

Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small prairie-margin stream

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Summary. *Campostoma anomalum* is an algae-grazing minnow, abundant in many streams of the central and eastern United States. In a small stream in south-central Oklahoma, *Campostoma* has a marked impact on standing crops of attached algae. Pools with schools of *Campostoma* are barren, while pools in which *Campostoma* are apparently excluded by bass (*Micropterus salmoides* or *M. punctulatus*) support large standing crops of filamentous green algae (predominantly *Spirogyra* sp. and *Rhizoclonium* sp.). *Campostoma* grazed actively on algae-covered cobbles transferred into their pools, and visibly reduced standing crops within one hour. After 24 h of exposure to *Campostoma*, standing crops of attached algae on cobbles were reduced from 22.0 to 6.3 mg ash-free dry weight cm^{-2} . When a largemouth bass was tethered in a pool with *Campostoma*, the minnows did not graze on algae-covered cobbles within 30–50 cm of the bass, but fed actively on cobbles that were more than 1.3 m away. These results indicate that interactions of *Campostoma* and their predators may be an important factor contributing to pool-to-pool variation in attached algae in small streams of the central and eastern United States.

Introduction

At low flow, Brier Creek, a prairie-margin stream in south-central Oklahoma, has two distinctly different types of pools. Some are barren, with bedrock and gravel substrates bare or thinly mantled with detritus. Other pools have luxuriant standing crops of filamentous green algae. This algae offers cover for a variety of fishes and invertebrates. For example, we observed snails (*Physa* sp.) on floating tops of attached green algal clumps, microhabitats which afforded them food as well as protection from predatory fishes.

Barren pools contain schools of *Campostoma anomalum* (Rafinesque), a minnow that is widespread and abundant in streams throughout the central and eastern United States (Burr 1980; Pflieger 1975). *Campostoma* is almost completely algivorous, with diatoms and filamentous algae comprising over 95% of the gut contents (Kraatz 1923). These minnows are eaten by bass (*Micropterus* spp.) (Scalet 1977; Funk and Fleener 1974; Lennon and Parker 1960; Gunning

and Lewis 1956). Here, we present data suggesting that the interactions of bass and *Campostoma* have major impacts on standing crops of attached algae in a small stream during periods of low flow, and may thereby exert important direct and indirect effects on other stream biota.

Study site

Brier Creek, in Marshall County, Oklahoma USA (34°0'N, 97°2'W), is a clear stream which flows over limestone bedrock and gravel, in a tree-lined channel cutting through pastureland. This stream has been described by Smith and Powell (1970). Our research was conducted in a 1 km reach which includes fourteen pools and twelve riffles (Fig. 1), and corresponds to Section 5 of Smith and Powell (1971). The study was carried out during November 1982, a period of low stream discharge ($0.012 \text{ m}^3 \text{ sec}^{-1}$). All pools in our study reach remained connected at this flow. This reach of Brier Creek has remained free-flowing throughout the year during all but one of the last twelve years (Smith and Powell 1970; Ross, Matthews and Echelle, in preparation). Minimum depths of thalwegs (the deepest part of the channel cross-section) of riffles between pools are shown in Fig. 1, and listed in Table 1 along with other physical attributes of the reach.

Field observations

Methods

We mapped the 1 km reach, measuring the maximum depth at five to ten positions in each pool and at two in each riffle. On 8 November and 19 November, we performed censuses in all pools. One observer snorkelled slowly upstream, spending 10–20 min underwater in each pool, recording the species, numbers and approximate sizes of all fish encountered. A second observer on the bank watched during the census to count any fish that escaped detection by the underwater observer. Pools were narrow and clear, so that few fish, even small individuals, escaped observation. On only one occasion did the observer on the bank note a fish (a bass) that the underwater observer failed to see.

