by egg-laying and recruitment occurred when the final instar larvae were replaced by first and second instars. The abruptness of these shifts indicates the degree of developmental synchrony among individuals comprising each population.

Late summer emergence of *H. orris* was not highly synchronous, although clearly evident. This population shifted from overwhelming dominance of fifth and fourth instars in July to dominance of first and second instars in September (Figure 6). A transitional phase was found in August, when the population consisted of approximately equal numbers of fifth through second instars. Reduction in fourth and fifth instars due to pupation was not evident until September. Developmental synchrony was very high among *Rheotanytarsus* sp. (Figure 7). For example, highly synchronous summer emergence was indicated

when the larval population clearly shifted from overwhelming dominance of fourth instars in June to dominance by first and second instars in July.

Sampling in 1987 began in mid-September just after the late-summer emergence/recruitment period for *H. orris* (Figure 6). The late-summer generation overwintered principally as fourth and third instars and emerged in late April. This emergence gave rise to the spring generation that comprised nearly all of the first 1988 sample taken in mid-May. By mid-July development of the 1988 spring generation was nearly complete, and this generation was dominated by fifth instars. August emergence was apparent from the declining abundance of fifth instars during that month. By September, the spring generation had been replaced by a late-summer generation of recently recruited first and second instars. The timing of late-summer recruitment was approximately the same in 1988 as in 1987. Thus, *H. orris* in the LMR is bivoltine (i.e., two generations per year).

A trivoltine life cycle (i.e., three generations per year) was evident in the *Rheotanytarsus* sp. population (Figure 7). The first sample obtained in September 1987 was dominated by fourth instars, but 1 month later (October 1987) the sample was dominated by second and third instars. This abrupt shift indicated that highly synchronous emergence/recruitment had occurred in late September and early October. The 1987 fall generation overwintered almost exclusively as the penultimate third instar. This generation probably emerged in late March to early April (prior to the onset of spring sampling) and gave rise to a 1988 spring generation that emerged in late June to early July.

Emergence in late March to early April is likely since fourth instars were dominant in mid-May, and larval growth rates were rapid. The 1988 summer generation required just 1 month, from mid-July to mid-August, to grow from first to fourth instars, and synchronous emergence was indicated in late September to early October. The rapid growth of the summer generation (from mid-July to mid-August) indicates that the fall 1987 generation, which entered winter principally as third instars, certainly accomplished their final larval molt before mid-June. It is very likely that completion of larval molts occurred in March as water temperatures began to rise (Figure 8) and was soon followed by spring emergence.

Production Estimates

Detailed information on patterns of instar growth and larval lifespan (Figures 6 and 7) was combined with density data (Table 2) to estimate the average standing crop and production of *H. orris* and *Rheotanytarsus* sp. The duration of each instar (Tables 3 and 4) was estimated based on growth rates determined from monthly changes in instar relative abundance (Figures 6 and 7). Mortality curves could not be directly estimated from raw density data because of variation in duration of each instar (i.e., developmental synchrony, although high, was not perfect). Thus, the size-frequency method of production estimation was used (Hynes and Coleman 1968) as modified by Hamilton (1969). The Pe/Pa ratios in Tables 3 and 4 provide factors needed to correct instar densities for each generation. These correction factors adjust underestimates and overestimates of relatively short- versus long-lasting instars, respectively (Hamilton 1969).

The confounding influence of river stage on density required that a single estimate of average density be applied to each generation before correcting with the Pe/Pa ratios. For example, the average density of the spring generation of *H. orris*, prior to Pe/Pa corrections, was actually the average of the May, June, July, and August samples (Table 2). Monthly estimates of each generation's density were apportioned among all larval instars according to observed instar relative abundance (Figures 6 and 7). High water prevented estimation of overwinter and early spring density of the late-summer generation of *H. orris* and the fall generation of *Rheotanytarsus* sp.

Overwinter mortality was assumed to decrease the average fall density of each population by 50% prior to spring emergence. This approximation of overwinter mortality was based on overwinter reductions in densities of lotic hydropsychid populations reported by Mackay (1986). However, it is noteworthy that initial production estimates assuming no overwinter mortality did not differ greatly from final estimates based on 50% mortality (reasons for this will be provided after generation production estimates have been fully developed). Relative abundance of instars during winter months was assumed to equal that observed in late fall, and further growth was not assumed to occur until mid-March when water temperature began to rise (Figure 8). Estimates of instar-specific densities, before and after Pe/Pa corrections, are shown for

each generation of *H. orris* and *Rheotanytarsus* sp. in Tables 5 and 6, respectively.

Average density of each instar was converted to a standing crop by multiplying by the DW of an average-sized individual. These weights were computed from the regressions (provided above) using the average IO (*H. orris*) or LPW (*Rheotanytarsus* sp.) for each instar. Losses to mortality and pupation must be incorporated into production estimates. The reduction in density observed between successive instars was used to estimate losses from the first to penultimate instar. All individuals of the final instar were assumed to pupate. The average size of individuals dying between two successive instars was estimated to be the geometric mean of the DW of the average-sized individual in adjacent instars.

The size of final instars at pupation was assumed to be substantially larger than the average-sized individual of that instar. For *H. orris* (average fifth instar IO = 0.94 mm and DW = 1,434 μ g), the IO at pupation was assumed to equal 1.00 (well within the IO range of this instar, Figure 4), corresponding to 1,702 μ g DW. For *Rheotanytarsus* sp. (average fourth instar LPW = 61.2 μ and DW = 15.5 μ g), the LPW at pupation was assumed to equal 65.0 μ (see Figure 5), corresponding to 17.0 μ g DW. The average DW and the DW at loss used in standing crop and production computations, respectively, are summarized for *H. orris* and *Rheotanytarsus* sp. in Tables 7 and 8, respectively.

Standing crop and production estimates for *H. orris* and *Rheotanytarsus* sp. are summarized in Tables 9 and 10. Summation of instar-specific estimates of standing crop provides an estimate of average generation standing crop (B). Values of B were greatest for the spring generations of both populations, reflecting the high population densities associated with the declining river stage throughout the spring and early summer of 1988. Production (P) of the spring generation of both populations contributed the most to total annual production (the latter is the sum of all generation P values). Annual P of the *H. orris* population equaled 10.10 g/m², with the spring and late-summer generations contributing 80% and 20%, respectively. Annual P of *Rheotanytarsus* sp. was 344.0 mg/m²; the spring generation contributed 79% of the annual total, whereas the summer and fall generations contributed only 11% and 10%, respectively.

Both annual and generation production were relatively insensitive to the exact level of overwinter mortality assumed for the late summer and fall generations of *H. orris* and *Rheotanytarsus* sp., respectively. As mentioned earlier, overwinter mortality was assumed equal to 50% for both populations. The reason for the minor effect (of assumed overwinter mortality) on annual P of both *H. orris* and *Rheotanytarsus* sp. is the fact that the majority of production is accounted for by the spring and not the overwintering generation (Tables 9 and 10).

The reason for the insensitivity of generation P to mortality has to do with the relationship among instars. For example, *H. orris* principally overwintered as third and fourth instars. As lower levels of mortality are assumed, the proportion of generation production due to loss of third and fourth instars decreases, but a concomitant increase occurs in the estimated production of the fifth instar. These trade-offs among instars reduce the sensitivity of generation P to mortality patterns among instars. *Rheotanytarsus* sp., which principally overwinters as third instar larvae, exhibits similar trade-offs between P of the third and fourth instars as assumed overwinter mortality is changed.

