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LARVICIDAL ALGAE

Gerald G. Marten[1]
New Orleans Mosquito and Termite Control Board, 6601 Stars & Stripes Blvd., New Orleans, LA 70126

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ABSTRACT. Although most algae are nutritious food for mosquito larvae, some species kill the larvae when ingested in large quantities. Cyanobacteria (blue-green algae) that kill larvae do so by virtue of toxicity. While blue-green algae toxins may offer possibilities for delivery as larvicides, the toxicity of live blue-green algae does not seem consistent enough for live algae to be useful for mosquito control.

Certain species of green algae in the order Chlorococcales kill larvae primarily because they are indigestible. Where these algae are abundant in nature, larvae consume them to the exclusion of other food and then starve. Under the right circumstances, it is possible to introduce indigestible algae into a breeding habitat so they become abundant enough to render it unsuitable for mosquito production. The algae can persist for years, even if the habitat dries periodically. The main limitation of indigestible algae lies in the fact that, under certain conditions, they may not replace all the nutritious algae in the habitat. More research on techniques to ensure complete replacement will be necessary before indigestible algae can go into operational use for mosquito control.

INTRODUCTION

Algae are a significant part of the diet for many kinds of mosquito larvae that feed opportunistically on microorganisms, small aquatic animals such as rotifers, and other small particulate food in their aquatic environment (Merritt et al. 1992). The larvae may filter algae from the water column, scrape them from the surface of containers or aquatic plants, or scoop them from the bottom of aquatic habitats where mosquitoes breed.

Mosquito biologists showed considerable interest in the gut contents of mosquito larvae during the 1920s (Boyd and Foot 1928, Senior-White 1928). By knowing the kind of food that makes habitats particularly favorable for mosquito production, it might be possible to manipulate the habitats to eliminate the food. The biologists found that algae are generally represented in the gut in proportion to their abundance among the microflora and microfauna where mosquito larvae are feeding. Coggeshall (1926) conducted an experiment in a pond with a high level of *Anopheles quadrimaculatus* production and an abundance of algae in both the water and the guts of the mosquito larvae. He treated the pond with copper sulfate to eliminate the algae, and the *An. quadrimaculatus* larvae disappeared.

Although an abundance of algae usually provides favorable conditions for mosquito production, Purdy (1924) discovered that some algae can kill mosquito larvae. He noticed that *Culex* and *Anopheles* larvae were virtually absent from a California rice field that had dense mats of the filamentous cyanobacterium (blue-green alga) *Tolypothrix* sp., although nearby fields without these algae had large populations of larvae. Larvae hatching naturally into this field survived less than 3 days, and they died equally rapidly when placed in a pure culture of *Tolypothrix* in the laboratory. Because larvae died in a small screened field enclosure where there were no algal mats inside the enclosure but algal mats immediately outside it, Purdy concluded that *Tolypothrix* released a toxin into the water.

Howland (1930) examined a number of algae species in the guts of *Aedes argenteus* larvae, using the appearance of the algae under the microscope and how much stain they absorbed to evaluate how thoroughly they were digested. The algae passed through the larval guts in about 15 min and were only partially digested. However, when he forced the larvae to hold algae in their guts for longer periods by first holding the larvae in water with algae and then transferring them to water with no food at all, most kinds of algae were thoroughly digested. The only exceptions were green algae in the order Chlorococcales (Philipose 1967), which were still incompletely digested. Some species (e.g., *Scenedesmus quadricauda)* showed no signs of digestion.

In Queensland, Australia, Hamlyn-Harris (1928) reported that *Cx. fatigans* and *Ae. argenteus* larvae died in water with dense mats of the filamentous green alga *Cladophora holsaltica*. He did not know the mechanism, but speculated that it was somehow connected to decomposition of the algae, though other filamentous algae that form mats (e.g., *Spirogyra)* were observed to serve as food and support high levels of mosquito production.

No development of larvicidal filamentous green algae for mosquito control has occurred since Hamlyn-Harris' observations, though *An. pseudopunctipennis* production has been reduced by removing *Spirogyra* that serve as food at their breeding sites in riverside pools (Bond et al. 2004). On the other hand, Purdy's discovery of

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[1] Present address: East-West Center, Honolulu, HI 96848.

toxicity in blue-green algae and Howland's report of indigestibility among green algae in the order Chlorococcales foreshadowed further discoveries along those lines and eventual demonstrations that larvicidal algae can be used for practical mosquito control.