We described algal standing crops in pools qualitatively and quantitatively in three ways. In all fourteen pools, we measured the height of benthic algae at sampling sites which were located at 1.0 or 0.5-m intervals along five cross-

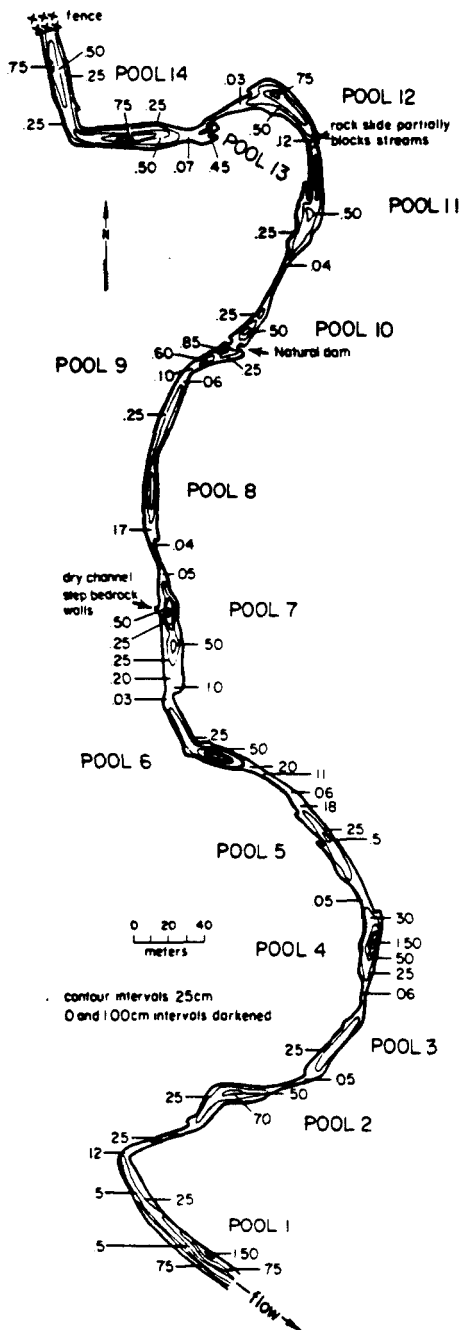


Fig. 1. Map, drawn to scale, of 1 km study reach in Brier Creek

stream transects spaced evenly along each pool. We noted the predominant material at each site (usually *Chara*, filamentous green algae (predominantly *Spirogyra* and *Rhizoclonium*), or loose deposits of detritus), and scored condition of the algae from 0 to 5 (0 = very senescent, 5 = very fresh). In six pools, we collected samples by scraping 2-cm² areas of substrate with a scalpel and aspirating detached material underwater. Samples were collected in small plastic containers and refrigerated for 3–5 days. Subsequently, samples were shaken, and drops were collected for microscopic examination. Sample composition was quantified under 400 \times , using a Whipple grid and the method of Jones (1968). Four fields were counted per sample, and 100 points (grid intersections) were examined per field. When the grid

Table 1. Physical characteristics of fourteen pools in a 1 km reach of Brier Creek, Marshall County, Oklahoma

| Pool | | | | Riffle | | |
|------|---------------|----------------------|----------------------|--------|----------------|------------------------------------|
| | Length (m) | Max. width (m) | Max. depth (m) | | Length (m) | Minimum thalweg depth (m) |
| 1)* | 100 | 8 | 1.50 | | | |
| 2) | 49 | 8 | 0.70 | 1-2 | 43 | 0.12 |
| 3) | 49 | 6 | 0.45 | 2-3 | 20 | 0.05 |
| 4) | 39 | 8 | 1.25 | 3-4 | 12.4 | 0.06 |
| 5) | 57.6 | 6.5 | 0.50 | 4-5 | 17.2 | 0.05 |
| 6) | 59.1 | 7 | 1.25 | 5-6 | 39 | 0.06 |
| 7) | 58 | 9 | 1.00 | 6-7 | 2 | 0.03 |
| 8) | 88 | 6.5 | 0.60 | 7-8 | 26 | 0.05 |
| 9) | 22 | 5.5 | 0.80 | 8-9 | 9 | 0.06 |
| 10) | 21 | 4.5 | 0.50 | 9-10 | 2 ^b | 0.02 |
| 11) | 74.9 | 10 | 0.60 | 10-11 | 29 | 0.04 |
| 12) | 43 | 9 | 0.75 | 11-12 | 11.3 | 0.04 |
| 13) | 6.4 | 2 | 0.45 | 12-13 | 15 | 0.12 |
| 14) | 120 | 9 | 1.00 | 13-14 | 5.3 | 0.07 |