Ratios of production to biomass for the spring and late-summer generations of *H. orris* equaled 4.1 and 4.0, respectively (Table 9). Generation P/B ratios for the spring, summer, and fall generations of *Rheotanytarsus* sp. equaled 4.2, 4.3, and 3.0, respectively (Table 10). The average annual B of each population was computed as the weighted (by length of lifespan) average of generation biomass. Annual P/B ratios equaled 10.1 and 20.7 for *H. orris* and *Rheotanytarsus* sp., respectively.

Productivity rates, in terms of milligrams DW/(m²·day), were estimated for each generation of each population by dividing production for each generation by larval lifespan. Productivity rates of the spring and late-summer generations of *H. orris* equaled 80.5 and 8.5, respectively. Productivity rates of the spring, summer, and fall generations of *Rheotanytarsus* sp. were 4.2, 0.6, and 0.3 mg/(m²·day). Thus, productivity of *Rheotanytarsus* sp. was considerably lower than *H. orris*. The spring generation exceeded late-summer generation productivity by a factor of 9.5 in the bivoltine *H. orris* population. In the trivoltine *Rheotanytarsus* sp. population, spring generation productivity exceeded the average productivity of the summer and fall generations by 9.3.

PART IV: DISCUSSION

Mackay and Waters (1986) estimated annual production of hydropsychid populations on cobble riffles above and below impoundments in Valley Creek, Minnesota. They estimated that hydropsychid production at three sites above impoundments was 0.9, 5.8, and 16.2 g/m², and production at three sites just below impoundments was 31.7, 34.9, and 40.0 g/m². The authors concluded that increased abundance or quality of seston below impoundments was the most likely cause of increased production. Based on a similar study, Parker and Voshell (1983) reported that hydropsychids on a cobble riffle just downstream of a major impoundment on the North Anna River in Virginia had annual production of 223.9 g/m². In contrast, hydropsychids at three other sites unaffected by impoundments had average annual production of 1.7, 6.8, and 36.5 g/m². Parker and Voshell noted that production at the site affected by impoundment greatly exceeded any previously reported value for any freshwater macroinvertebrate population or community. Krueger and Waters (1983) estimated annual production of hydropsychids on riffles in three first-order streams in Minnesota to be 2.2, 14.4, and 28.7 g/m².

Thus, excluding sites affected by seston-enriched discharge from impoundments, annual production of hydropsychids on natural cobble riffles has been reported to average 12.6 g/m² (Krueger and Waters 1983, Parker and Voshell 1983, Mackay and Waters 1986). Annual production of *H. orris* on LMR dikes was very similar, equaling 10.1 g/m² (Table 9).

Benke et al. (1984) estimated production of heavily dominant *Hydropsyche* populations on snags at two sites in the Saltilla River in Georgia. *Hydropsyche elissoma* (which accounted for 91% of caddisfly production in the upper river) had annual production estimated at 10.8 g/m². *Hydropsyche incommoda* (which represented 80% of caddisfly production in the lower river) had annual production of 21.0 g/m². Benke et al. (1984 and references within) concluded that snags are among the most productive components of riverine habitats. Annual production of *H. orris* on LMR dikes was essentially the same as hydropsychid production on natural snags in the upper Saltilla River.

Average annual density of *H. orris* on stone dikes equaled 2,877 individuals/m² (Table 2). This is within the range reported for other hydropsychid populations. Riffles sampled by Mackay and Waters (1986) upstream of Valley Creek impoundments supported hydropsychid assemblages with

average annual densities of 101 to 2,509 individuals/m². The three riffles below impoundments had average annual densities of 4,828 to 7,854 individuals/m². The dominant *H. elissoma* population studied by Benke et al. (1984) in the upper Saltilla River had an average annual density of 4,017 individuals/m², and the dominant *H. incommoda* population at the lower Saltilla River site had an average annual density of 8,149 individuals/m².

Krueger and Waters (1983) included midges of the subfamily Tanypodinae in their production study of three first-order streams in Minnesota. Annual production of midges equaled 0.07, 0.02, and 0.9 g/m² in the three streams. They assumed a univoltine life history in order to make these production estimates. Benke et al. (1984) estimated annual production of Tanytarsini midges in the upper and lower Saltilla River in Georgia, based on an assumed average generation production interval of approximately 12 days (i.e., approximately 30 generations per year were assumed). Based on this assumption, estimated annual production was 2.4 and 2.3 g/m² at the upper and lower river sites, respectively.

Results of the present study indicate that Krueger and Waters' (1983) assumption of an average generation lifespan of 12 days for Tanytarsini midges is too low. Average generation lifespan equaled 106 days for midges in the LMR (Table 4). The assumption of a single generation per year by Krueger and Waters (1983) may slightly underestimate the voltinism of Minnesota populations. However, higher water temperatures and longer growing seasons allow more generations per year in large rivers than northern coldwater streams. If the average generation production interval of 106 days is applied to production estimates of Benke et al. (1984), then annual production of midges at both Saltilla River sites equals 344.0 mg/m². Interestingly, this adjusted value equals the average production noted by Krueger and Waters (1983) and that reported for the LMR.

The average annual density of *Rheotanytarsus* sp. on LMR dikes was 3,676 individuals/m². Benke et al. (1984) observed slightly lower densities of Tanytarsini midges on snags in the upper and lower Saltilla River. Densities at the upper and lower sites averaged 2,132 and 2,308 individuals/m², respectively.

Waters (1987) noted that the average generation P/B ratio of larval insect populations is relatively constant (among species and populations) and ranges from 2 to 5. The two generations of the bivoltine *H. orris* population

on Lower Mississippi River dikes had P/B ratios of 4.1 and 4.0 (Table 9). Caddisfly generation P/B ratios have been reported to range from 2.4 to 5.2 (Caspers 1978, Iversen 1980, Elliot 1982, Krueger and Waters 1983, Benke et al. 1984). The trivoltine *Rheotanytarsus* sp. population showed P/B ratios of 4.3, 4.2, and 3.0 (Table 10). Estimated generation P/B of other midges ranges from 2.4 to 3.9 (Menzie 1981, Butler 1982, Soluk 1985). Thus, the estimated generation P/B of both *H. orris* and *Rheotanytarsus* sp. on LMR dikes closely corresponds to published values for related insects, and provides additional evidence of the relative constancy of generation P/B ratios as discussed by Waters (1987).

Annual P/B ratios are not constant among species or populations, and depend greatly on voltinism (Waters 1969, 1979). The higher annual P/B of the trivoltine *Rheotanytarsus* sp. population (= 20.7) relative to the bivoltine *H. orris* population (= 10.1) demonstrates the inverse relationship between average generation lifespan and annual P/B as discussed in detail by Waters (1969, 1979).

Knowledge of life history pattern is crucial to production estimation. This LMR study provides the only detailed account of the life history of *Rheotanytarsus* sp. Fremling (1960) published the first detailed investigation of the life history of *H. orris*. His report was based on studies conducted in the Upper Mississippi River (UMR) near Keokuk, Iowa. Fremling concluded that *H. orris* in the UMR was bivoltine with emergence peaks from mid-May to mid-June and from mid-August to mid-September. However, the population data reported by Fremling appear to reflect a principally univoltine life cycle. Certainly, the extent of bivoltinism of *H. orris* in the UMR Mississippi River population of *H. orris* appeared variable between years, and strict bivoltinism involving complete replacement of generations was not conclusively demonstrated.

