

## Abundance, composition, and dynamics of the invertebrate fauna of a tidal freshwater wetland

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**Abstract.** The benthic and epiphytic faunas of Tivoli South Bay, a freshwater tidal wetland on the Hudson River, New York, were studied in the summers of 1986 and 1987. Total macroinvertebrate density in the sediments ranged from  $5.0 \times 10^3$  individuals/m<sup>2</sup> to  $11.0 \times 10^3$  individuals/m<sup>2</sup>. Chironomids made up 15 to 50% of the total number of macroinvertebrates in the sediment.

Artificial substrates were used to document short-term population dynamics of chironomids. Colonization of artificial substrates placed in the field in June of 1986 was rapid, with the maximum number of chironomid genera being present in <2 wk. Peak abundance on these substrates ( $8.3 \times 10^3$  individuals/m<sup>2</sup>) was reached after 22 d of exposure, and densities were comparable to densities of chironomids found on the predominant macrophyte ( $9.5 \times 10^3$  individuals/m<sup>2</sup>). Substrates placed in the field later in the summer collected fewer individuals and genera, and there were changes in taxonomic composition.

From late June to August, water-chestnut (*Trapa natans*) thoroughly covered the surface of this bay and was an important habitat for macroinvertebrates. The average abundance of epiphytic invertebrates was consistently greater than  $1.0 \times 10^4$  individuals/m<sup>2</sup> of bottom surface area and ranged as high as  $3.0 \times 10^4$  individuals/m<sup>2</sup>. From June to August, epiphytic invertebrates were more abundant than benthic invertebrates, illustrating the importance of the water-chestnut habitat.

In July, abundance of epiphytic chironomids declined sharply, with densities dropping from  $7.7 \times 10^3$  individuals/m<sup>2</sup> of bottom surface area to  $0.7 \times 10^3$  individuals/m<sup>2</sup>. Emerging adults collected over this period totalled  $0.4 \times 10^3$  individuals/m<sup>2</sup>, leaving much of the decline unexplained. Predation by fishes and predatory or competitive interactions among the Chironomidae are possible alternative explanations for the decline.

**Key words:** macroinvertebrates, chironomids, macrophytes, wetlands.

Tidal freshwater wetlands are known to have some of the highest rates of primary production of any aquatic ecosystem (Whigham et al. 1978, Brinson et al. 1981) and are important feeding areas for fishes and waterfowl (e.g., Weller 1981, Odum et al. 1984, Schmidt 1986). Despite the apparent importance of invertebrates in the trophic structure of wetlands, there have been few studies of invertebrate abundance or dynamics in tidal freshwater wetlands. Recent reviews (Simpson et al. 1983, Odum et al. 1984, Mitsch and Gosselink 1986, Odum 1988) reveal that the few studies of invertebrates are largely taxonomical in focus and contain few quantitative data on abundance or dynamics.

The expectation of high invertebrate abun-

dance is particularly valid when macrophytes are present in the system. Macrophytes provide an additional habitat with a high surface area per area of the bottom, and abundances on macrophytes can be very high (Soszka 1975, Menzie 1980, Downing and Cyr 1985). This increased animal density due to the presence of macrophytes may therefore have favorable consequences in the form of higher predator production.

Chironomids are recognized as one of the most abundant and productive taxa in freshwater ecosystems (Waters 1977, Simpson and Bode 1980, Menzie 1981, Benke et al. 1984, Coffman and Ferrington 1984, Strayer and Likens 1986). Their importance as food for fishes in freshwater ecosystems has been well documented (Keast and Webb 1966, Pinder 1986) and they were an important component of fish diets in the wetland we studied (Duryea and Schmidt 1986, Richard and Schmidt 1986). For these reasons, we have emphasized the chironomid com-

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ponent of macroinvertebrates in this study. Our objectives were (1) to describe macroinvertebrate abundance and composition in the sediments and on water-chestnut (*Trapa natans*) in Tivoli South Bay, and (2) to examine short-term population dynamics of chironomids by looking at the rate of colonization of a series of artificial substrates.