* Pool 1 is the most downstream (Fig. 1)

^b Pools 9 and 10 are also separated by a 38 cm high natural water-fall

intersection touched an alga or an animal, it was scored. Mineral particles, detritus and empty space were not scored. The following eight categories sufficed to describe all other material encountered: full and empty diatoms, full and empty green algal filaments, full and empty blue-green algae, full unicellular green algae and animals. After examination, material on slides was rinsed back into appropriate containers with distilled water, and the entire sample was filtered onto tared Whatmen No. 1 filter paper, dried 24 h at 70° C and combusted for 3–3.5 h at 510° C for determination of ash-free dry weight.

Results

Distributions of *Campostoma* and large (> 70 mm SL) bass among pools showed significant complementarity ($P < 0.025$ and $P < 0.05$ (Fisher's exact test) on 8 November and 19 November, respectively). Counts of *Campostoma* in given pools were similar on the two census dates ($r^2 = 0.91$, $P < 0.001$). Numbers of bass per pool varied more between the two dates ($r^2 = 0.50$, $P < 0.10$) but in only one case (Pool 5) was a pool found with bass on one date but not the other (Table 2).

Pools in which bass longer than 70 mm SL occurred and *Campostoma* were absent ("bass pools") had lush standing crops of filamentous green algae (predominantly *Spirogyra* sp. and *Rhizoclonium* sp.) and beds of *Chara* spp. heavily covered with epiphytes. In pools where *Campostoma* schools occurred and bass were absent ("Campostoma pools") filamentous green algae were visible only along the margins, in depths of no more than 15 and usually less than 3 cm. *Chara*, where it occurred in *Campostoma* pools, was stripped of epiphytes and many of its branches. The bedrock and gravel substrates in *Campostoma* pools were bare or thinly mantled with fine detritus. Figure 2 shows the thickness of algal mats or detritus deposits in nine bass and four *Campostoma* pools at various depths. Table 3 sum-

Table 2. Numbers of bass longer than 70 mm SL and of *Campostoma* counted in fourteen pools of Brier Creek, and the abundance of filamentous green algae (– = scant or absent, + = abundant)

| Pool | 8 November 1982 | | | 19 November 1982 | | |
|------|-----------------|-------------|--------------------|--------------------------|-------------|--------------------|
| | Bass | Cam-postoma | Fila-mentous algae | Bass | Cam-postoma | Fila-mentous algae |
| 1 | 6 | 0 | + | 4 | 0 | + |
| 2 | 3 | 0 | + | 4 | 0 | + |
| 3 | 0 | 400 | – | 0 | 300 | – |
| 4 | 3 | 0 | + | 6 | 0 | + |
| 5 | 0 | 300 | – | 5 | 200 | + |
| 6 | 4 | 0 | + | 7 | 0 | + |
| 7 | 8 | 200 | +/- | 7 | 200 | +/- |
| 8 | 3 | 0 | + | 2 | 0 | + |
| 9 | 4 | 0 | + | 4 | 0 | + |
| 10 | 0 | 340 | – | 0 | 350 | – |
| 11 | 7 | 0 | + | 7 | 0 | + |
| 12 | 3 | 0 | + | omitted due to turbidity | | |
| 13 | 0 | 70 | – | 0 | 50 | – |
| 14 | 5 | 0 | + | 3 | 0 | + |

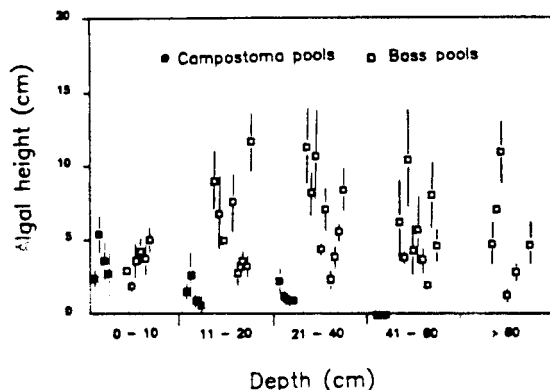


Fig. 2. Height of attached algae ($\bar{x} \pm 1$ S.E.) at sites along cross-stream transects in four *Campostoma* and nine bass pools. Data are grouped into depth intervals. Heights of attached algae are significantly greater in bass pools than *Campostoma* pools at depths of 11–20 cm, 21–40 cm and 41–60 cm (P 's from Mann-Whitney U tests < 0.002, 0.01 and 0.006, respectively)