In contrast, seasonal changes in larval size demography of *H. orris* in the LMR (Figure 6) clearly indicated a bivoltine population with complete replacement of the spring generation a late-summer generation. This larval population was overwhelmingly dominated by first and second instars and included hardly any fifth instars in both September 1987 and 1988. Thus, complete replacement of generations was clearly indicated. Such full replacement of generations was not apparent in Fremling's study (1960) of an UMR population. In contrast to Mackay's generalization (1986 and references within)

that hydropsychid species overwintering in the final instar are likely to be bivoltine, the late-summer generation in the Lower Mississippi River appears to overwinter principally as third and fourth instars (see November sample in Figure 6). In contrast, late-October samples collected by Fremling were dominated by fifth instars, although he concluded that these larvae arose from late-summer recruitment. Fall growth of late-summer recruits in the LMR is likely to be at least equal if not faster than that of late-summer recruits in the UMR due to more rapid cooling of water in the fall in the upper river. Thus, the fall larval demography observed by Fremling is likely to have resulted from a principally univoltine rather than bivoltine life cycle pattern.

Spring emergence appears to occur earlier in the lower than upper river. Spring emergence in late April to early May was indicated by the overwhelming dominance of first instar larvae in the mid-May sample of larvae in 1988 (Figure 6). In contrast, spring emergence in the upper river appears to occur principally from late May to mid-July (Fremling 1960). Later spring emergence in the upper river probably reflects the later onset of spring warming of both water and air temperature. Later spring emergence of *H. orris* in the upper than in lower river is concordant with the view that Fremling's results indicate a principally univoltine population with occasional and incomplete replacement of the dominant spring generation by a less abundant late-summer generation.

Beckett (1982) provides the only other account of the life history of *H. orris* in a large river. His study of an Ohio River population near Cincinnati provided evidence of more complete bivoltinism than Fremling (1960) observed in the UMR, but less complete bivoltinism than noted in the LMR. On the Ohio River a well-defined emergence and recruitment peak in May was evident from a shift in a larval population dominated by fifth instars in early May to dominance of second and third instars with complete absence of fourth and fifth instars in early June.

Summer and fall emergence was less clearly defined than in the LMR. Beckett's (1982) data did not show a clear shift from one heavily dominated by fifth and fourth instars to one heavily dominated by first and second instars. Nonetheless, a substantial late-summer and fall emergence and recruitment period was evident in the Ohio River population from declining abundance of fifth instars in July and August, which was accompanied by increased abundance

of second instars and appearance of at least some first instars. As in the LMR (Figure 6), but unlike the UMR (Fremling 1960), Beckett's samples of late-fall larvae in the Ohio River were dominated by third and fourth instars. In summary, the completeness and clarity of bivoltinism among *H. orris* populations in the Mississippi and Ohio Rivers follows this pattern: LMR near Greenville, Miss. > Ohio River near Cincinnati, Ohio > UMR near Keokuk, Iowa.

Life history and production have been quantified for the first time for populations of two abundant species of macroinvertebrates on dikes in the LMR. *Hydropsyche orris* showed a bivoltine life cycle and heavily dominated macroinvertebrate production. Annual production of this species was 10.1 g/m^2 . This value approximately equals published estimates of annual production of hydropsychid caddisflies on natural riffles and snags. The annual production of *Rheotanytarsus* sp. equaled 344.0 mg/m^2 , which was similar in magnitude to production of related midges on natural cobble riffles.

As of September 1988, 221 miles of dikes had been constructed in the LMR. These habitats support an abundant macroinvertebrate fauna dominated by relatively few species. Representative dikes studied in the LMR support naturally high levels of macroinvertebrate production. These studies demonstrate that stone dikes provide a valuable substrate for aquatic invertebrates that are important in the nutrition of fishes and other vertebrates of recreational and ecological value.

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Table 1

Macroinvertebrate Taxa Found on Lower Cracraft and Leota Dikes,
Lower Mississippi River, 1987-88

<u>Taxonomic Group</u>	<u>Species</u>
<u>Dominant Taxa (Comprised Greater Than 95% of the Community)</u>	
Arthropoda	
Insecta	
Trichoptera	<i>Hydropsyche orris</i>
Diptera	<i>Rheotanytarsus</i> sp.
Crustacea	
Amphipoda	<i>Corophium lacustre</i>
Platyhelminthes	
Tricladida	<i>Dugesia tigrina</i>
<u>Other Taxa (Comprised Less Than 5% of the Community)</u>	
Arthropoda	
Insecta	
Trichoptera	<i>Potamyia flava</i>
	<i>Ceraclea</i> sp.
	<i>Neotrichia</i> sp.
	<i>Neureclipsis</i> sp.
	<i>Cyrnellus fraternus</i>
Diptera	<i>Polypedilum convictum</i>
	<i>Cricotopus</i> sp.
	<i>Nanocladius</i> sp.
	<i>Glyptotendipes</i> sp.
	<i>Thienemanniella</i> sp.
	<i>Dicrotendipes</i> sp.
	<i>Cladotanytarsus</i> sp.
	<i>Tanytarsus</i> sp.
	<i>Eukiefferiella</i> sp.
	<i>Chironomus</i> sp.
	<i>Micropsectra</i> sp.
	<i>Simuliidae</i> *
Ephemeroptera	<i>Stenonema</i> sp.
	<i>Baetis</i> sp.

(Continued)

* A single unidentified species.

(Sheet 1 of 3)

Table 1 (Continued)

Taxonomic Group	Species
<u>Other Taxa (Comprised Less Than 5% of the Community) (Continued)</u>	
Arthropoda	
Insecta	
Ephemeroptera (Cont.)	<i>Stenacron</i> sp. <i>Isonychia</i> sp. <i>Heptagenia</i> sp. <i>Caenis</i> sp. <i>Potamanthus</i> sp. <i>Tricorythodes</i> sp. <i>Pseudocloeon</i> sp.
Plecoptera	<i>Perlesta</i> sp. <i>Neoperla</i> sp.
Odonata	<i>Neurocordulia</i> sp. <i>Dromogomphus</i> sp. <i>Coenagrionidae</i> *
Coleoptera	Elmidae*
Collembola	
Hemiptera	
Lepidoptera	
Crustacea	
Amphipoda	<i>Gammarus</i> sp.
Isopoda	<i>Lirceus</i> sp.
Arachnoidea	Hydracarina**
Mollusca	
Gastropoda	
Prosobranchia	<i>Lithasia armigera</i> <i>Pleurocera</i> sp. <i>Ferrissia</i> sp. <i>Campeloma</i> sp.
Bivalvia	<i>Corbicula fluminea</i>

(Continued)

* A single unidentified species.

** Several unidentified species.

(Sheet 2 of 3)

Table 1 (Concluded)

Taxonomic Group	Species
Annelida	
Oligochaeta	
Naididae*	
Tubificidae*	
Aelosomatidae**	
Nematoda*	
Nemertea**	
Cnidaria	
Hydrozoa	<i>Hydra</i> sp. <i>Cordylophora</i> sp.

* Several unidentified species.