### Study Area

Tivoli South Bay is one of four marsh components of the Hudson River National Estuarine Research Reserve and is located on the eastern bank of the Hudson River approximately 163 km north of Battery Park, New York (Fig. 1). The bay is a freshwater tidal wetland that was partially separated from the main channel of the Hudson by the construction of a filled railroad bed in 1851. Three bridges allow water to pass in and out of the bay as the tide changes. The average tidal range is 1.3 m, but saline water does not intrude this far upriver. Summer water temperatures range from 15 to 25°C. Nutrient concentrations are high, with  $\text{NO}_3$  commonly exceeding 1 mg/L and  $\text{PO}_4$  greater than 50  $\mu\text{g/L}$ . Water entering the bay is usually saturated with oxygen but ebb-tide concentrations may be only half saturation.

Water-chestnut is the dominant aquatic macrophyte except in the northern fringe of the bay, where *Typha*, *Nuphar*, and *Pontederia* are common, and the deeper, open-water tidal channels. By late June of 1985–1988 the water-chestnut formed a thick mat which almost completely covered the surface of the bay.

All sampling for this study was conducted at a single site near the center of the bay (Fig. 1) where the water was about 1 m deep at mean low water. Sediment samples taken on an east-west transect across the bay showed a gradient in sediment organic matter (ash-free dry mass [AFDM] ranging from 6.0 to 12.0% of dry mass [DM]). The sampling station had a mean sediment organic content of 7.8% AFDM, similar to the average for the entire transect (8.5%). The water-chestnut biomass at the sampling station on 27 August 1987 was 377 g DM/m<sup>2</sup>, when the average over the same east-west transect was 367 g DM/m<sup>2</sup> (range = 301–453). Therefore, we are assuming that the particular location is representative of a large proportion of Tivoli South Bay.

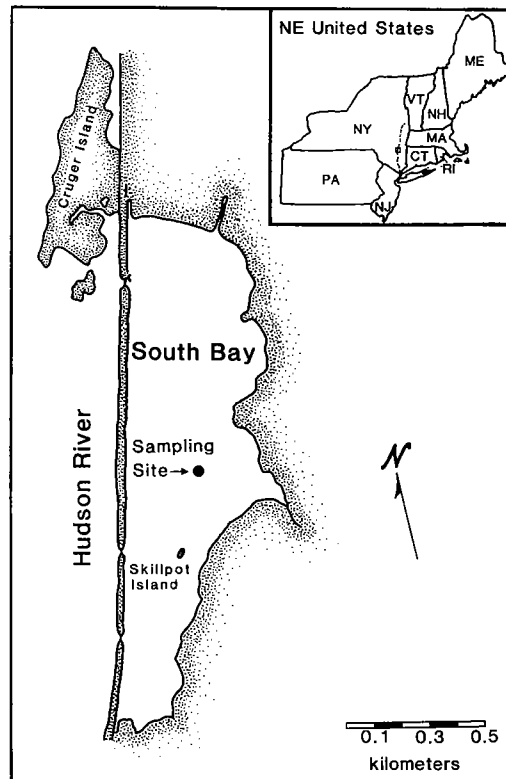


FIG. 1. Location of Tivoli South Bay, Hudson River, New York (42°N, 74°W). All sampling was conducted at the central site.

### Methods

#### *Benthic invertebrate sampling*

Sediment samples were taken monthly from April through August 1987. On each date, five 30-cm<sup>2</sup> cores consisting of the top 5 cm of sediment were collected with a pole-mounted coring device (Gillespie et al. 1985). All samples were preserved in a 5% formalin solution with Rose Bengal dye added as a sorting aid. In the laboratory the cores were sieved through a 0.5-mm mesh sieve and at a later date the organisms were sorted into taxonomic groups with the aid of a dissecting microscope.