BLUE-GREEN ALGAE (CYANOBACTERIA)

Thirty years after Purdy discovered *Tolypothrix* killing mosquito larvae in California rice fields, Gerhardt (1953, 1955, 1956, 1961) surveyed the same fields to explore the matter further. *Tolypothrix* was no longer present, but mosquito larvae were missing from fields with dense mats of the filamentous blue-green algae *Anabaena* sp. or *Aulisira implexa*. When Gerhardt placed *A. implexa* mats and *Cx. tarsalis* larvae in a small enclosure in a rice field that did not have these algae and supported normal mosquito production, the larvae quickly died. If he placed larvae in the enclosure when it was covered to exclude sunlight, the larvae survived. He concluded that the larvicidal mechanism was a photometabolite toxic to the larvae.

Anabaena unispora and *A. circinalis* killed *Ae. aegypti* larvae in the laboratory and sometimes attained sufficient numbers to kill larvae when introduced to breeding habitats (Griffin 1956). Ilyaletdimova (1976) and Semakov and Sirenko (1985) attributed unusually low populations of mosquito larvae in Russia to high densities of blue-green algae in breeding habitats.

Marten (1986a) conducted a laboratory study assessing the survival of *Ae. albopictus* and *Cx. quinquefasciatus* larvae in pure cultures of 17 species of blue-green algae. The following species often (but not always) killed the larvae: *Anabaena cylindrica*, *A. flosaquae*, *A. sphaerica*, *Gloeotrichia echinulata*, and *Plectonema boryanum*. *A. flosaquae* was tested with *Cx. tarsalis*, *An. albimanus*, *An. freeborni*, and *An. quadrimaculatus* larvae and performed the same as with *Ae. albopictus* and *Cx. quinquefasciatus*. The larvicidal mechanism was presumed to be toxicity, because the algae were highly digestible. Larvae were not killed by other species of *Anabaena* tested. Nor were they killed by species of *Chroococcus*, *Cylindrospermum*, *Eucapsis*, *Lyngbya*, *Microcystis*, *Nodularia*, *Nostoc*, *Oscillatoria*, *Phormidium*, or *Spirulina* that were tested.

Aedes aegypti larvae died when fed *Oscillatoria agardhii* and *Anabaena circinalis* in the laboratory (Kiviranta and Abdel-Hameed 1994, Abdel-Hameed et al. 1994). Saario et al. (1994) killed *Ae. aegypti* larvae by feeding them strains of *Oscillatoria agardhii* and *Anabaena circinalis* known to produce microcystins toxic to vertebrates and invertebrates. Microscopic examination of the dead larvae revealed lesions in their midgut epithelial cells. Larvae survived and manifested no midgut lesions when fed strains of *O. agardhii* and *Anabaena solitaria* known not to produce toxic microcystins.

Amonkar (1969) isolated unidentified metabolites from blue-green algae that were toxic to mosquito larvae. A methanol extract of *Westielopsis* sp. killed *Ae. aegypti*, *An. stephensi*, *Cx. quinquefasciatus*, and *Cx. tritaeniorhynchus* in the laboratory (Rao et al. 1999). Nassar et al. (1999) observed that an aqueous extract of unspecified blue-green algae killed *Cx. pipiens* larvae. Adults from the few surviving larvae were deformed and unable to produce viable offspring.

It appears that toxicity is always the mechanism by which blue-green algae kill mosquito larvae. The same kinds of blue-green algae that kill larvae are well known to produce toxic blooms in ponds, killing animals such as fish and cattle (Ingram and Prescott 1954). Although the larvicidal capacity of blue-green algae does not seem consistent enough to make live algae a reliable tool for mosquito control, their toxins may have potential as larvicides.

GREEN ALGAE

Fifty years passed from the studies of the 1920s until larvicidal green algae were once again the object of investigation. Dhillon and Mulla (1982) observed that larval populations of *Cx. quinquefasciatus* and *Cs. incidens* were reduced by 85% in cemetery vases with natural blooms of the green alga *C. ellipsoidea*. *C. ellipsoidea* suspensions, as well as supernatant from centrifuging the algae, killed 80% of 1st instar *Cx. quinquefasciatus* in the laboratory (Dhillon and Mulla 1981). Ether extracts from *C. ellipsoidea* and the filamentous green alga *Rhizoclonium hieroglyphicum* behaved like growth hormones, killing *Cx. quinquefasciatus*, *Cs. incidens*, and *Ae. aegypti* larvae in the laboratory (Dhillon et al. 1982).