** A single unidentified species.

Table 2

Average Density of Major Macroinvertebrate Taxa on Lower Cracraft and Leota Dikes,
Lower Mississippi River, 1987-88 ($\pm$ Standard Error)

Date	Density (Individuals/m ²)					Total Macroinvertebrates
	<i>Hydropsyche orris</i>	<i>Rheotanytarsus sp.</i>	<i>Corophium lacustre</i>	<i>Dugesia tigrina</i>		
9/16/87	1,297 ± 816	2,773 ± 1,075	90 ± 34	64 ± 22	4,892 ± 1,684	
10/14/87	546 ± 454	2,175 ± 765	1,781 ± 431	524 ± 300	6,415 ± 1,742	
11/13/87	119 ± 80	3,823 ± 1,959	70 ± 43	19 ± 8	4,783 ± 2,359	
5/13/88	75 ± 20	1,745 ± 317	6 ± 3	2 ± 1	182 ± 38	
6/14/88	16,350 ± 2,099	17,989 ± 1,909	560 ± 193	2,159 ± 357	47,990 ± 3,429	
7/22/88	3,923 ± 1,092	646 ± 173	6,152 ± 3,423	7,894 ± 2,181	21,950 ± 7,220	
8/12/88	2,845 ± 986	1,203 ± 348	20,987 ± 7,080	4,920 ± 1,346	32,776 ± 8,700	
9/9/88	2,231 ± 1,081	2,338 ± 915	38,937 ± 9,165	3,379 ± 1,308	51,103 ± 11,096	
10/17/88	4,522 ± 1,385	514 ± 212	5,133 ± 2,006	4,207 ± 1,347	15,684 ± 3,548	

Table 3

Duration of Larval Life Spent in Each Instar of the Spring and Late-Summer
Generations of *H. orris*

<u>Generation</u>	<u>Larval Instar</u>	<u>Duration (days)</u>	<u>Pe/Pa*</u>
Spring	I	12	1.67
	II	18	1.11
	III	19	1.05
	IV	20	1.00
	V	<u>31</u>	0.65
		Total = 100	
Late-summer	I	11	4.36
	II	30	1.60
	III	75	0.64
	IV	75	0.64
	V	<u>44</u>	1.09
		Total = 235	

* Pe/Pa ratio represents the expected versus the actual proportion of larval life spent in each instar, with the expected proportion based on the assumption that an equal amount of time is spent in each instar (Hamilton 1969). For example, in larval instar I of the spring generation, the expected proportion (Pe) equals $100/5 = 20$; the actual proportion equals 12. Thus, the Pe/Pa ratio is $20/12$, or 1.67.

Table 4

Duration of Larval Life Spent in Each Instar of the Spring, Summer,
and Fall Generations of *Rheotanytarsus* sp.

<u>Generation</u>	<u>Larval Instar</u>	<u>Duration (days)</u>	<u>Pe/Pa*</u>
Spring	I	2	9.50
	II	6	3.17
	III	17	1.12
	IV	<u>51</u>	0.37
	Total = 76		
Summer	I	2	9.50
	II	6	3.17
	III	17	1.12
	IV	<u>51</u>	0.37
	Total = 76		
Fall	I	2	21.00
	II	6	7.00
	III	135	0.31
	IV	<u>25</u>	1.68
	Total = 168		

* Pe/Pa ratio represents the expected versus the actual proportion of larval life spent in each instar, with the expected proportion based on the assumption that an equal amount of time is spent in each instar (Hamilton 1969). For example, in larval instar I of the spring generation, the expected proportion (Pe) is equal to $76/4$ or 19 days, although the actual duration was 2 days. The Pe/Pa ratio is $19/2$, or 9.50.

Table 5

Estimated Density (Individuals/m²) per Instar Throughout the Lifespan of
Each Generation of the Bivoltine *Hydropsyche orris* Population

Generation	M	J	J	A	S	O	N	D	J	F	M	A	Average	Multiplied by Pe/Pa
Spring														
I	4,012	551	267	174	--	--	--	--	--	--	--	--	1,251	2,089
II	771	2,339	672	1,206	--	--	--	--	--	--	--	--	1,248	1,385
III	151	1,703	528	1,977	--	--	--	--	--	--	--	--	1,090	1,145
IV	0	828	2,032	1,165	--	--	--	--	--	--	--	--	1,007	1,007
V	864	377	2,299	1,276	--	--	--	--	--	--	--	--	1,205	783
Late-summer														
I	--	--	--	--	861	476	59	53	17	42	0	0	192	837
II	--	--	--	--	425	690	207	187	166	145	0	0	228	365
III	--	--	--	--	178	345	709	639	568	497	524	44	438	294
IV	--	--	--	--	199	176	561	505	449	393	314	262	357	229
V	--	--	--	--	80	54	207	187	166	145	209	523	196	214

Table 6

Estimated Density (Individuals/m²) per Instar Throughout the Lifespan of
Each Generation of the Trivoltine *Rheotanytarsus* sp. Population

Generation	A	M	J	J	A	S	O	N	D	J	F	M	Average	Multi- plied by Pe/Pa
Spring														
I	3,680	0	0	--	--	--	--	--	--	--	--	--	1,227	3,509
II	3,493	671	187	--	--	--	--	--	--	--	--	--	1,450	2,639
III	2,260	2,723	2,082	--	--	--	--	--	--	--	--	--	2,355	2,473
IV	434	6,483	7,598	--	--	--	--	--	--	--	--	--	4,838	2,274
Summer														
I	--	--	--	521	0	0	--	--	--	--	--	--	174	609
II	--	--	--	494	173	59	--	--	--	--	--	--	242	469
III	--	--	--	320	395	311	--	--	--	--	--	--	342	315
IV	--	--	--	61	828	1,026	--	--	--	--	--	--	638	300
Fall														
I	--	--	--	--	--	--	486	0	0	0	0	0	81	573
II	--	--	--	--	--	--	861	54	48	41	34	0	173	433
III	--	--	--	--	--	--	661	2,063	1,805	1,290	1,290	217	1,264	430
IV	--	--	--	--	--	--	163	54	48	41	34	870	202	407

Table 7
Average Dry Weight (for Standing Crop Estimates) and Dry Weight at Loss (for
 Production Estimates) per Instar of *Hydropsyche orris*

Larval Instar (1)	Average Dry Weight* (μg)	Dry Weight at Loss** (μg)
I	9	19
II	41	85
III	175	313
IV	561	897
V	1,434	1,702 ⁺

* $(W_1)^{1/2}$.

** $(W_1 W_{1+1})^{1/2}$.

+ Average individual lost to pupation was assumed to be slightly larger
 (IO = 1.00 mm) than the average-sized (IO = 0.94) individual of instar V.

Table 8
Average Dry Weight (for Standing Crop Estimates) and Dry Weight at Loss
 (for Production Estimates) per Instar of *Rheotanytarsus* sp.

Larval Instar (1)	Average Dry Weight* (μg)	Dry Weight at Loss** (μg)
I	0.51	0.89
II	1.57	2.86
III	5.20	10.50
IV	21.00	26.14 ⁺

* $(W_1)^{1/2}$.

** $(W_1 W_{1+1})^{1/2}$.

+ Average individual lost to pupation was assumed to be slightly larger
 (LPW = 65.0 μ) than the average (LPW = 61.2 μ) individual of instar IV.