#### *Colonization of artificial substrates*

We used a time series of artificial substrates to determine short-term population dynamics of chironomids in the summer of 1986. Ceramic tile samplers (Fig. 2) were designed to permit

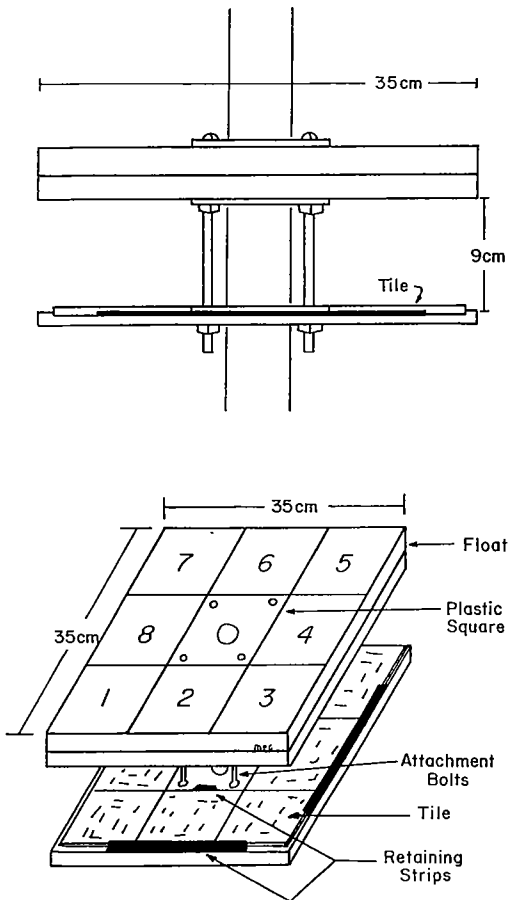


FIG. 2. Schematic of the apparatus for holding the ceramic tile sampling units. Numbers on the upper surface of the float are for identifying the tiles.

retrieval and replacement of individual tiles (sampling units) with minimal disturbance. The samplers held eight  $11 \times 11$ -cm ( $0.012 \text{ m}^2$ ) unglazed tiles on a lower platform attached to an upper styrofoam float. A plastic pipe passed through the center of the sampler to hold it in place, yet allowed the entire apparatus to float up and down with the tides. Therefore, the tiles were always about 10 cm below the water surface. The upper surface of tiles was available for colonization. On water-chestnut, the lower surface of leaves was colonized, probably because the upper surfaces were frequently out of water.

Three ceramic tile samplers (each with eight new tiles) were placed at the site near the center of Tivoli South Bay on 19 June 1986. Tiles were

collected beginning on 23 June, and every few days thereafter. One tile from each sampler on each date was collected and replaced with a new tile. This pattern of collection and replacement resulted in the initial set of tiles all starting on 19 June and being exposed for varying lengths of time. The replacement tiles all started at different times, but all were exposed for either 28 or 29 d.

Tiles were collected by carefully sliding them into plastic bags. The water in the bags was poured through a 0.123-mm mesh sieve, which was then backwashed with 70% isopropyl alcohol into the bags. Rose Bengal was added as a sorting aid, and bags were filled one-third full with 70% isopropyl alcohol.

In the lab, each tile was brushed with a small toothbrush to remove organisms. The tiles were rinsed with 70% isopropyl alcohol. The contents of the bags were poured onto a 0.5-mm mesh sieve and gently washed with tap water. All organisms retained on the sieve were backwashed into a petri dish with 70% isopropyl alcohol. The organisms were counted and sorted into taxonomic groups with the aid of a dissecting microscope. Samples containing  $>50$  chironomids were subsampled such that 25% of the total number of larvae was mounted for identification.

#### *Water-chestnut invertebrate sampling*

Water-chestnut rosettes were collected twice during the course of the 1986 colonization study. Each rosette was clipped at the base and carefully pushed into a plastic bag. Isopropyl alcohol was added to the bags until they were half full.

In 1987, five water-chestnut rosettes were collected weekly from 8 June to 13 August. Collection methods were the same as in 1986, except that 5% formalin was used as a preservative. Water-chestnut samples were processed in the laboratory by first vigorously shaking the bag containing the rosette to dislodge most of the organisms. Then, each leaf was clipped off at its base and 25% of the total number of leaves was examined under a dissecting microscope to remove any remaining organisms. Less than 10% of the total number of animals was found on the leaves after shaking. The rest of the plant was placed on a 0.5-mm mesh sieve and washed with tap water to remove any organisms that

had not come off in the sample bags. The preservative from the sample bags was also sieved and, as above, the organisms were sorted, identified, and counted.