Table 3. Percent of sites* sampled in fourteen pools where the following predominated

| | Bare rock | Detritus | Chara | Fila-mentous algae |
|---|-----------|----------|-------|--------------------|
| Bass pools (1, 2, 4, 6, 7, 8, 9, 11, 12, 14) | 0 | 9 | 30 | 61 |
| <i>Campostoma</i> pools (3, 5, 10, 13) | 11 | 56 | 9 | 23 |

* Number of sites in Bass Pools: 273; in *Campostoma* Pools: 87

marizes data on the macroscopic appearance of algae described at sites along 60 cross-stream transects in fourteen pools. There was a higher proportion of bare rock and detritus in *Campostoma* pools, while *Chara* and filamentous green algae were proportionately more abundant in bass

Table 4. Composition of algal samples collected in three bass and three *Campostoma* pools

| | Mean proportion (\pm S.E.) | |
|-------------------------|-------------------------------|-------------------------|
| | Bass pools | <i>Campostoma</i> pools |
| Diatoms | | |
| Full | 0.42 \pm 0.12 | 0.14 \pm 0.05 |
| Empty | 0.10 \pm 0.02 | 0.37 \pm 0.06 |
| Filamentous green algae | | |
| Full | 0.39 \pm 0.14 | 0.10 \pm 0.07 |
| Empty | 0.01 \pm 0.01 | 0.20 \pm 0.08 |
| Blue-green algae | | |
| Full | 0.05 \pm 0.02 | 0.09 \pm 0.07 |
| Empty | 0.03 \pm 0.01 | 0.10 \pm 0.06 |

pools ($P < 0.001$ from t -tests on arcsin-transformed data (Sokal and Rohlf 1969) for all four comparisons).

Results from microscopic examinations of samples from three bass and three *Campostoma* pools are summarized in Table 4. Diatoms and filamentous green algae with intact cell contents occurred in significantly higher proportions in bass pools, while empty cells of both types were proportionately more abundant in *Campostoma* pools ($P < 0.001$ for all four comparisons from t -tests on arcsin-transformed proportions). Blue-green algae (*Oscillatoria* sp.) made up a smaller proportion of algae in both types of pools (Table 4), and both intact and empty blue-green filaments were proportionately more abundant in *Campostoma* pools ($P < 0.01$ and $P < 0.001$, respectively). Unicellular green algae and microscopic animals each comprised less than 1% of 539 and 806 points scored in bass and *Campostoma* pools, respectively.

Experimental studies of bass-*Campostoma*-algae interactions

To test the hypotheses that grazing by *Campostoma* affected pool-to-pool occurrence of filamentous green algal mats, and that bass influenced *Campostoma* grazing on these algae, we conducted two experiments. In the first, nine cobbles and one log, covered with thick mats of filamentous green algae, were transferred from Pool 9 (a bass pool) to the next pool upstream, Pool 10 (a *Campostoma* pool). The two pools were separated by a rock ledge 38 cm high. The minimum thalweg depth in the riffle between Pools 9 and 10 was only 2 cm, over the lip of this ledge. Before cobbles and the log from Pool 9 were placed in Pool 10, their standing crops of attached algae were sampled by scraping and aspirating material from 1–2 cm² areas on each. Two bare cobbles were also moved within Pool 10 to serve as controls for "novelty effects" that might attract minnows to any displaced rock. The log and eleven cobbles were placed in a single row, parallel to the banks of the pool. The two control cobbles were in the first and fourth positions from the downstream end. All cobbles were located within an area where *Campostoma* had formerly been seen, in water 20–50 cm deep. For 30 min after the cobbles were positioned, two observers on the bank scanned the downstream seven cobbles at 2-min intervals, recording the number of *Campostoma* actively feeding on each.

