

Natural Control of *Culex quinquefasciatus* Larvae in Residential Ditches by the Copepod *Macrocyclus albidus*

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ABSTRACT: Natural populations of three larvivoracious copepod species live in residential roadside ditches in Louisiana: *Macrocyclus albidus*, *Acanthocyclops vernalis*, and *Megacyclus latipes*. *Macrocyclus* is most common and killed an average of 27 first-instar *Culex quinquefasciatus* larvae/copepod/day in the laboratory. Although severe pollution from septic tank effluent in some parts of the ditches creates havens for *Cx. quinquefasciatus* production by excluding predatory copepods and fish (*Gambusia affinis*), *Macrocyclus* and the fish substantially reduce *Cx. quinquefasciatus* larval survival when present where pollution is not so severe. At natural abundance, *Macrocyclus* reduced the survival of *Cx. quinquefasciatus* larvae (during their first four days) to 2.6%, compared with 46% survival in controls without *Macrocyclus*. During one year of field observation, *Macrocyclus* was common in the spring but disappeared during the summer when fish (which prey on copepods) appeared in many ditches, reduced water flows led to more severe pollution, and water temperatures in very shallow water were sometimes higher than *Macrocyclus* could survive. *Macrocyclus* reappeared in many ditches during autumn and winter, when water temperatures and pollution declined and fish disappeared. Introduction of *Macrocyclus* to ditches in October accelerated its reappearance during autumn and winter and reduced the number of sites with *Cx. quinquefasciatus* larvae to one-quarter the number in control ditches. The most effective way to control *Cx. quinquefasciatus* is to eliminate pollution so predators like fish and copepods can live throughout the ditches, but timely introduction of fish and copepods could also contribute to control. More experience will be necessary to ascertain whether copepod introductions are cost effective.

Keyword Index: Copepod, mosquito larvae, mosquito control, biological control, *Culex*, predation.

INTRODUCTION

Roadside drainage ditches in residential areas can be a major breeding habitat for *Culex quinquefasciatus* Say, particularly where effluent from septic tanks empties into the ditches. The pollution generates an abundant supply of bacterial food for *Cx. quinquefasciatus* larvae, but impacts of the pollution on predators of the larvae may also influence mosquito production.

Cyclopoid copepods are known to provide effective natural control of *Aedes* larvae in water storage containers and rain-fed tires (Marten et al. 1994, Nam et al. 1998). However, the relation of cyclopoids to mosquito larvae in other aquatic habitats has only begun to be explored

(Marten et al. 1989, Marten et al. 1994). Louisiana is known to have at least 34 species of cyclopoids that might live where mosquitoes breed (Reid and Marten 1995). We investigated the ecological interaction of natural cyclopoid populations with *Cx. quinquefasciatus* larvae in residential ditches polluted by septic tank effluent.

MATERIALS AND METHODS

Field Survey

The approximately 100 km of roadside ditches in Slidell, a small city in Louisiana, were sampled for cyclopoid copepods at random locations throughout the

year—a total of 300 samples, each sample consisting of 25 dips with a conventional dipper for mosquito larvae. *Macrocyclus albidus* (Jurine) collected from ditches were established in laboratory culture to supply animals for the predation experiments and *Macrocyclus* field introductions described below. Culture methods followed Marten et al. (1997), a system based on wheat seed, *Chilomonas*, and *Paramecium caudatum*, similar to the copepod production system described by Suárez et al. (1992).

Laboratory Predation Experiments

The capacity of *Macrocyclus albidus*, *Acanthocyclops vernalis* (Fischer), and *Megacyclus latipes* (Lowndes) to kill *Cx. quinquefasciatus* larvae was evaluated in the laboratory. Single adult female copepods were placed in tissue culture plate wells (35 mm diameter, 18 mm deep) with ditch water. Fifty newly hatched *Cx. quinquefasciatus* larvae were placed in each well with a small quantity of yeast to ensure food for the larvae. The number of surviving larvae was counted after 24 hours at a temperature of 24°-26°C. Control wells contained larvae and yeast but no copepods.

Field Predation Experiments

In September 1990, eight cylindrical sheet-metal enclosures (90 cm diameter, 60 cm high) were placed in residential roadside ditches by imbedding the bottom 15 cm of each cylinder in the mud. The water in the enclosures was 10-15 cm deep and contained typical ditch vegetation. Moderate organic pollution was apparent, and natural food for *Cx. quinquefasciatus* larvae was abundant. *Cx. quinquefasciatus* larvae were common at the sites.