INDIGESTIBLE GREEN ALGAE

Marten (1984) observed that *Ae. albopictus* larvae failed to grow, and died within a week after hatching, when in water containing a dense natural population of *Kirchneriella irregularis* (Fig. 1). Confirmation that *K. irregularis* was in fact responsible and that larvae died because *K. irregularis* was indigestible came from 3 lines of evidence. First, water that contained *K. irregularis* and killed mosquito larvae was transformed to supporting normal larval development when *K. irregularis* was filtered out of the water but bacteria were not. Second, adding yeast to water with *K. irregularis* transformed the water from killing larvae to supporting normal development. Third, mixing water containing *K. irregularis* with water containing other kinds of algae that

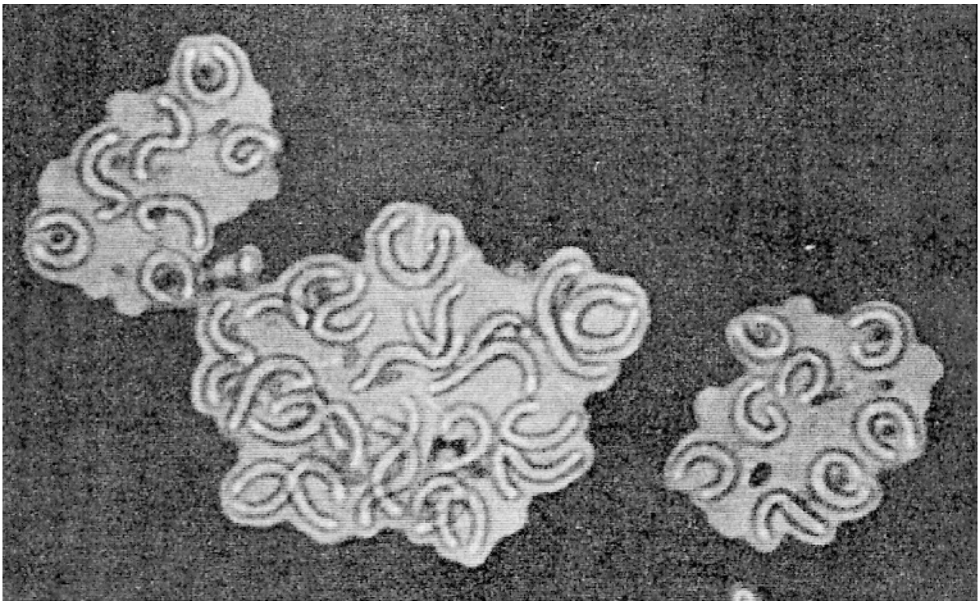

Fig. 1. *Kirchneriella irregularis*. The horseshoe-shaped algal cells are held together by a gelatinous matrix highlighted in this photo by India ink in the water. Source: Marten (1986b).

supported normal larval development resulted in water that supported normal larval development.

Marten (1986a, 1986b, 1987) assessed larval survival in pure cultures of 92 species of green algae from a broad taxonomic spectrum. The assessment was conducted in both tap water and pond water. Before the pond water was inoculated with each algae species, other species of algae in the water, but not bacteria, were removed by filtration. *Ae. albopictus* and *Cx. quinquefasciatus* larvae always died in water containing the following species (all in the order Chlorococcales): *Coelastrum reticulatum*, *Dactylococcus dissociatus*, *Dictyosphaerium pulchellum*, *Elakatothrix viridis*, *Kirchneriella contorta*, *K. cornuta*, *K. irregularis*, *Scenedesmus abundans*, *S. bijugatus*, *S. dimorphus*, *S. dispar*, *S. longus*, *S. parisiensis*, *S. quadricauda*, *Selenastrum gracile*, *Tetradesmus cumbricus*, and *Tetrallantos lagerheimii*. *Culex quinquefasciatus* larvae always died, but *Ae. albopictus* occasionally survived, in water containing *Botryococcus brownii*, *Franceia amphitricha*, *Keratococcus bicaudatus*, *Nephrochlamys rotunda*, *N. subsolitaria*, *Nephrocytium alantoideum*, and *Scotiellopsis oocystiformis*. *Coelastrum reticulatum*, *E. viridis*, *K. irregularis*, *S. bijugatus*, *S. quadricauda*, and *S. gracile* were tested with *Cx. tarsalis*, *An. albimanus*, *An. freeborni*, and *An. quadrimaculatus*, and killed them consistently.