Table 9

Average Standing Crop (B) and Production (P) of the Bivoltine

Hydropsyche orris Population

Larval Instar	Density (Ind./m ²)	Dry Weight (µg/Ind.)	Standing Crop (g/m ²)	Density Loss per Instar (Ind./m ²)	Dry Weight at Loss (µg/Ind.)	No. of Times Loss Occurs	Production (g/m ²)
Spring Generation							
I	2,089	9	0.018	704	19	5	0.067
II	1,385	41	0.057	240	85	5	0.102
III	1,145	175	0.200	138	313	5	0.216
IV	1,007	561	0.565	224	897	5	1.005
V	783	1,434	1.123	783	1,702	5	6.663
B = 1.963							P = 8.053
Late-Summer Generation							
I	837	9	0.008	472	19	5	0.045
II	365	41	0.015	85	85	5	0.036
III	280	175	0.049	51	313	5	0.080
IV	229	561	0.129	15	897	5	0.067
V	214	1,434	0.307	214	1,702	5	1.821
B = 0.508							P = 2.049

Annual production of *H. orris*: 10.102 g/m²

Table 10

Average Standing Crop (B) and Production (P) of the Trivoltine
Rheotanytarsus sp. Population

Generation	Larval Instar	Avg Instar Density (Ind./m ²)	Dry Weight (µg/Ind.)	Standing Crop (mg/m ²)	Density Loss per Instar (Ind./m ²)	Dry Weight at Loss (µg/Ind.)	No. Times Time Loss Occurs	Production (mg/m ²)
Spring	I	11,657	0.51	5.9	7,060	0.89	4	25.1
	II	4,597	1.57	7.2	1,959	2.86	4	22.4
	III	2,638	5.20	13.7	848	10.50	4	35.6
	IV	1,790	21.00	37.6	1,790	26.14	4	187.2
				B = 64.4				
Summer	I	1,653	0.51	0.8	886	0.89	4	3.2
	II	767	1.57	1.2	384	2.86	4	4.4
	III	383	5.20	2.0	147	10.50	4	6.2
	IV	236	21.00	5.0	236	26.14	4	24.7
				B = 9.0				P = 38.5
Fall	I	1,701	0.51	0.9	490	0.89	4	1.7
	II	1,211	1.57	1.9	819	2.86	4	9.4
	III	392	5.20	2.0	53	10.50	4	2.2
	IV	339	21.00	7.1	339	26.14	4	21.9
				B = 11.9				P = 35.2