The surface area (stem and leaves) of water-chestnut rosettes was determined with a LiCor 3100 Area Meter. These calculations were used to obtain density estimates of organisms per square meter of leaf surface area (LSA). These surface area measurements include only one side of the leaf because macroinvertebrates were seen only on the undersurface of the leaves. The upper surface was frequently out of the water and so would not be available to aquatic invertebrates.

After leaf area was measured, the rosettes were dried at 70–75°C for approximately 24 hr and weighed. Water-chestnut biomass in the field was determined by clipping, drying, and weighing all rosettes in five replicate 0.15-m<sup>2</sup> quadrats. The standard error of the mean was always less than 20% of the mean. To facilitate comparison between epiphytic invertebrate densities and densities in the sediment, water-chestnut biomass data were used to calculate the relationship of water-chestnut LSA to bottom surface area (BSA):

$$\text{LSA/BSA} = (\text{m}^2 \text{ LSA/rosette}) / (\text{g DM/rosette}) \times \text{g DM/m}^2 \text{ BSA}$$

Epiphytic invertebrate densities are thus presented as number of animals per m<sup>2</sup> BSA with the equation:

$$\# \text{ indiv/m}^2 \text{ BSA} = (\# \text{ indiv/m}^2 \text{ LSA}) \times (\text{m}^2 \text{ LSA/m}^2 \text{ BSA})$$

Chironomid larvae from both water-chestnut and sediment samples were mounted in CMC-10 mounting medium according to Beckett and Lewis (1982) and identified to the lowest taxon possible. The primary taxonomic references were Merritt and Cummins (1984) and Simpson and Bode (1980).

#### Chironomid emergence

Three floating emergence traps were deployed at the central sampling site on 18 June 1987. Traps were tethered to an anchor and could move around with the currents. Collections from these traps were made on 19 June, 22 June, and once per week thereafter until their removal in mid-September. Traps were pyramid-shaped

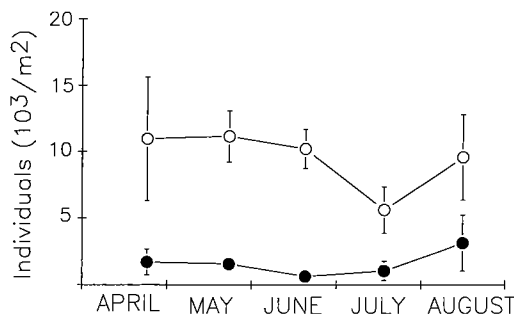


FIG. 3. Density of total invertebrates (O) and chironomids (●) in sediments of Tivoli South Bay in 1987. Each point is the mean of five cores ( $\pm 1$  SE).

with a 0.25-m<sup>2</sup> wood base and walls of plastic screening (1 mm mesh) supported by wires. A plastic funnel was attached to the wires at the top. The sample container was a plastic bag attached to the neck of the funnel by a rubberband. Sample collection involved removing the bag and replacing it weekly. Organisms were removed from the bag in the laboratory, stored in vials, and frozen until identified and counted. Emergence rate was calculated from the number of individuals in the trap divided by the area of the trap opening (0.25 m<sup>2</sup>) and number of days deployed.

## Results

### Benthic invertebrates

Total invertebrate densities in the sediments ranged from  $5.6 \times 10^3$  individuals/m<sup>2</sup> to  $11.1 \times 10^3$  individuals/m<sup>2</sup> (Fig. 3) with a mean density of  $9.5 \times 10^3$  individuals/m<sup>2</sup>. Neither total invertebrate nor chironomid density changed significantly over this time period (ANOVA,  $p > 0.05$ ). The most common macroinvertebrates in the sediment were chironomids, oligochaetes, and copepods which collectively made up about 90% of the individuals. Gastropoda, Ostracoda, Cladocera, Trichoptera, and Collembola were also found but in very low abundance.