Macrocyclus albidus was introduced to all of the enclosures, which were covered with mosquito netting to prevent mosquito oviposition. Six weeks later, when the *Macrocyclus* populations had increased to several adult copepods per dip, all enclosures were checked with an aquarium net to ensure that they contained no fish or mosquito larvae. Ten *Cx. quinquefasciatus* egg rafts (approximately 2,000 larvae/m²) were placed in four of the enclosures, and 20 egg rafts (4,000 larvae/m²) were placed in each of the other four enclosures. The number of larvae that hatched into each enclosure was estimated from an average of 130 larvae per egg raft observed to hatch in the laboratory. Four days after eclosion, when the larvae had grown too large for copepods to kill, all surviving larvae were removed from each enclosure with a net and counted.

The same experiment was repeated two weeks later in all eight enclosures. At the same time, ten egg rafts and twenty egg rafts, respectively, were placed in two

additional enclosures, which contained no copepods or fish and served as controls.

Bioassays for Pollution

Approximately 150 water samples were collected from different ditch locations to assess toxicity for copepods and fish. The degree of pollution of each water sample was judged subjectively on the basis of physical appearance and smell. *Macrocyclus albidus* was collected from ditches, and ten adults were placed in 300 ml of each water sample for one week of observation in the laboratory. *Gambusia affinis* (Baird and Girard) from the ditches were observed for one week in one-liter water samples from ten moderately to severely polluted ditches. Five *Gambusia* were placed in each sample.

Field Sites

Two residential areas with roadside ditches were selected for a year of observation. The first site consisted of four adjacent dead-end streets on which the houses were nearly continuous. The second site consisted of four adjacent streets with small woodlots between many of the houses. Pollution due to septic tank effluent was conspicuously greater in the ditches at the first site.

Macrocyclus were introduced to two streets at each site to explore the possibility of increasing their presence in the ditches. *Macrocyclus* were introduced to 300 m of ditch on both sides of two streets at the first site in late April 1991. Two other streets served as controls to which *Macrocyclus* was not introduced. *Macrocyclus* were introduced to 500 m of ditch on both sides of two streets at the second site in early May 1991, and they were introduced again to the same two streets in mid-October. Two adjacent streets at the second site served as controls. *Macrocyclus* were applied to both sites using a two-gallon backpack sprayer (SP Systems Survivor) at a rate of 10 adult females per meter of ditch.

Macrocyclus, *Gambusia*, and mosquito larvae were monitored on a biweekly basis at both sites from April 1991 to April 1992. Each side of the four streets at the first site had seven sampling stations at 25 m intervals. Each side of the streets at the second site had ten sampling stations at 30 m intervals during April-June 1991, three sampling stations at 150 m intervals from July to early September, and the same ten sampling stations at 30 m intervals from late September 1991 to April 1992.

The inspection procedure was to make five dips within 5 m of each station, recording the number of *Macrocyclus* and mosquito larvae in the dips. Dips were directed toward spots in the ditch (e.g., vegetation

or conspicuous pollution) that were judged subjectively to be most suitable for *Cx. quinquefasciatus* larvae. The presence or absence of *Gambusia* at the station was assessed visually.

RESULTS

Field Survey

Natural populations of three copepod species large enough to prey on mosquito larvae were found in the ditches. They were *Macrocyclus albidus*, *Acanthocyclops vernalis*, and *Megacyclus latipes*. *Acanthocyclops* and *Megacyclus* appeared in scattered populations, primarily during winter and spring. *Megacyclus* was particularly associated with sites that had pine needles in the ditch.

Macrocyclus albidus was the most common larvivorous copepod in the ditches. It was particularly abundant in the spring but disappeared from many ditches during the summer. *Macrocyclus* started to reappear in the ditches by October or November, spreading through many of them as autumn and winter progressed. Regardless of the season, *Macrocyclus* was seldom observed in the visibly polluted water that was typically within 5 m of septic tank outlets, even in ditches where this copepod was common further from the outlets. Large numbers of *Macrocyclus* were observed only at sites without *Gambusia*.