Annual production of *Rheotanytarsus* sp.: 344 mg/m²

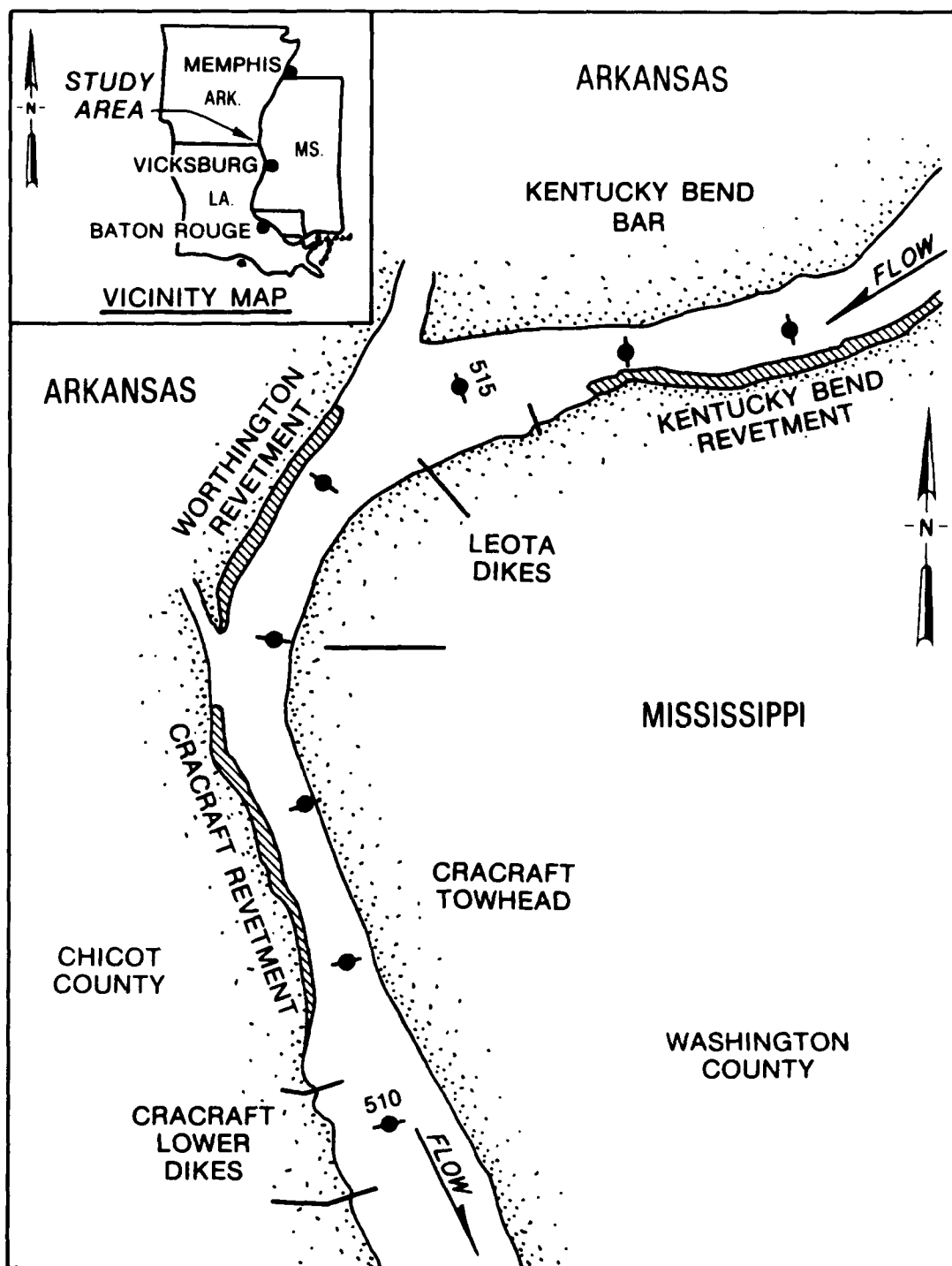


Figure 1. Location map of Leota and Lower Cracraft dike fields

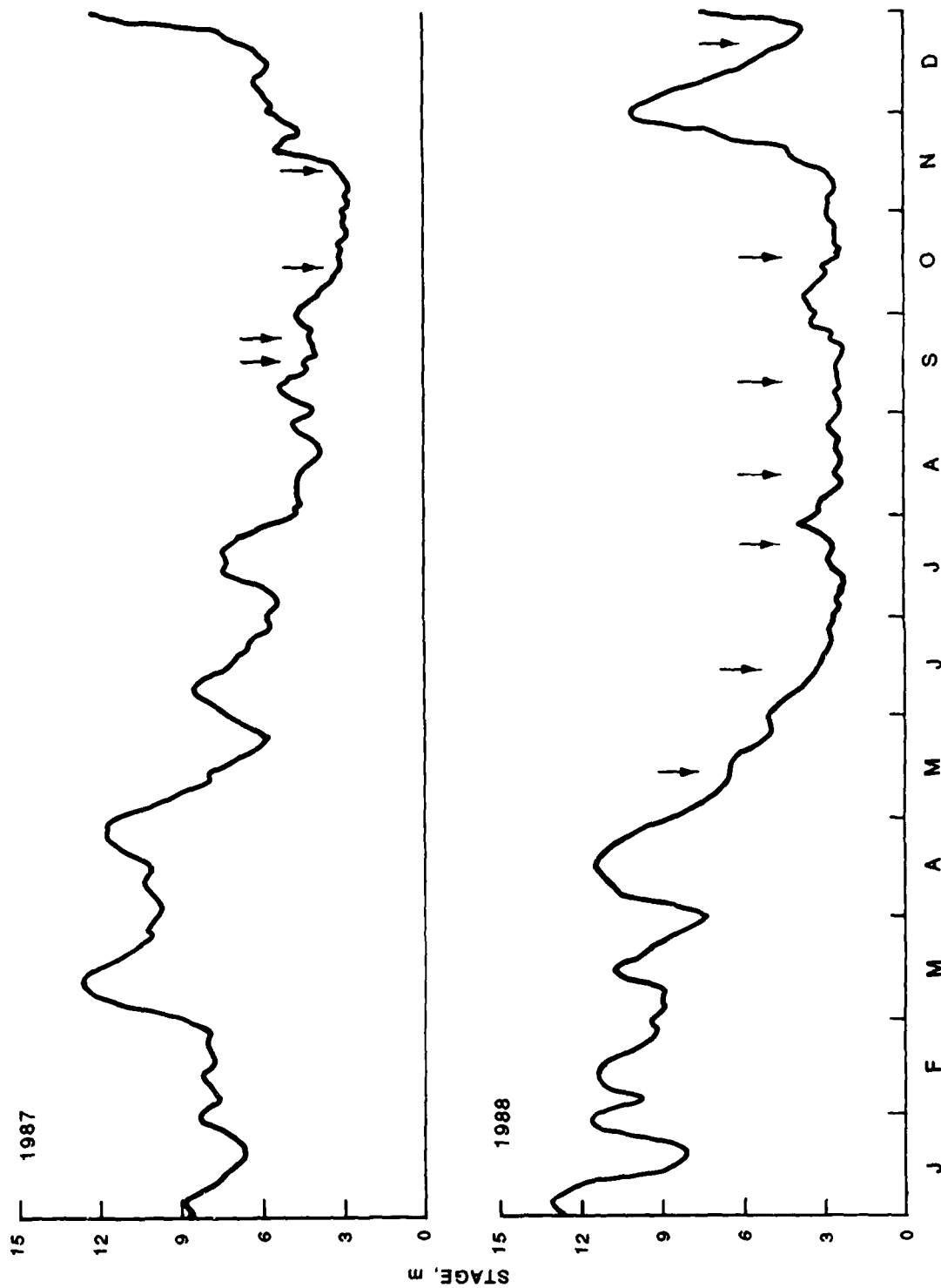


Figure 2. Daily stage records of Lower Mississippi River (Greenville gage) for 1987-1988. Arrows indicate dates of sampling for macroinvertebrates on stone dikes

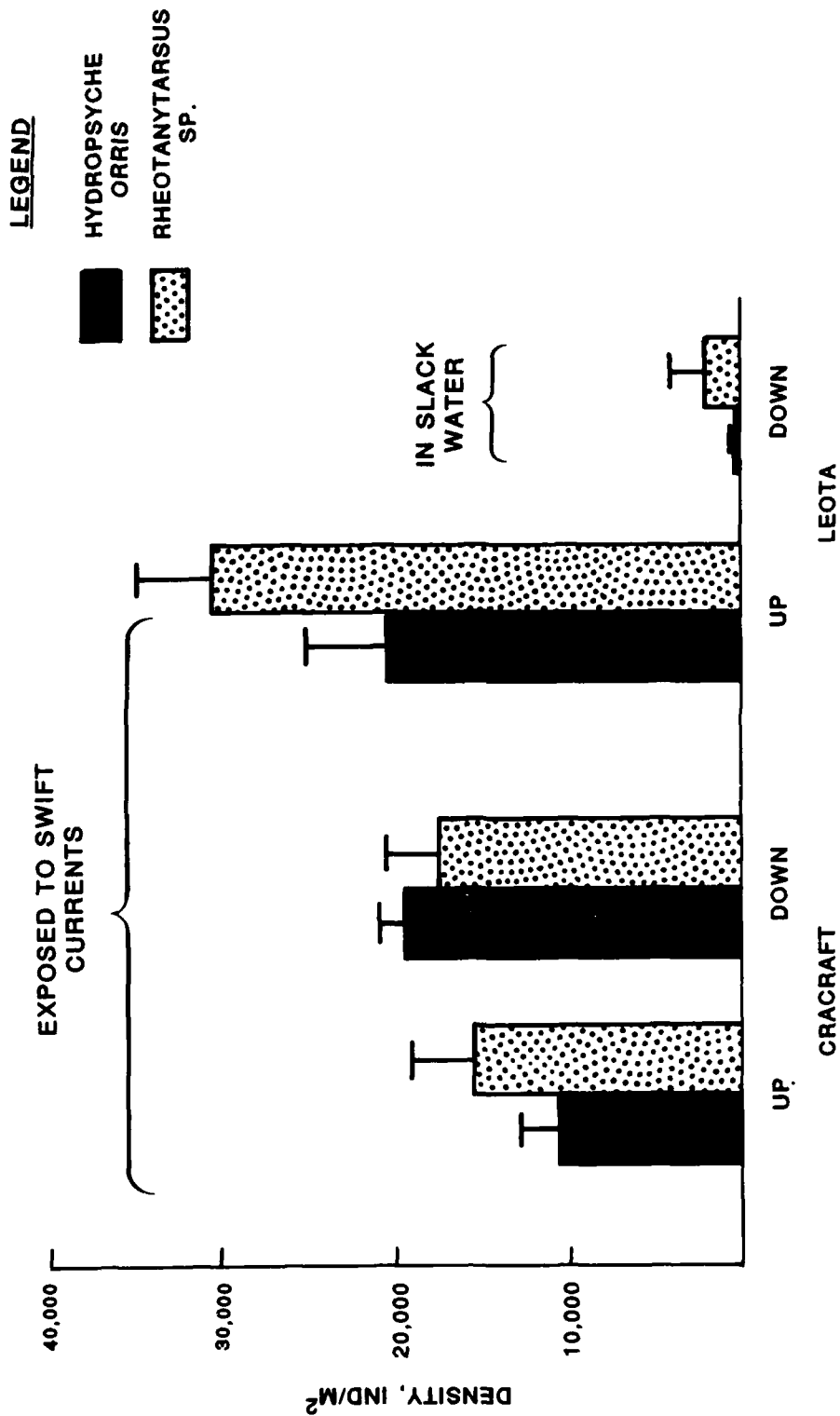


Figure 3. Average density ($\pm$ SE) of *H. orris* and *Rheotanytarsus* sp. on Cracraft and Leota Dikes on 14 June 1988. Note the markedly low density of both species on the downstream Leota dike that was exposed to slackwater conditions