Several other species of *Coelastrum*, *Kirchneriella*, and *Scenedesmus* always killed *Cx. quinquefasciatus*, but *Ae. albopictus* occasionally survived, particularly if the algae were in pond water. *Cx. quinquefasciatus* was more vulnerable to indigestible algae than *Ae. albopictus* because *Cx. quinquefasciatus* fed more or less exclusively on algae in the water column, whereas *Ae. albopictus* also grazed bacteria from surfaces on the sides and bottom of the containers. Indigestible algae were most effective against *Ae. albopictus* when the algae were so dense that they coated the surfaces.

Although all the larvicidal green algae in this study were in the order Chlorococcales, some Chlorococcales algae were not larvicidal. Larvae thrived with the tested species of *Ankistrodesmus*, *Pediastrum*, *Micractinium*, *Gloenkinia*, and *Tetraedron*. Larvicidal capacity even varied from species to species in the same genus. Whereas many species of *Scenedesmus* were consistently larvicidal, mosquito larvae developed normally with other species of *Scenedesmus*.

That indigestibility was responsible for the lethal impact of many species of Chlorococcales algae was confirmed by 3 lines of evidence (Marten 1986a). First, the larvae developed normally when yeast was added to the cultures. Second, different algae species tagged with C^{14} tracer were fed to mosquito larvae. The larvae assimilated substantial quantities of C^{14} from algae on which they grew normally, but C^{14} assimilation was barely detectable from species of algae that killed them. Third, observation of 1st instars with ultraviolet illumination under a microscope revealed that algae supporting normal development fluoresced bright red in the foregut but only faintly in the hindgut, indicating that their chlorophyll had been destroyed by digestive enzymes. Algae that killed mosquito larvae fluoresced brightly in both foregut and

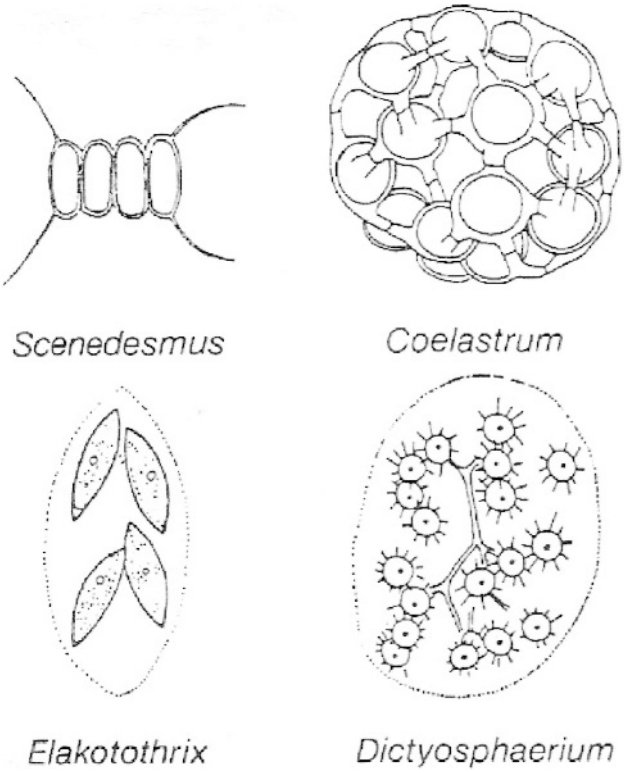

Fig. 2. Four common genera of algae in the order Chlorococcales that include species indigestible to mosquito larvae. *Coelastrum*, *Elakatothrix*, and *Dictyosphaerium* occur in small colonies held together by a gelatinous matrix. Source: Marten (1986b).

hindgut, and they were viable when cultured after passing through the gut.

Ahmad et al. (2001, 2004) assessed concentrations of digestive enzymes in the guts of *Ae. aegypti* larvae fed indigestible *Chlorella* (presumably in the *Chlorella vulgaris* species group). The purpose was to examine the hypothesis that the algae were indigestible because they inhibited digestive enzymes. The hypothesis was rejected. *Chlorella* passed undigested through larval guts despite normal concentrations of enzymes necessary to digest them.