Laboratory Predation Experiments

All three copepod species killed substantial numbers of *Cx. quinquefasciatus* larvae in the laboratory (TABLE

1). *Macrocyclus albidus* killed the most larvae, and *Acanthocyclops vernalis* killed the least. *Macrocyclus* and *Acanthocyclops* killed fewer *Cx. quinquefasciatus* larvae than Marten (1990) reported for *Aedes albopictus* (Skuse). The difference can be explained by our observation that these copepods made numerous aborted attacks on *Cx. quinquefasciatus* larvae before actually seizing and killing one. In contrast, nearly all attacks on *Aedes* larvae were carried through to completion. As cyclopoid copepods are known to avoid preying on animals much larger than themselves (Roche 1990), it may be that the prominent bristles on *Cx. quinquefasciatus* larvae intimidate the copepods by giving them the impression the larvae are larger than they really are.

Field Predation Experiments

At the time *Cx. quinquefasciatus* egg rafts were placed in the enclosures containing *Macrocyclus*, the number of *Macrocyclus* varied from one to five adults/dip, corresponding to several hundred to several thousand adults in each enclosure. While 46% of the *Cx. quinquefasciatus* larvae were still alive in control enclosures four days after hatching, only 2.6% of the larvae were still alive in enclosures that contained *Macrocyclus* (TABLE 2). The number of mosquitoes that actually emerged was not counted. It is conceivable that the difference in adult mosquito production between enclosures with and without *Macrocyclus* would not be so great because of density dependent survival after the fourth day. Nonetheless, differences in four-day-old larvae should reflect differences in mosquito production

TABLE 1. Predation by three species of cyclopoid copepods on *Culex quinquefasciatus* and *Aedes albopictus* larvae in the laboratory.

Copepod Species	Number of larvae killed per day ¹	
	<i>Culex quinquefasciatus</i>	<i>Aedes albopictus</i> ²
<i>Macrocyclus albidus</i>	26.8 ± 1.8 (38)	44.3 ± 0.7 (72)
<i>Megacyclus latipes</i>	22.1 ± 3.5 (19)	18.3 ± 2.7 (20)
<i>Acanthocyclops vernalis</i>	16.6 ± 2.0 (21)	33.3 ± 2.7 (27)
Controls (no copepod)	0.1 ± 0.1 (14)	0.1 ± 0.1 (13)

¹Average ± SE. Fifty mosquito larvae available to each copepod for 24 hours at 24-26°C. Number of replicates shown in parentheses.

²Source: Marten (1990).

because third/fourth instar larval survival in this food-rich habitat is generally high in the absence of predators.

Bioassays for Pollution

The survival of *Macrocyclus* in water samples from the ditches was associated strongly with pollution from septic tanks. Assessment of survival was unambiguous because all the *Macrocyclus* in a particular sample either died within 1-3 days or were all still alive after a week. *Macrocyclus* died in 93% (N=43) of the samples of visibly polluted water, which always came from within 5 meters of septic outlets. *Macrocyclus* was killed in 52% (N=46) of the less polluted water samples (cleaner in appearance).

Gambusia survived in 6 of the 10 moderately to severely polluted water samples in which it was held for one week. In every case, all the fish survived or they all died. With one exception, *Macrocyclus* survived or died in the same samples as *Gambusia*, the exception being a sample in which *Macrocyclus* died and *Gambusia* survived. *Gambusia* was sometimes (though not often) observed at sampling stations where the water killed *Macrocyclus* when tested in the laboratory.

Pollution from septic tank effluent was particularly visible on one of the streets at the first field site. Water from every station on this street killed *Macrocyclus* in laboratory bioassays during summer, autumn, and winter. Only in the spring, when the ditch was flushed by heavy rainfall, were there stations with water that was not

lethal. Water from 40% of the stations on this street killed *Macrocyclus* when field observations began in April, and water from 50% of the stations killed *Macrocyclus* the following March.

The other three streets at the first field site had a patchwork of polluted and unpolluted water. *Macrocyclus* died in water from 27% of the stations on those streets in April. Pollution was visibly greater during summer, autumn, and winter, when the percentage of stations with water that killed *Macrocyclus* fluctuated between 65% and 75%.

There was no conspicuous pollution at the second site when field observations began in April. *Macrocyclus* and *Gambusia* survived in all water samples taken from the second site at that time. Water from 15% of the stations—always the same stations and the only ones with conspicuous pollution—consistently killed *Macrocyclus* during summer, autumn, and winter.