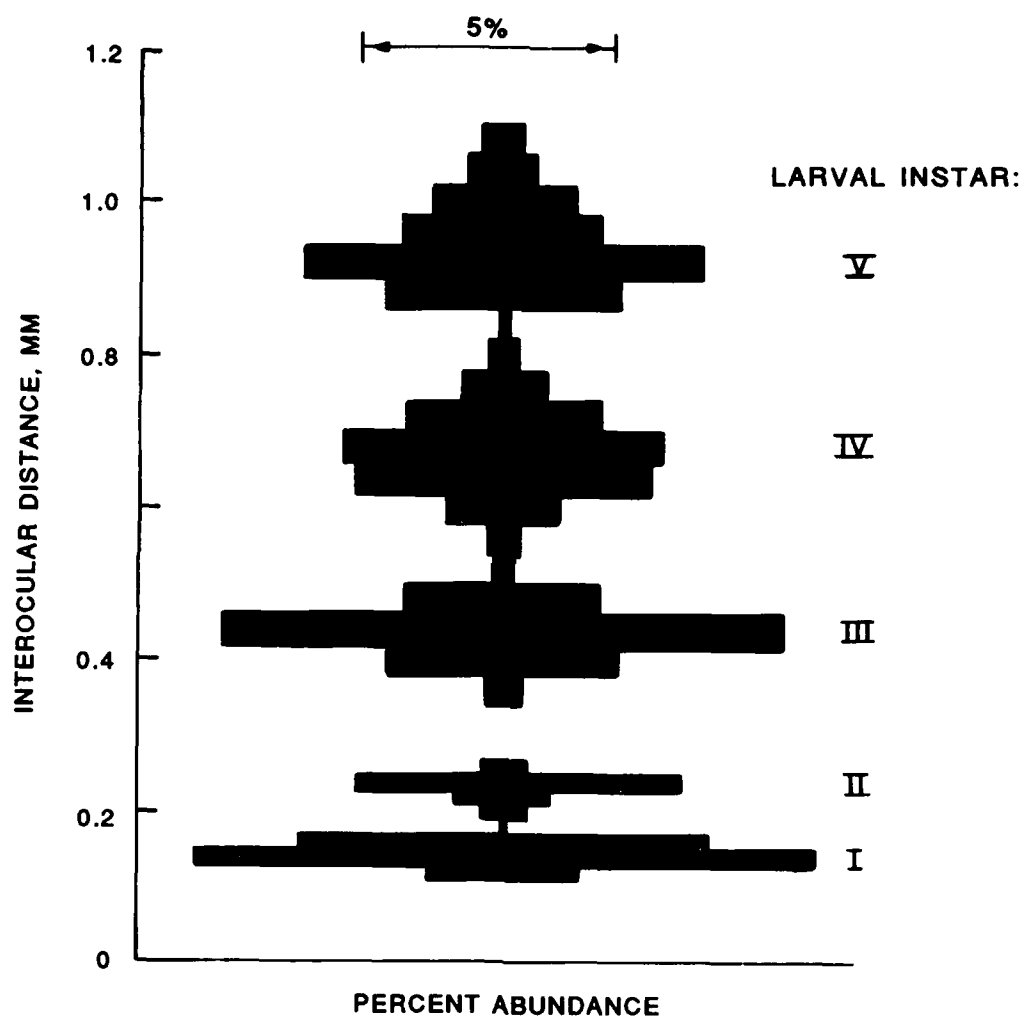


Figure 4. Five instars of *H. orris* as delineated by interocular distance measurements

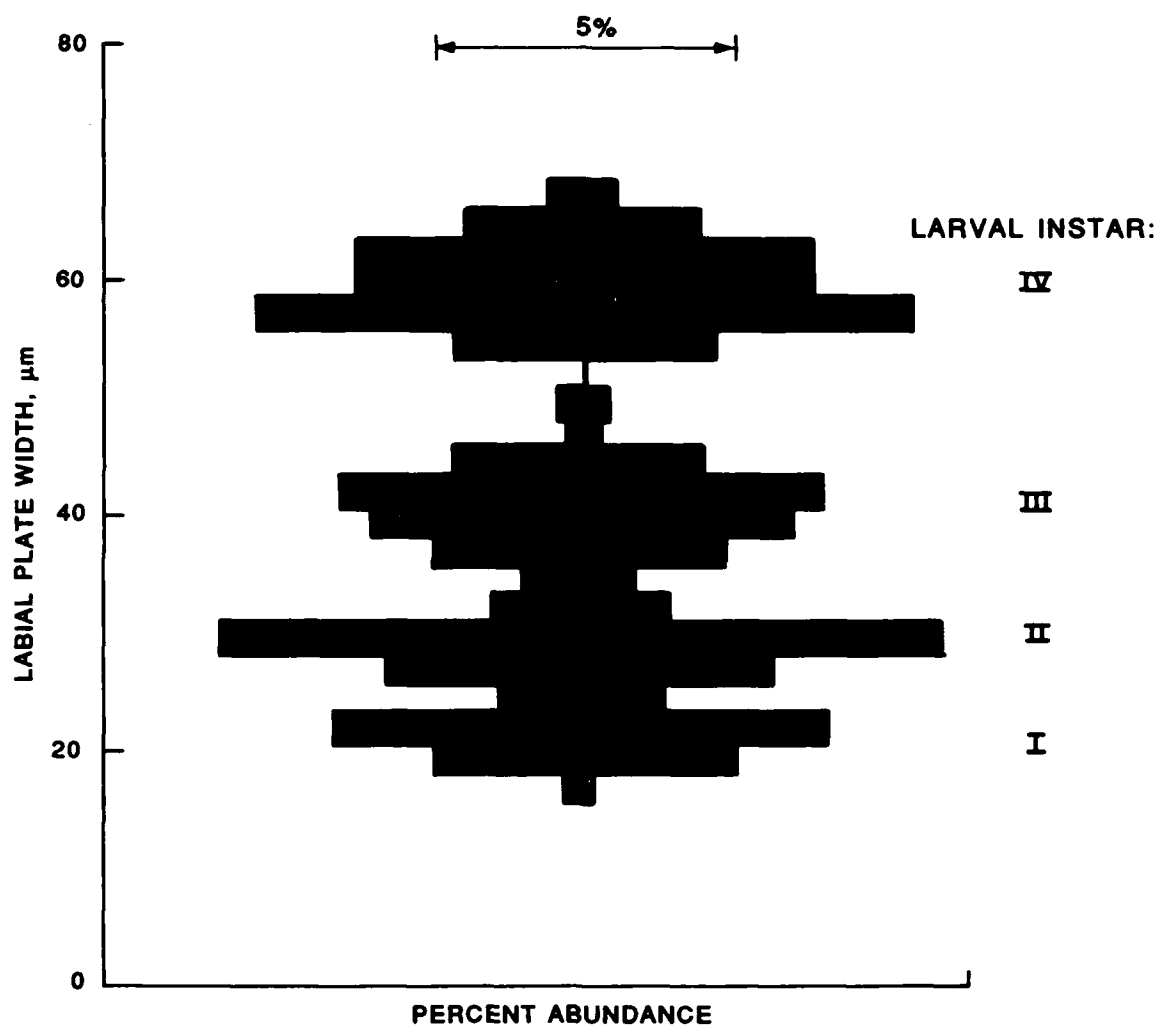


Figure 5. Four instars of *Rheotanytarsus* sp. as delineated by labial plate width measurements

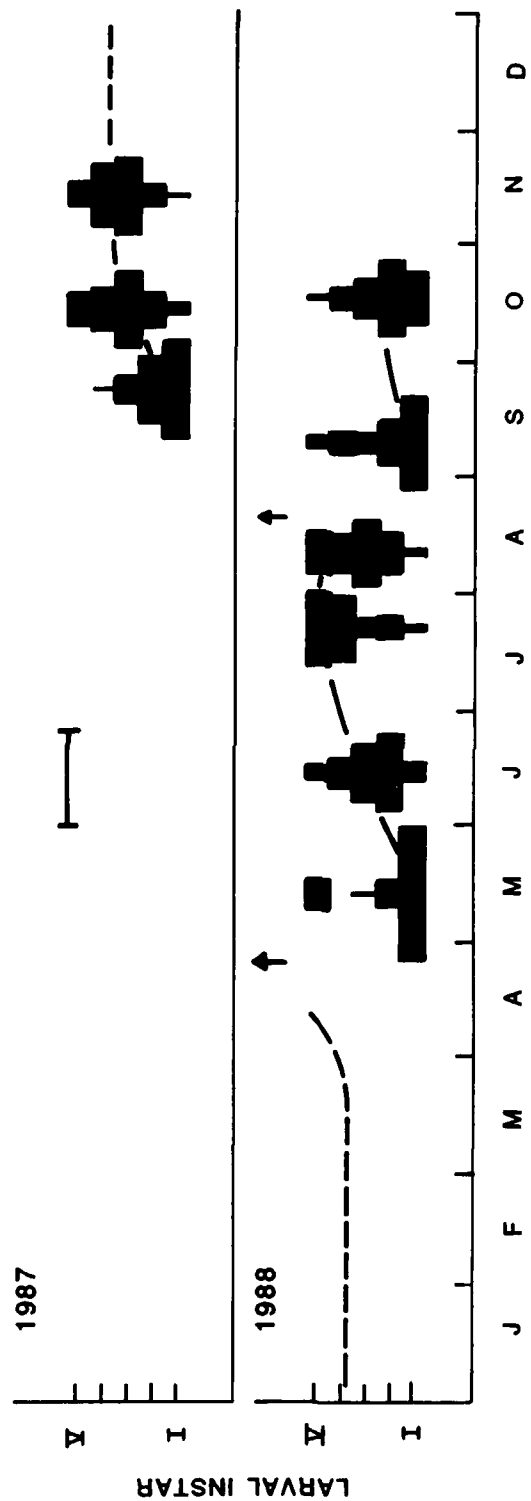


Figure 6. Seasonal changes in the relative abundance of larval instars of *H. orris*. Arrows indicate peak emergence periods