Total chironomid densities in the sediments ranged from  $0.6 \times 10^3$  individuals/m<sup>2</sup> to  $3.1 \times 10^3$  individuals/m<sup>2</sup> during the sampling period (Fig. 3). The subfamily Chironominae was most common and two genera, *Tanytarsus* and *Polypedium*, dominated. *Chironomus*, *Harnischia*, and the tanyptodine *Procladius* were also found in

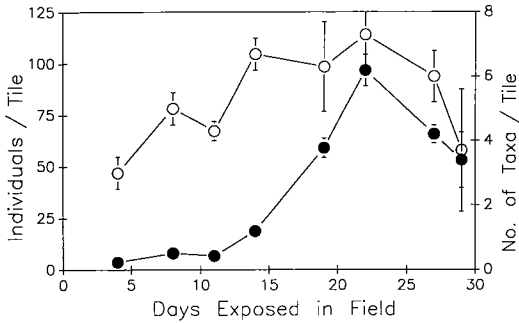


FIG. 4. Rate of colonization of tiles by chironomids (●) and accumulation of number of chironomid taxa (○) in 1986. Each point is the mean of three tiles ( $\pm 1$  SE).

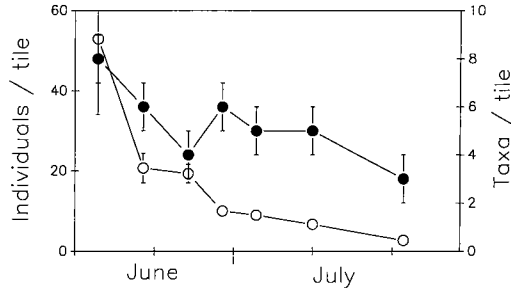


FIG. 5. Density of chironomids (○) and number of chironomid taxa (●) collected after 28 or 29 d of exposure on tiles started progressively later in the summer of 1986. Each point is the mean of three tiles ( $\pm 1$  SE).

the sediment. Many chironomids collected from the sediments were very small and therefore difficult to identify below the subfamily level.

The nauidids *Stylaria*, *Chaetogaster*, and *Dero* were the oligochaetes most frequently encountered, both in the sediment and on water-chestnut in our study.

#### Chironomid colonization of tiles

For the first set of tiles (started 23 June 1986), the mean abundance of chironomid larvae increased gradually during the first week of exposure and then increased rapidly to a peak abundance (96/tile) on Day 22 (15 July) (Fig. 4). The number of genera present on tiles levelled off after less than 2 weeks in the field (Fig. 4).

The staggered replacement of tiles resulted in seven sets of three tiles each, all of which were started on different dates, but had the same duration of exposure. Regression analysis showed that tiles started later in the summer had a lower abundance and number of taxa after 29 d in the field (Fig. 5, slopes significantly less than zero,  $p < 0.05$ ).

Parallel to the decline in abundance on tiles, a decline in abundance was also observed in the two 1986 water-chestnut samples. Chironomid density was  $9.5 \times 10^3/\text{m}^2$  LSA on 5 July and decreased to  $0.2 \times 10^3/\text{m}^2$  LSA by 7 August.

Larvae from the subfamily Chironominae constituted 61% of the total number (994) of midges on the first series of tiles collected between 23 June and 18 July 1986. Within the Chironominae, the most common genera were

*Endochironomus*, *Dicrotendipes*, *Tanytarsus*, and *Polypedilum*. Tanypodinae larvae (primarily *Procladius*) constituted 14% of the total. Orthocladinae made up 14% of the total, with the vast majority (93%) of individuals belonging to the genus *Cricotopus*. The remaining 12% was divided among taxa that individually made up less than 1% of the total, or were unidentifiable larvae.

In the later tile samples, collected 22 July to 26 August 1986, only 412 larvae were collected over all the samples, so data from all tiles were combined. Larvae in two Chironominae genera (*Endochironomus* and *Tanytarsus*) were predominant, each genus making up about 20% of the total number. *Cricotopus* and *Procladius* were absent from these later samples. About 45% of the chironomid larvae could not be identified because of their small size (early instars); certainly young *Cricotopus* and *Procladius* could have been present among these unidentified animals.