Many indigestible green algae occur in small colonies held together by a gelatinous matrix (Fig. 2). Porter (1973) speculated that the gelatinous covering could make algal cells indigestible by obstructing digestive enzymes. However, some indigestible algae do not have a gelatinous matrix, and some highly digestible algae do have it. Marten (1986a) concluded that the explanation for indigestibility lies in a thin layer of sporopollenin (100 μm thick) around the outside of the cell wall. Sporopollenin is impervious to all digestive enzymes (Atkinson et al. 1972). Algae with the most complete sporopollenin protection pass through the guts of mosquito larvae without being killed.

FIELD TRIALS WITH *KIRCHNERIELLA IRREGULARIS*

The potential of *Kirchneriella irregularis* for mosquito control was demonstrated by introducing it to pig-farm waste water in small artificial ponds (Marten 1986a). The water previously contained an abundance of other algae species and supported normal development of *Cx. quinquefasciatus* larvae. *K. irregularis* replaced the other algae within a month in 30% of the replicates. Larvae were not able to survive after this happened. The success rate for replacing other algae with *K. irregularis* increased to 70% when an algae-grazing cladoceran (*Daphnia* sp.) was introduced at the same time as *K. irregularis*. Because *Daphnia* digested the original algae, but not *K. irregularis*, *Daphnia* grazing provided a competitive advantage for *K. irregularis* over the other algae, enabling *K. irregularis* to permanently replace them.

FIELD TRIALS WITH *CHLORELLA PROTOTHECOIDES*

Dense natural populations of *Kirchneriella* sp. or *Chlorella protothecoides* (also known as *Palmellococcus protothecoides*) (Fig. 3) were

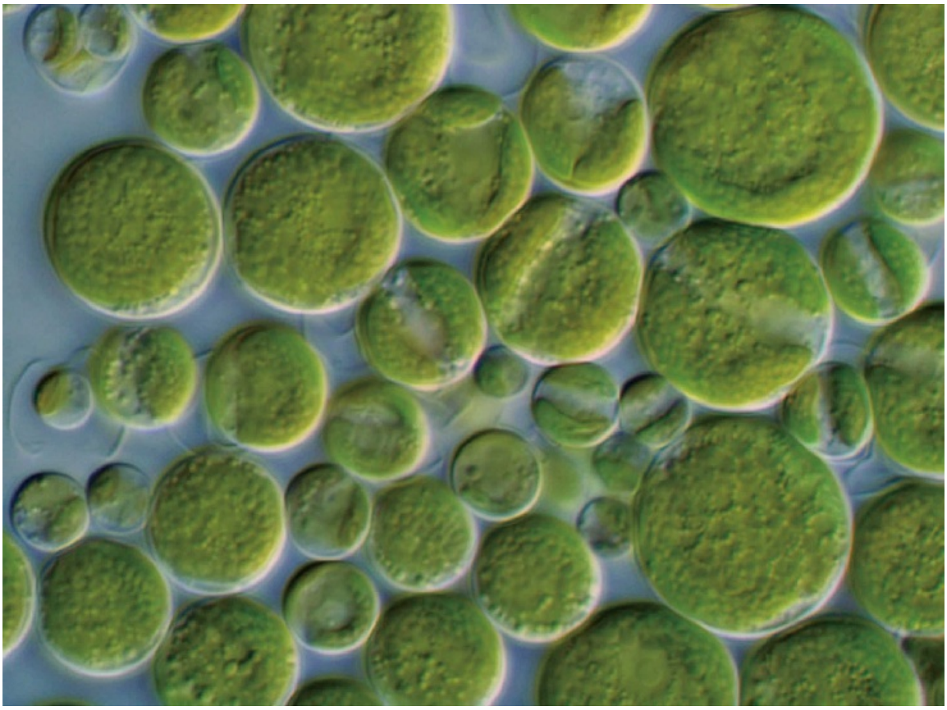

Fig. 3. *Chlorella protothecoides*. Source: Algae Resources Data Base (http://shigen.lab.nig.ac.jp/algae/images/strainsimage/nies-0629.jpg).