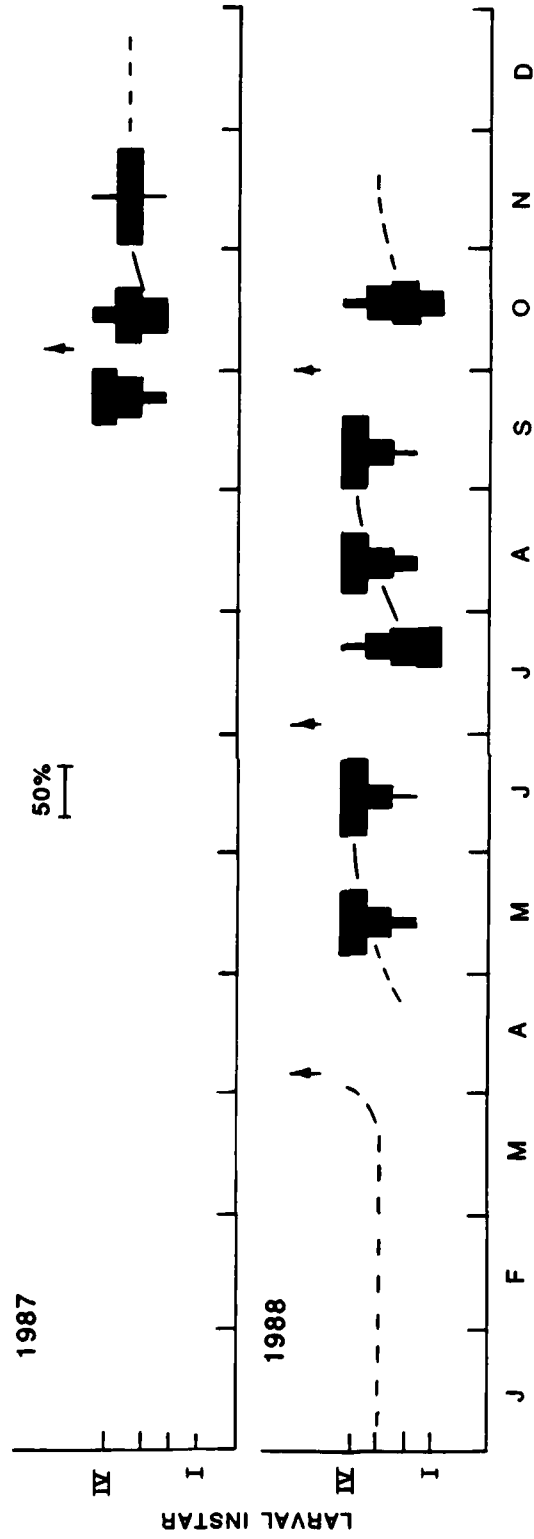


Figure 7. Seasonal changes in the relative abundance of larval instars of *Rheotanytarsus* sp.
Arrows indicate peak emergence periods

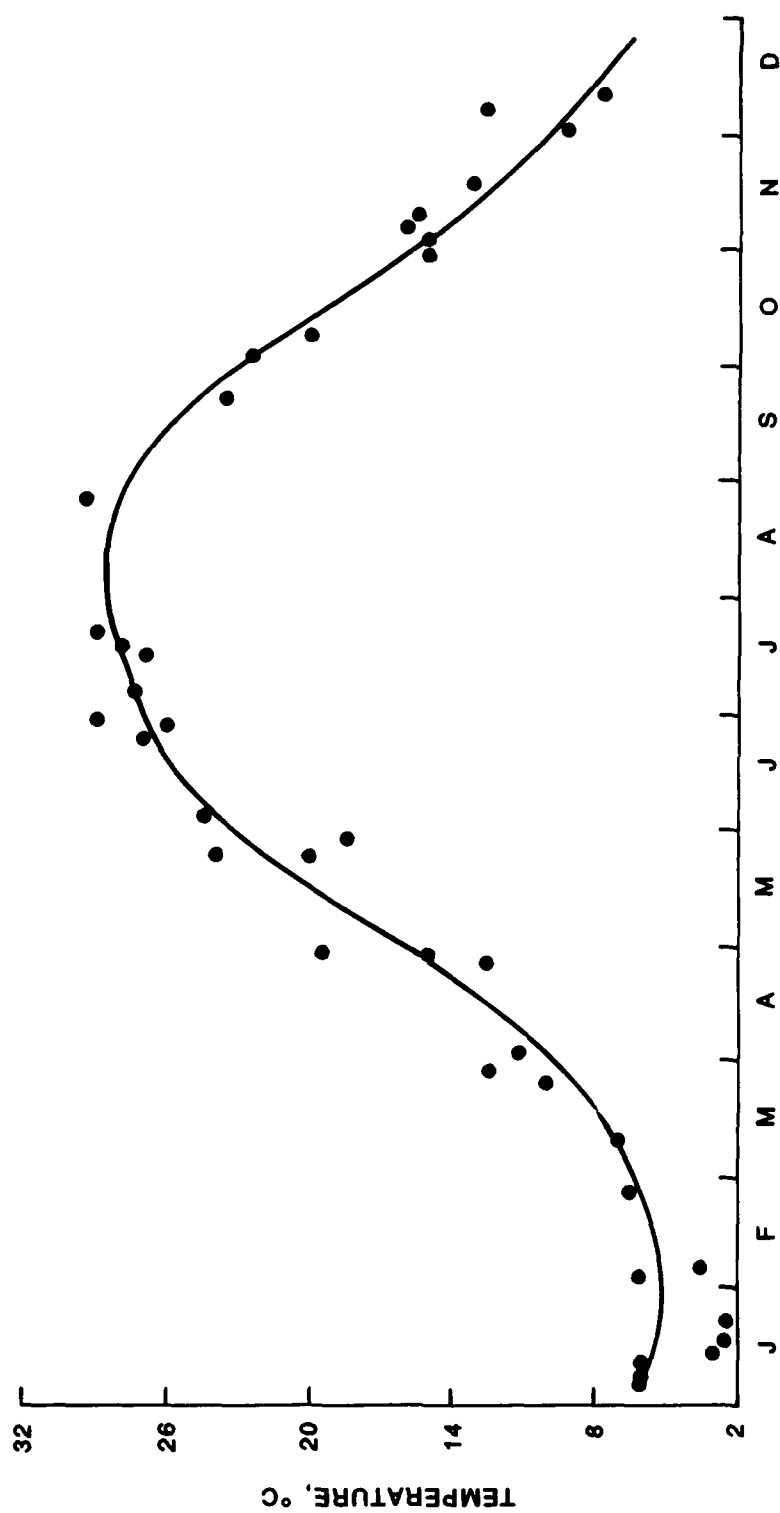


Figure 8. Seasonal pattern of surface water temperature, Mississippi River at Vicksburg, Miss.
(based on data gathered from 1980 to 1985 by the US Geological Survey)