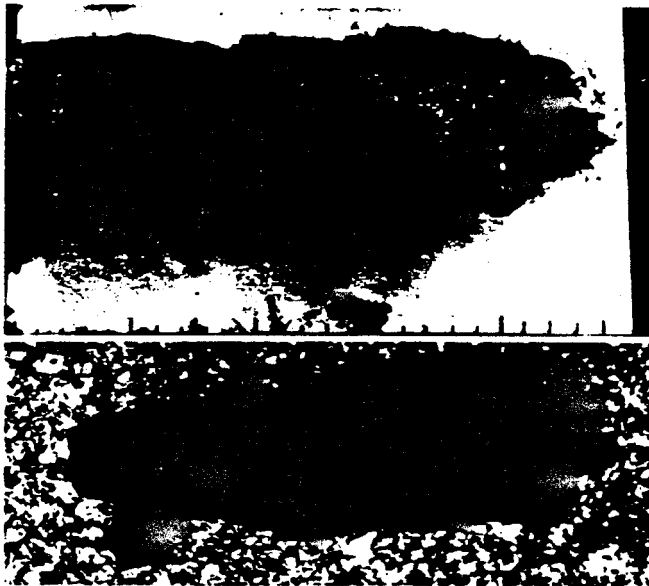


Fig. 3. Attached filamentous algae on a submerged log before and 1 h after it was transferred into a pool with *Campostoma*

Table 5. Average numbers of *Campostoma* feeding on transferred cobbles and controls (cobbles 1 and 4). N = 24 scans for all cobbles

| Cobble | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|-----------|-----|-----|-----|-----|-----|-----|------|
| \bar{x} | 0.0 | 7.5 | 7.3 | 0.0 | 5.4 | 6.4 | 14.5 |
| S.E. | 0.0 | 0.6 | 0.4 | 0.0 | 0.2 | 0.5 | 0.8 |

Campostoma fed actively on algae on the transferred cobbles and log within 10 min after they had been placed in Pool 10. Control cobbles were virtually never visited (Table 5). Figure 3 shows the transferred log just before and 1 h after it was exposed to *Campostoma* grazing. Standing crops of attached algae ($\bar{x} \pm \text{S.E.}$) decreased from 22.0 ± 0.3 to 6.3 ± 2.7 mg ash-free dry weight cm^{-2} after 24 h of *Campostoma* grazing. Standing crops of algae on control cobbles were not measurable before or after the experiments.

In a second experiment, conducted 7 days after the first, cobbles with attached algae were again transferred from Pool 9 to Pool 10, but placed in two groups of four. Each cobble was 20–30 cm from the others in its group, and the groups were 1.3 m apart. The eight cobbles were scanned by one observer at 5-min intervals for 25 min. Then a large-mouth bass, 300 mm SL, was introduced into Pool 10. The bass was tethered to a cobble on the streambed by a 0.8 m nylon line fastened through the fish's lower jaw. This cobble was placed in the center of the upstream group of transferred cobbles. The bass lunged once upon being placed in the pool, and afterwards, hovered quietly in mid-water. After the bass was in position, the numbers of minnows grazing on the eight cobbles was again recorded during 5 scan samples made at 5-min intervals. The bass and the eight cobbles were left in the pool for 72 h, after which the bass was removed and standing crops of attached algae were sampled from the eight cobbles.

Campostoma fed actively on attached algae on the eight transferred cobbles before the introduction of the bass. More fish visited the upstream group than the downstream

Table 6. Numbers of *Campostoma* feeding on algae-covered cobbles transferred into their pool, before and after the introduction of a tethered bass

| Time | Cobble | | | | | | | |
|-------|----------------------------------|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 16:00 | cobbles 1–8 introduced into pool | | | | | | | |
| 16:15 | 1 | 1 | 2 | 3 | 2 | 6 | 6 | 2 |
| 16:20 | 1 | 1 | 2 | 3 | 4 | 1 | 1 | 2 |
| 16:25 | 2 | 1 | 4 | 3 | 4 | 2 | 4 | 5 |
| 16:30 | 3 | 2 | 2 | 6 | 8 | 1 | 7 | 5 |
| 16:35 | 5 | 2 | 1 | 6 | 6 | 2 | 6 | 5 |
| 16:37 | bass tethered near cobbles 5–8 | | | | | | | |
| 16:40 | 4 | 5 | 2 | 4 | 0 | 0 | 0 | 0 |
| 16:45 | 5 | 3 | 4 | 2 | 0 | 0 | 0 | 0 |
| 16:50 | 5 | 4 | 6 | 5 | 0 | 0 | 0 | 0 |
| 16:55 | 5 | 3 | 4 | 6 | 0 | 0 | 0 | 0 |
| 17:00 | 7 | 5 | 6 | 7 | 0 | 0 | 0 | 0 |