First Field Site

Macrocyclus and fish were never observed on the most heavily polluted street at the first field site (except a small number of *Macrocyclus* at one end of the street in April). Sixty-two percent of the sampling stations on that street had >50 *Cx. quinquefasciatus* larvae/dip throughout the year. The other stations on that street also had larvae through almost all of the year (except August), though in lower numbers. The following results are based on the other three streets at the first site, where pollution from septic tanks did not completely exclude *Macrocyclus* and *Gambusia*.

Forty percent of the stations on those three streets had natural *Macrocyclus* populations when observations began in April (Fig. 1). Only one station had fish in April. Most stations with *Macrocyclus* had no *Cx. quinquefasciatus* larvae; the average number of larvae at stations with *Macrocyclus* was 1.9 larvae/dip (SE = 0.5, N = 16). Most stations without *Macrocyclus* had large numbers of *Cx. quinquefasciatus* larvae in April. The average for all stations without *Macrocyclus* was 30.8 larvae/dip (SE = 8.0, N = 22).

Gambusia spread through all three streets during May and June, occupying 35% of the sampling stations by early July (Fig. 1). *Macrocyclus* and *Cx. quinquefasciatus* larvae disappeared from each station as soon as *Gambusia* appeared. During July and August, *Gambusia* disappeared from some of the stations it had just invaded and then expanded briefly on one of the streets in early September. *Gambusia* remained at a smaller number of stations on all three streets through autumn and winter (Fig. 1).

Introduction of *Macrocyclus* at the end of April did not increase the subsequent distribution or abundance

TABLE 2. Survival of *Culex quinquefasciatus* larvae in field predation experiments.

Number Introduced ¹	Number of Surviving Larvae ²	
	<i>Macrocyclus</i> Present ³	<i>Macrocyclus</i> Absent ⁴
1300	30 ± 14 (0-99)	614
2600	74 ± 41 (0-290)	1,208

¹Number of larvae estimated to have hatched from egg rafts placed in the enclosures.

²Average number of larvae (±SE) in the 0.64 m² enclosures four days after introducing egg rafts. Range shown in parentheses.

³Eight replicates for 1300 larvae introduced; seven replicates for 2600 larvae introduced.

⁴Controls (one replicate for 1300 larvae and one replicate for 2600 larvae).