In the two 1986 water-chestnut samples, *Cricotopus* made up 86.4% of the total number (655) of midge larvae on 5 July, but was absent from the 7 August samples. Two taxa (*Ablabesmyia* and *Endochironomus*) which had not been identified in the 5 July samples were common in the 7 August samples. *Polypedilum* sp. increased in relative abundance.

#### Water-chestnut invertebrates

Sampling of water-chestnut invertebrates during 1987 showed total invertebrate densities ranging from  $0.03 \times 10^3/\text{m}^2$  BSA on 8 June to

a high of  $30.4 \times 10^3/\text{m}^2$  BSA on 29 June, with a mean of  $12.3 \times 10^3/\text{m}^2$  BSA (Fig. 6A). As in the sediments, chironomids and oligochaetes were the predominant invertebrate taxa on water-chestnut. Chironomid density ranged from 0.02 to  $7.2 \times 10^3/\text{m}^2$  BSA (Fig. 6B) and chironomids made up as much as 55% of the total invertebrates on water-chestnut. Oligochaetes were found at densities of 0.07 to  $3.9 \times 10^3/\text{m}^2$  BSA; from 16 July to 13 August they represented an average of 24% of total invertebrates. Oligochaete densities increased steadily over the course of this study from an initial density of 81/m<sup>2</sup> BSA in mid-June to over  $4.0 \times 10^3/\text{m}^2$  BSA by mid-August 1987. Significant changes in density were seen in both total epiphytic invertebrates and epiphytic chironomids over the course of this study (ANOVA,  $p < 0.001$ ).

As summer progressed, the ratio of water-chestnut leaf surface area to bottom surface area increased from 0.7 in June to a maximum of 4.2 by late July 1987. Because of this increase in surface area, fluctuations per m<sup>2</sup> LSA were less pronounced than fluctuations per m<sup>2</sup> BSA. The fact that densities/LSA do in fact increase indicates an absolute increase in numbers of organisms over the early summer. Therefore, the increases per m<sup>2</sup> BSA were not due simply to increasing surface area of macrophytes.

*Sida crystallina*, a cladoceran, was found at extremely high densities for part of the summer. *Sida* reached a peak abundance of  $21.9 \times 10^3/\text{m}^2$  BSA on 29 June; from 8 June to 13 August it averaged  $4.5 \times 10^3/\text{m}^2$  BSA. On 18 and 29 June, *Sida* represented 82.6 and 72.0%, respectively, of the total number of invertebrates on water-chestnut. Later in the summer *Sida* decreased sharply, and on 31 July and 13 August it represented only 8.5 and 0.8%, respectively. It is probable that many *Sida* went through the 0.5-mm sieve, so our estimates of *Sida* abundance were almost certainly too low.

*Cricotopus* was the most common chironomid on water-chestnut throughout most of the summer, reaching a peak density of  $5.0 \times 10^3/\text{m}^2$  BSA (73% of the total chironomids) on 6 July. After this date, *Polypedilum* became abundant, representing over 50% of the chironomids collected in late July. *Ablabesmyia* was first collected at roughly the same time that *Polypedilum* was increasing, and gradually increased in

abundance until on 13 August it was dominant and represented 43% of the chironomids. On 13 August, 41% of the chironomids collected were too small to be identified.

#### *Chironomid emergence*

Emergence rate ranged from 1.9 chironomids  $\text{m}^{-2} \text{d}^{-1}$  to a high of  $21.0 \text{m}^{-2} \text{d}^{-1}$  (Fig. 7). Emergence rates were variable through June and July and had declined by August. While the emergence traps were in the bay, 18 June to 20 August, we estimated a total emergence of  $454 \pm 132$  (mean  $\pm$  SE,  $n = 3$ ) chironomids/m<sup>2</sup>. These numbers are probably underestimates of emergence rate; some insects, including midges, were collected by hand from the mesh inside the trap, but it is possible that some emerging insects were lost. It is unknown to what degree this affected the emergence estimate.

#### Discussion

Tidal wetlands have high rates of primary production (Whigham et al. 1978, Brinson et al. 1981), but it is not yet clear that secondary production is correspondingly high. Densities of benthic organisms found in this study were within the range reported in other studies of soft sediments from lakes, rivers, and other wetlands (e.g., Gerking 1957, Good et al. 1975, Diaz et al. 1978, Simpson et al. 1986).