group (Table 6). When we introduced the bass, all *Campostoma* initially stopped grazing. Within three min of the introduction, however, *Campostoma* resumed grazing the downstream group of cobbles. Upstream cobbles were no longer visited by *Campostoma* after the bass was tethered near the center of this group (Table 6). *Campostoma* sometimes swam toward the "guarded" cobbles, but veered sharply away when within 50 cm of the bass.

By the third day, the bass had assumed an acentric position near three of the transferred cobbles, but more than 50 cm away from the fourth. We observed sporadic grazing by *Campostoma* on this fourth cobble. Individuals would dart in for several bites and then leave. Standing crops of algae on the four guarded cobbles were 15.2 ± 3.3 mg cm^{-2} . On the three guarded, ungrazed cobbles they averaged 17.9 ± 2.6 mg cm^{-2} , while standing crops on cobbles 1.3 m away were 5.2 ± 0.7 , not significantly different from cobbles exposed to 24 h of grazing in the first experiment. The difference in standing crops of the four guarded and four unguarded cobbles after 72 h was significant ($P = 0.03$, Mann-Whitney U test).

Discussion

Certain grazers of attached algae exert strong effects on aquatic communities (Paine 1980; Lubchenko and Gaines 1981; Vine 1974; Hay 1981; Kesler 1981; Hunter 1980). When densities of such grazers change, changes ensue not only in the food available to other grazers, but also in the physical structure of the environment. For example, if sea urchin densities fluctuate due to experimental manipulations or changes in the abundances of their predators, strong effects on kelp bed communities follow (Paine and Vadas 1969; Mann and Breen 1972; Estes and Palmisano 1974; Duggins 1980).

Similarly, *Campostoma* schools can quickly reduce standing crops of filamentous green algae. In Brier Creek, this algae provides much of the cover in stream pools, a factor of great importance to fish and invertebrates in small freshwater habitats (Crowder and Cooper 1979; Werner et al. 1977). At low flow in Brier Creek, *Campostoma* was usually not present in pools where bass longer than 70 mm

SL occurred. (Largemouth bass become totally piscivorous when they are 80–100 mm long (Keast 1970; Clady 1974; Kramer and Smith 1962). Where large bass and *Campostoma* did co-occur in Brier Creek (Pool 7 and 8 November and Pools 5 and 7 on 19 November), they were spatially segregated, with bass in deeper areas and *Campostoma* in shallower areas of the pool. Barren areas and standing crops of filamentous green algae were correspondingly located in shallower and deeper regions of the pool, respectively.

Two different processes may account for the complementary distributions of *Campostoma* and bass in Brier Creek. Bass predation may eliminate these minnows from pools in which both species originally co-occur. Alternatively, *Campostoma* may actively avoid bass by selecting pools in which bass are absent. Fraser and Cerri (1982) found that avoidance of piscivorous fish by the minnows *Semotilus* and *Rhinichthys* affected their distribution among compartments in an artificial stream. Our results from the experimental introduction of a tethered bass indicate that *Campostoma* avoid bass over short distances, but do not indicate whether this behavior plays a role in their habitat selection.

However the bass-*Campostoma* complementarity arises, it explains a conspicuous pattern of pool-to-pool variation in the quantity and quality of attached algae in Brier Creek. *Campostoma* are widespread throughout the central and eastern United States (Burr 1980) and in some streams, outweigh and outnumber all other species of fishes combined (Lennon and Parker 1960; Beets 1979). Therefore, the interaction described here may be an important factor producing spatial variation in attached algae in many North American streams.

Acknowledgments. We would like to thank Art Stewart for discussion and help with algal identifications, and Ray Drenner and Bill Dietrich for comments on the manuscript. The University of Oklahoma Biological Station and the University of Oklahoma Department of Zoology Visiting Faculty Program provided logistical and financial support for this research.

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Received March 22, 1983