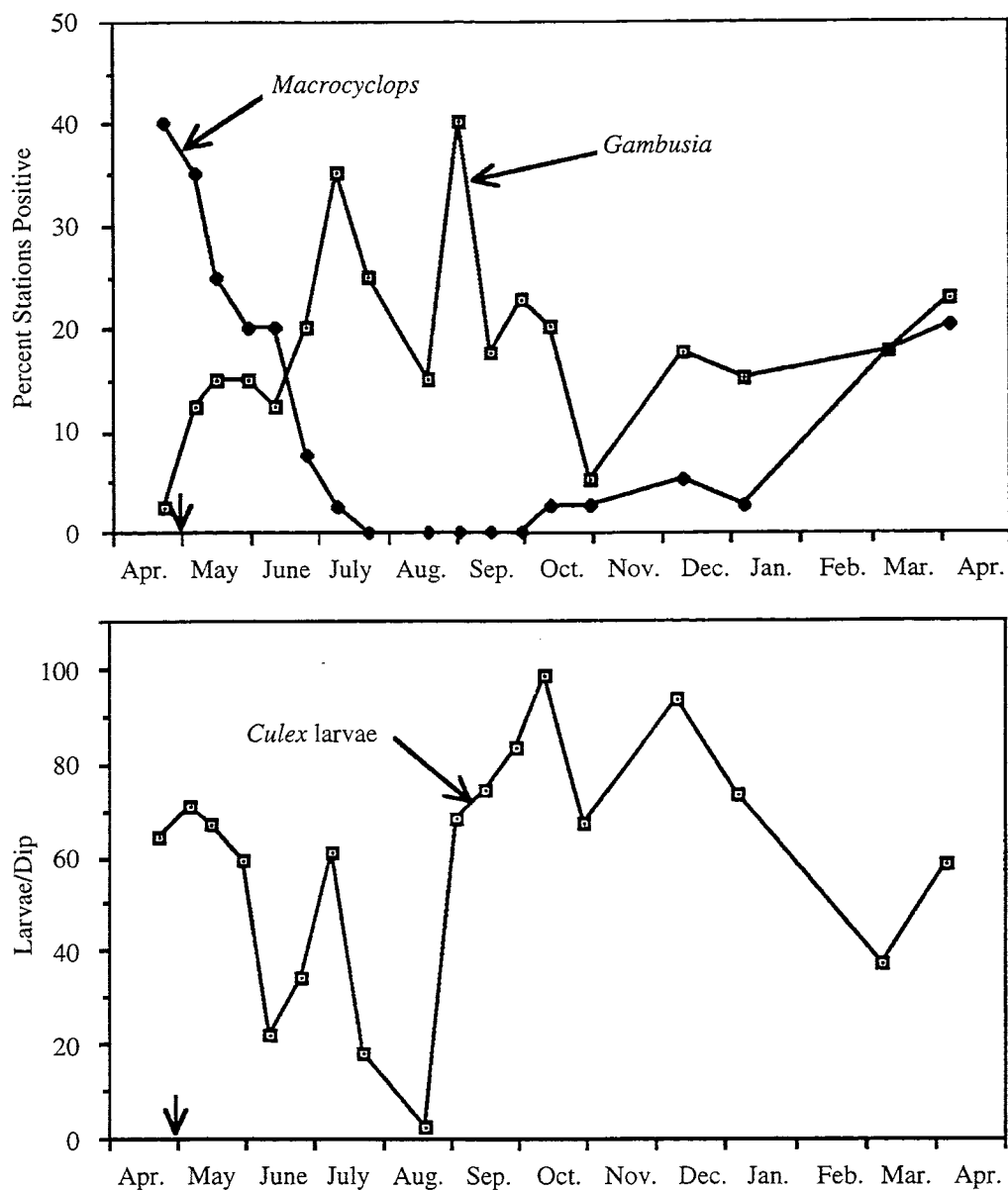


Figure 1. *Macrocyclus albidus*, *Gambusia affinis*, and *Culex quinquefasciatus* larvae in the ditches of three streets at the first site from April 1991 to April 1992. There was a patchwork of severe septic tank pollution on all three streets. The vertical arrow at the end of April indicates the introduction of *Macrocyclus* to two of the streets. Because most stations at this site had *Cx. quinquefasciatus* larvae almost all year, seasonal changes in larval abundance are best seen as average larvae/dip.

of *Macrocyclus* on the treated streets. *Macrocyclus* disappeared from all stations on both treatment and control streets by July (Fig. 1). A few *Macrocyclus* were observed during November to February. They reappeared in large numbers on one of the streets starting in March, occupying 36% of the stations on that street when observations terminated at the beginning of April.

Stations that had large numbers of *Cx. quinquefasciatus* larvae when observations started in April continued to have large numbers during summer, autumn, and winter if *Gambusia* was not present. The larval population at these stations dropped to zero in August when polluted parts of the ditches dried up. At the less polluted stations, which had *Macrocyclus* and

few *Cx. quinquefasciatus* larvae when observations began in April, there were no larvae during the summer, when *Gambusia* occupied nearly all these stations. The less polluted stations had small numbers of larvae on an intermittent basis during autumn and winter.

Second Field Site

There was a conspicuous negative association between the presence of *Gambusia* and the presence of *Cx. quinquefasciatus* larvae at the second site. Over the entire year of observation, *Cx. quinquefasciatus* larvae were present in 12.4% of the inspections at stations with neither *Gambusia* nor *Macrocyclus* (SE = 2.0%, N = 275, range at positive stations: 1-100 larvae/dip). In contrast, *Cx. quinquefasciatus* larvae were observed in only 1.5% of the inspections at stations where *Gambusia* was present (SE = 0.5%, N = 472, number of larvae at positive stations almost always <1 larva/dip). *Gambusia* was also associated negatively with *Macrocyclus*. While *Macrocyclus* was abundant enough to be detected by five dips during 37% of the inspections at stations without *Gambusia* (SE = 2.9%, N = 279), *Macrocyclus* was detected during only 18% of the inspections at stations where *Gambusia* was present (SE = 3.5%, N = 120).

Gambusia populations were low on all streets in the spring, but *Gambusia* spread through all the ditches during May and was at 71% of the stations by June. The fish continued at most of the same stations through the summer, being absent primarily from parts of the ditches that were heavily polluted or dry most of the time. *Gambusia* disappeared from most of the stations during September-October, even though they still had water. *Gambusia* repopulated the same stations by December and repeated the same sequence of disappearing and repopulating two more times during the period from January to April (Fig. 2).