occasionally observed in rainwater that collected in discarded tires in New Orleans. The number of mosquito larvae in tires with *Kirchneriella* or *C. protothecoides* was very low, and pupae were nearly absent (Marten [NOMCB] June 1991 p 10–11). In the laboratory, *Ae. aegypti* larvae never survived when placed in water from tires containing dense populations of *Kirchneriella* or *C. protothecoides*. The larvae usually died in the 1st instar. Larvae in water with *Kirchneriella* grew slowly, sometimes surviving as far as the 4th instar but never emerging as adults. Larvae developed normally when yeast was added to water with *Kirchneriella*, confirming that it killed the larvae because of indigestibility. The same usually happened with *C. protothecoides*, but sometimes larvae died when yeast was added to water, suggesting that toxicity could possibly have been involved along with indigestibility. Avissar et al. (1994) confirmed the indigestibility of *C. protothecoides* with radiotracer experiments in which *Cx. pipiens* larvae assimilated no C^{14} from *C. protothecoides* that they ingested.

Chlorella protothecoides from a pure culture was introduced to the water in several hundred discarded tires at the edge of a woodlot in New Orleans (Marten [NOMCB] April 1992 p 7–9). The environment varied from open and sunny to semi-shaded by large oak trees. All untreated control tires at the site contained natural populations of *Ae. albopictus* larvae that developed normally. *Chlorella protothecoides* established dense populations, to the exclusion of all other algae, in tires whose water had no algae or a moderate algae population at the time of *C. protothecoides* introduction. *Aedes albopictus* production was completely suppressed in all those tires (Marten [NOMCB] July 1992 p 8–10). In tires that had natural populations of digestible algae species dense enough to color the water deep green at the time of *C. protothecoides* introduction, *C. protothecoides* usually established a dense population as a mixture with some of the other species. In some of those tires, *C. protothecoides* dominated the mixture and reduced or eliminated *Ae. albopictus* production. In other tires *C. protothecoides* did not dominate, and *Ae. albopictus* was not suppressed.

Though the water in tires where *C. protothecoides* successfully eliminated mosquito production sometimes dried out for several weeks, a dense population of the algae reappeared within days after the tire again filled with water. Larval suppression continued. When the copepod *Mesocyclops longisetus* (Marten et al. 1994) was introduced into some of the tires with dense *C. protothecoides* populations, the result was control from both algae and copepods. The copepods maintained populations large enough (typically 25–50 copepods per tire) to eat all the larvae, although copepod populations in tires with *C. protothecoides* were somewhat lower than the populations in tires without *C. protothecoides*.

Almost all the tires that acquired dense populations of *C. protothecoides* soon after introduction still had dense populations of *C. protothecoides* when they were inspected 2 years later (Marten [NOMCB] April 1994 p 6–7, August 1994 p 14, October 1994 p 7). *Chlorella protothecoides* was still suppressing mosquito production in most of the tires. Production was completely suppressed or greatly reduced in tires where *C. protothecoides* constituted more than 90% of all the algae. *Aedes albopictus* production was normal when the *C. protothecoides* percentage was less than 70%.

CONCLUSIONS

The following conclusions can be drawn from the laboratory and field studies reviewed above:

- Some species of blue-green algae kill mosquito larvae because of toxicity. The toxicity does not appear consistent enough to be of use for mosquito control. Blue-green algae toxins may have potential for use as insecticides.
- Many species of green algae in the order Chlorococcales are resistant to digestion by mosquito larvae. Some are completely indigestible.
- Mosquito larvae are unable to complete their development if indigestible algae are numerous enough in the aquatic habitat to prevent the larvae ingesting enough other food to satisfy their nutritional needs. This sometimes happens in nature.
- Indigestible algae can achieve the necessary abundance to eliminate mosquito production when introduced to confined breeding habitats such as tires or ponds. They continue to suppress mosquito production for years, even if the habitat dries out periodically.
- If digestible algae are numerous at the time of indigestible algae introduction, the result can be a mixture of digestible and indigestible algae that does not completely suppress mosquito production.
- Introduction of an herbivore that feeds on digestible algae, at the same time indigestible algae are introduced, can facilitate the replacement of digestible algae by the indigestible algae.

So far, no larvicidal algae have been put into operational use for mosquito control. Further research and development will be necessary before their use is sufficiently reliable. The key improvement will be a method to ensure that larvicidal algae replace other algae in the aquatic habitat as completely as possible. One possibility is chemical treatment of the habitat to eliminate other algae before introducing larvicidal algae. For indigestible algae, simultaneous introduction of a herbivore that grazes on the digestible algae is a possibility that has already been demonstrated.

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