Comparing our epiphytic invertebrate densities with literature data is complicated by the variety of mesh sizes and normalizing units employed. Epiphytic invertebrate numbers may be per g of macrophyte, per m<sup>2</sup> of plant surface area, or per m<sup>2</sup> of bottom surface area. The simplest comparison is per g of macrophyte, although this ignores potential effects of plant architecture (see Brown et al. 1988, Cyr and Downing 1988). The mean number of invertebrates on water-chestnut from our study (94 individuals/g DM) was in the same range as other epiphytic invertebrate densities collected with a 0.4–0.5-mm mesh (e.g., 114/g DM [Gerking 1957], 223/g DM [Soszka 1975]). These comparisons suggest that invertebrate densities in the sediments and on macrophytes in Tivoli South Bay were not particularly high, despite the apparently abundant food resources.

Chironomid taxa composition in the sedi-

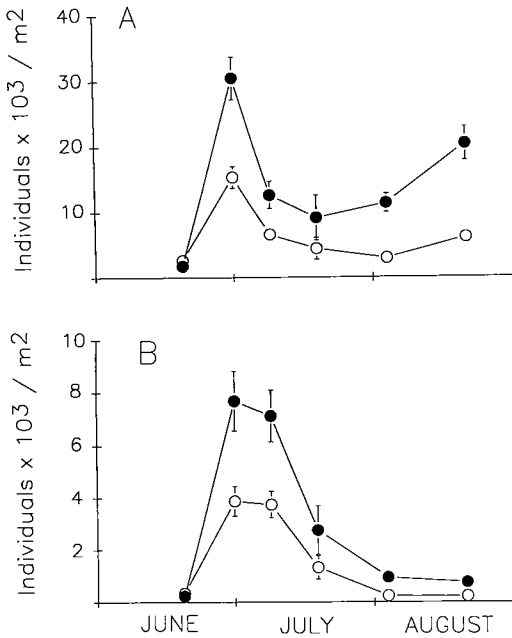


FIG. 6. Density of total invertebrates (A) and chironomids (B) on water-chestnut in 1987. Each point is the mean of 5 rosettes ( $\pm 1$  SE). BSA (●) is number of organisms per  $m^2$  of bottom surface area; LSA (○) is number of organisms per  $m^2$  of leaf surface area.

ment was similar to that found by Menzie (1980), who found mostly *Chironomus* and *Tanytarsus* in the sediments of Bowline Pond in Haverstraw Bay of the lower Hudson River. *Tanytarsus* was clearly dominant in the Tivoli South Bay sediment; however, *Chironomus* was not common. Similarly, *Cricotopus* was the most common genus on *Myriophyllum* in Haverstraw Bay (Menzie 1980) and *Cricotopus* was also the most common genus on water-chestnut in Tivoli South Bay. In a detailed study of oligochaetes on water-chestnut, Juget (1976) reported a taxonomic composition and range in densities ( $7.2 \times 10^3$  to  $5.4 \times 10^4$  individuals/ $m^2$  LSA) similar to our results for Tivoli South Bay.

For most of the summer, the abundance of epiphytic invertebrates was greater than the abundance of benthic invertebrates (Figs. 3, 6), showing the importance of macrophytes as habitats in this wetland. Benthic invertebrates apparently did not fluctuate in density over the course of this study, whereas epiphytic invertebrates, particularly chironomids, showed large changes in abundance.

The mid-summer decrease in population den-

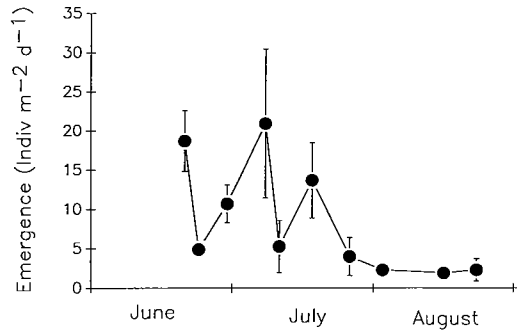


FIG. 7. Emergence rate of chironomids collected in floating emergence traps in 1987. Each point is the mean of three traps ( $\pm 1$  SE).

sities of chironomids on the tiles in 1986 and in the water-chestnut samples in 1987 suggests that these organisms are being removed by unknown processes. Several possible explanations include emergence, predation, competition, or some change in habitat suitability.