There were natural *Macrocyclus* populations at 18% of the stations before *Macrocyclus* was introduced to two of the streets in early May. *Macrocyclus* populations were not increased by the introduction. *Macrocyclus* disappeared from all stations on both treatment and control streets by early June and none were seen again until September. *Macrocyclus* was observed at about 5% of the stations on all streets immediately before its introduction to two of the streets in October.

There were few *Cx. quinquefasciatus* larvae in the ditches at the second site when field observations began in April, and they were virtually absent from the ditches throughout the summer (always <1 larva/dip). *Cx. quinquefasciatus* larvae increased dramatically during September as *Gambusia* declined, and by early October

they had large numbers (10-85 larvae/dip) at 7% of the sampling stations. They were present in smaller numbers at an additional 17% of the stations.

The abundance of *Macrocyclus* and *Cx. quinquefasciatus* larvae was distinctly different on treated and control streets after *Macrocyclus* introduction in October (Fig. 2). On control streets, the number of stations with *Macrocyclus* was about the same from October to February, and the same was true for *Cx. quinquefasciatus* larvae (1-25 larvae/dip) after a decline from October to November. The number of control stations with *Cx. quinquefasciatus* larvae did not decline again until *Macrocyclus* spread naturally through the ditches on one of the control streets during March.

The number of stations with *Macrocyclus* on treatment streets increased dramatically within a few weeks after *Macrocyclus* introduction (Fig. 2). From November to March *Macrocyclus* was recorded at three times as many stations on treatment streets compared to control streets. The difference between treatment and control streets during November-April was significant at $P = .008$ ($T = 0$, $N = 7$), using Wilcoxon's rank sum test for matched pairs (Rohlf and Sokal 1995, p. 135). During this period 32%-50% of the stations on the treatment streets had enough *Macrocyclus* to be detected by the inspection procedure of five dips per station. More intensive sampling in January revealed that 80-90% of the remaining stations also had *Macrocyclus*, but in numbers too small to be detected by five dips. Most stations with very low *Macrocyclus* populations had fish.

The treatment streets had twice as many stations positive for *Cx. quinquefasciatus* larvae compared to control streets during the first month after *Macrocyclus* introduction (Fig. 2). However, stations on the treatment streets that had large numbers of *Cx. quinquefasciatus* larvae during September-October experienced a dramatic drop in larval numbers as soon as *Macrocyclus* reached significant numbers in November. Many of those stations continued to have a small number of larvae until December. The remaining larvae, too large for *Macrocyclus* to kill, probably stayed in the ditches because of slow development at cool autumn/winter temperatures. By January there were no larvae on the treatment streets, even when *Gambusia* was absent from most stations (Fig. 2). Small numbers of larvae appeared at a few stations with *Macrocyclus* during March and April.

The impact of *Macrocyclus*, separate from *Gambusia*, can be evaluated by comparing *Cx. quinquefasciatus* at stations having only *Macrocyclus* (but no *Gambusia*) with stations that had neither predator. Using information from all four streets during November-

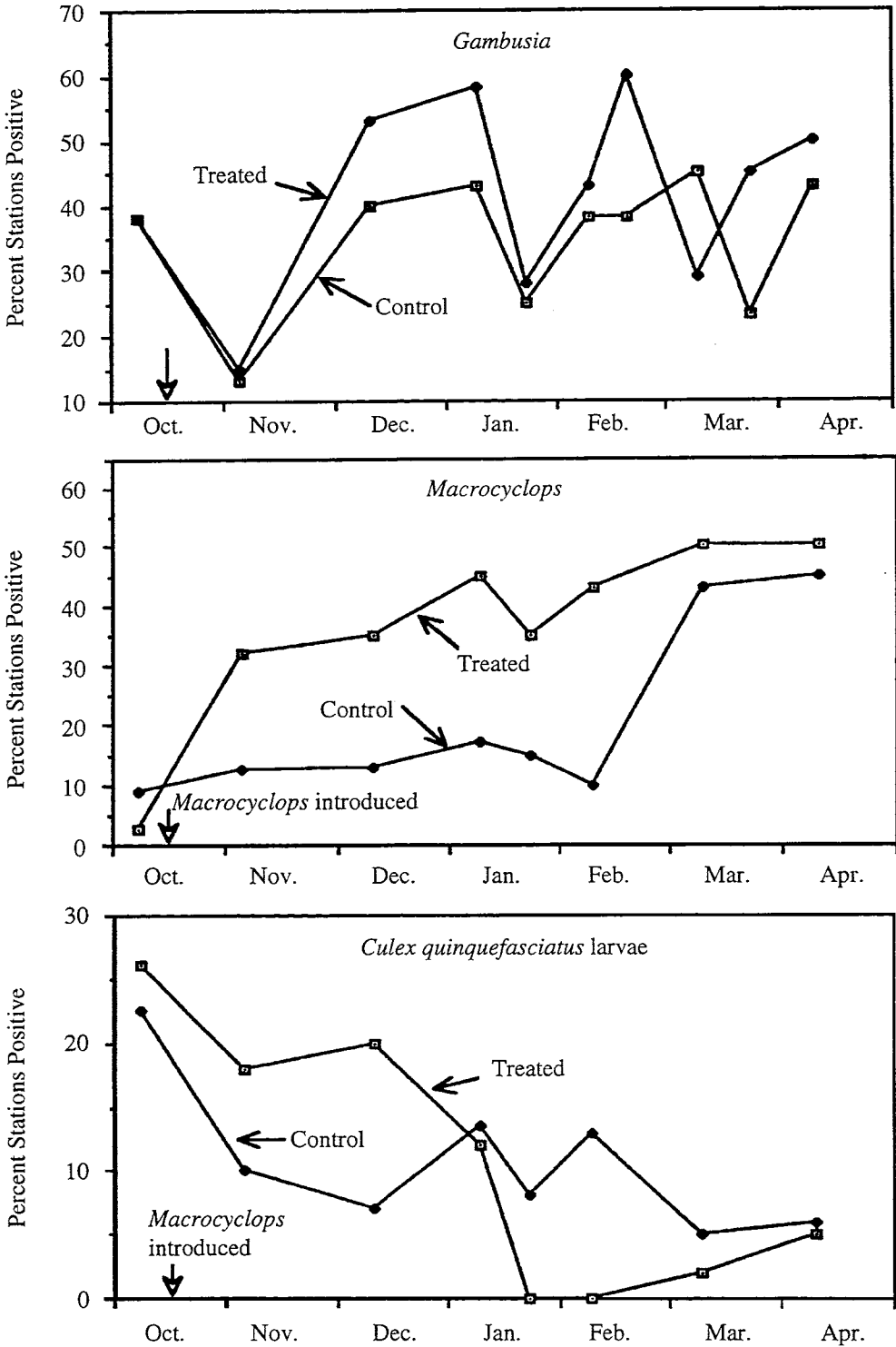


Figure 2. Populations of *Gambusia affinis*, *Macrocyclus albidus*, and *Culex quinquefasciatus* larvae at the second site after introduction of *Macrocyclus* to two of the streets in October. Pollution on both treated and control streets was moderate and scattered. Because changes in larval numbers at a few highly polluted stations could dominate average larval/dip, seasonal changes and the impact of *Macrocyclus* introduction on *Cx. quinquefasciatus* larvae at the more numerous less-polluted stations are best seen in terms of the number of stations positive for larvae.

April, 21.2% of the stations with neither *Macrocyclus* nor *Gambusia* had *Cx. quinquefasciatus* larvae (SE = 2.6%, N = 250). On the same streets during the same period, 5.8% of the stations with *Macrocyclus* (but not *Gambusia*) had *Cx. quinquefasciatus* larvae (SE = 2.0%, N = 137).

DISCUSSION

It is apparent from the field observations that *Cx. quinquefasciatus*, *Macrocyclus albidus*, and *Gambusia affinis* occupy the ditches in a dynamic patchwork that is shaped by seasonal weather fluctuations, ditch hydrology, pollution, and predator-prey relations. Predation by *Gambusia* is a dominant factor. *Cx. quinquefasciatus* larvae are virtually eliminated wherever and whenever *Gambusia* is present, and *Gambusia* suppresses (but does not eliminate) *Macrocyclus*. We consistently observed that if *Macrocyclus* was present on a street, it rapidly increased its numbers at a particular station when *Gambusia* disappeared.