The total decline in epiphytic chironomid abundance during July 1987 was over 6900 individuals/ $m^2$  (Fig. 6B). The cumulative emergence from 18 June to 20 August was only  $454 \pm 132$  individuals/ $m^2$ , apparently leaving much of the decrease in abundance to be explained by other factors. The efficiency of emergence traps is uncertain and we must consider the possibility that our traps badly underestimated the number of emerging chironomids. The absolute trapping efficiency is impossible to determine but the common approach has been to compare the decline in abundance of larvae with the capture of adults (Davies 1984). This approach underestimates the efficiency because it is not certain that all larvae that disappeared had actually emerged. Davies (1984) reviewed the trap efficiency of a variety of funnel traps and reported a range from 2 to 343%. The average (excluding values  $>100\%$  and using the mid-point when a range was reported) was 37.3% ( $\pm 5.6$  SE,  $n = 25$ ). Floating traps (as used in this study) usually give greater captures than the submerged traps used to calculate the average efficiency. The efficiency of our traps would have had to be less than 6.5% to explain the discrepancy between disappearance of larvae and emergence. While we cannot rule out the possibility that our trap efficiency was that low, we feel that the discrepancy is large enough for us to consider alternative explanations for the decline in chironomid abundance.



It is feasible that the decline in chironomid abundance in Tivoli South Bay could be related to the arrival of juvenile fishes. Midge larvae constitute perhaps 60% of the diet of younger (30–40 mm) *Fundulus diaphanus* (Keast and Webb 1966). Data obtained from Tivoli North Bay show that chironomid larvae make up a significant part of the diet of *Fundulus* and tessellated darters (*Etheostoma olmstedi atramaculatum*) (Duryea and Schmidt 1986, Richard and Schmidt 1986). We do not have quantitative data on fish abundance in Tivoli South Bay, so we cannot say whether numbers were high enough that fish predation could explain the decline in chironomids.

Invertebrate predators such as damselfly naiads (Menzie 1981) or even some predaceous chironomid larvae (Coffman and Ferrington 1984) may contribute to the decline. Early in the summer when chironomid numbers were high, *Cricotopus*, a collector-gatherer/filter-feeder (Merritt and Cummins 1984), was by far the dominant chironomid on water-chestnut. Gradually the taxonomic composition changed, first to dominance by *Polypedilum* and then to dominance by *Ablabesmyia*. *Ablabesmyia* is a known predator (Simpson and Bode 1980, Merritt and Cummins 1984) and some species of *Polypedilum* are predators (Merritt and Cummins 1984). Therefore, trophic structure shifted among chironomids towards a predator-dominated community. Perhaps predation by *Ablabesmyia* and *Polypedilum* reduced the *Cricotopus* population and the overall chironomid density. Damselfly naiads were not common in our samples but have been shown to be significant consumers of chironomids in Haverstraw Bay (Menzie 1981).

The decline in chironomid abundance on water-chestnut in the later samples could also be caused by thick growths of this plant in mid-summer. The plants became so crowded together that they forced many of the leaves and stems out of the water so that only the lower petioles and main stems were underwater. Early in the summer the rosettes were smaller and less densely packed, so the leaves lay flat on the water surface and the petioles remained underwater. Therefore, the leaf area available as invertebrate habitat might have declined in late summer. The fact that oligochaete densities increased throughout this study makes it unlikely that lack of surface area was responsible for the decline in chironomids.

In summary, the macroinvertebrate fauna of this wetland was abundant and relatively simple in taxonomic composition. Macrophytes were more important than sediments as invertebrate habitat for much of the summer, owing to the high densities of animals per leaf area and the high leaf area per bottom area. The dynamics of the epiphytic chironomids suggested that some processes other than emergence were responsible for a mid-summer decline in numbers; predation by fishes or by invertebrates was an equally feasible explanation.

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