Macrocyclus is also a significant predator, though the impact of *Macrocyclus* predation on *Cx. quinquefasciatus* larvae is not as absolute as *Gambusia*. The impact of *Gambusia* and *Macrocyclus* on *Cx. quinquefasciatus* production is limited by expansion and contraction of their populations through the ditches during the year. *Gambusia* is particularly limited in ditches that dry out frequently, and it disappears from many ditches during the winter. Both *Gambusia* and *Macrocyclus* are excluded from severely polluted water. Organic pollution is not responsible for excluding *Macrocyclus* because *Macrocyclus* thrives in the heavy organic pollution of the New Orleans Mosquito and Termite Control Board's mass production system for copepods, which is based on rotting wheat seed (Marten et al. 1997). Further evidence that organic pollution is not responsible came from the survival of *Macrocyclus* in some of the ditch water samples that appeared (and smelled) severely organically polluted. The fact that *Macrocyclus* was sometimes killed by ditch water that lacked noticeable organic pollution suggests that household chemicals are responsible.

Pollution from septic tanks is particularly important because it creates refuges where *Cx. quinquefasciatus* larvae are protected from predation by *Gambusia* or *Macrocyclus*. Although the complementary distribution of *Cx. quinquefasciatus* larvae vis-à-vis *Gambusia* and *Macrocyclus* is probably due in part to selection of organically polluted water by *Cx. quinquefasciatus* for oviposition, existence of the complementary distribution where water was not so severely polluted suggests it was

also due to predation.

Natural factors—pollution, fish, and temperature—appear to limit the distribution of *Macrocyclus* during the summer. *Macrocyclus* is suppressed in some parts of the ditches by the expansion of *Gambusia* during early summer. Severe pollution from septic tank effluent is more extensive in the summer because of less water flow. Most ditch water is only a few inches deep during the summer and readily heats up during the day. *Macrocyclus* is killed by temperatures exceeding 37°C (Marten et al. 1994) and was observed to retreat to cooler water in shaded areas and culverts during the hottest times of the summer.

Dispersal seems to be the main factor limiting the distribution of *Macrocyclus* during autumn and winter. Pollution and water temperatures declined sufficiently by October for *Macrocyclus* to be able to live in many parts of the ditches, but natural restocking of the ditches took about six months, perhaps in part because polluted segments (and possibly *Gambusia*) obstructed copepod movement through the ditches. In contrast, *Macrocyclus* was abundant in nearly all suitable parts of the ditches within a few weeks after introduction in October.

Implications for Mosquito Control

What are the implications of this study for operational control of *Cx. quinquefasciatus*? First and foremost is the significance of pollution. Not only does pollution create an abundant supply of bacterial food for *Cx. quinquefasciatus* larvae, it also excludes natural predators. The most obvious and effective way to reduce *Cx. quinquefasciatus* production is to eliminate pollution so predators can provide natural control. Further study could verify whether household chemicals are in fact responsible for excluding copepods from severely polluted parts of the ditches, and if so, which specific chemicals.

Unfortunately, ditch pollution is a fact of life in many places. While the heaviest *Cx. quinquefasciatus* production comes from severely polluted sites where only a larvicide can eliminate production, production from the many kilometers of less polluted segments can also be substantial in the aggregate. It is in these places that appropriately timed introduction of fish and copepods—October for *Macrocyclus* in Louisiana—could reduce the need for larviciding by facilitating natural control. Copepods can help to fill the gap when and where fish are absent. In ditches treated with a larvicide, copepods can help to kill larvae missed by the larvicide.

The lag in the decline of *Cx. quinquefasciatus* larvae observed after introducing *Macrocyclus* in October (Fig. 2) could be eliminated by applying BTI

simultaneously and following up with a single BTI application once the copepod population has built up its numbers (early November). Because BTI kills mosquito larvae of all sizes, it can eliminate larvae that are too large for copepods to kill, and the copepods will prey on new larvae after that. BTI has no detrimental effect on copepods (Marten et al. 1993).

The practical utility of *Macrocyclus* introductions remains to be seen. It is clear that *Macrocyclus* does not eliminate *Cx. quinquefasciatus* larvae with the same completeness that it eliminates *Aedes* larvae in containers. At best, copepods could fill a specific and limited role in a comprehensive package of integrated *Cx. quinquefasciatus* control. Though millions of copepods can be produced at reasonably low cost (Marten et al. 1997), only further experience will show whether the benefits from introductions are sufficient to justify the cost and effort.

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