An Ecological Survey of *Anopheles albimanus* Larval Habitats in Colombia

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ABSTRACT: The flora and fauna of 69 aquatic sites in Colombia were surveyed to identify ecological conditions that favor production of *Anopheles albimanus*. *Anopheles albimanus* larvae were most numerous at sun-exposed sites with abundant *Culex* larvae and grass at the edge of the water. Only 29% of the sites with *An. albimanus* larvae contained pupae, suggesting that poor larval survival prevented the production of adult mosquitoes at many sites. In the Atlantic region, *An. albimanus* production was highest from large ponds with an abundant and varied aquatic insect fauna, including many kinds of predators of *An. albimanus* larvae. Although productive sites were often covered with water hyacinth, aquatic vegetation was generally not a reliable indicator of *An. albimanus* production. In the Pacific region, *An. albimanus* production was highest from small water bodies with few aquatic macrophytes and an abundance of cladocera, reflecting an abundance of microalgal food for mosquito larvae. In both regions, *An. albimanus* production was negatively associated with a complete cover of *Lemna*, fish, hydrometrid nymphs, large species of cyclopoid copepods, and dragonfly or mayfly nymphs. *Anopheles albimanus* production was also negatively associated with dytiscid beetle larvae in the Pacific region.

Keyword Index: Mosquito, ecology, habitat, larvae, biological community.

INTRODUCTION

Anopheles albimanus Wiedemann is a common and widely-distributed neotropical mosquito species that breeds in a variety of aquatic habitats (Breeland 1972): ditches, temporary pools, ponds of all sizes, lakes, streams, and estuaries. Source reduction for such extensive larval habitat would appear to be an overwhelming task.

The prospects for source reduction might be improved if ecological common denominators could be identified that cut across the apparent diversity of habitats. Such information might provide ecological indicators for recognizing sites that are most important for *An. albimanus* production, so that larviciding or other forms of source reduction could be focused on those sites. Ecological information might also help to identify key characteristics of *An. albimanus* larval habitats that could be modified to render the habitats unsuitable for *An. albimanus* production.

Anopheles albimanus larvae are generally found at sites that are well exposed to sunlight (Breeland 1972). One way to expand and refine this characterization is to look for discernable communities of aquatic flora and fauna. Plants and animals that share aquatic ecosystems with *An. albimanus* larvae should have profound impacts on the larvae as food, shelter, predators, or competitors.

Savage et al. (1990), Rejmankova et al. (1991, 1992), and Rodríguez et al. (1993) surveyed aquatic habitats on the Pacific coastal plain of southern Mexico, where *An. albimanus* larvae were associated with emergent aquatic plants, planktonic algae, pasture grasses, or water hyacinth. In Belize, Rejmankova et al. (1993) observed *An. albimanus* larvae to be associated with cyanobacterial mats and submerged plants covered with periphyton.

Anopheles albimanus is common throughout the coastal zone of Colombia (Quiñones et al. 1987) (Fig. 1). We conducted a field survey of aquatic habitats in Colombia to identify ecological conditions that support the production of *An. albimanus*. We particularly wanted to know if the habitat associations were the same in Colombia's Pacific and Atlantic regions. The survey emphasized aquatic flora and fauna, their organization into biotic communities, and their associations with *An. albimanus* larvae and pupae.

MATERIALS AND METHODS

The survey was designed to cover the full range of aquatic habitats that might produce *An. albimanus* on the Pacific and Atlantic coasts of Colombia. Twenty-seven sites were sampled on the Pacific coast from October 1986 to April 1987 in the vicinity of Tumaco (Fig. 1) and extending 50 km inland along the highway east of Tumaco. Mangroves dominate the coastal part of the area surveyed, while farther inland the landscape is dominated by small-scale agriculture (coconut and palm plantations, sugar cane, and subsistence crops). The rainy season on the Pacific coast extends from September to June with peaks in January, February, and May. Small bodies of water are numerous because much of the land is only slightly above sea level, rainfall is plentiful, and the water table is high. Sample sites on the Pacific coast included borrow pits, stream impoundments, roadside ditches, and temporary pools.

Forty-two sites were sampled on the Atlantic coast (from May 1987 to October 1987) in the vicinity of Las Flores, Santa Catalina, and Carmen de Bolivar (Fig. 1). Cattle ranches dominate the Atlantic landscape along with small-scale agriculture. There are two rainy seasons on the Atlantic coast—September to November and May to June—with distinct dry seasons between them. Small bodies of water are unusual on the Atlantic coast. Large cattle ponds and impoundments to store water for household use are common.

A total of seven physical/chemical factors, ten categories of terrestrial or aquatic plants, and 39 categories of aquatic animals (five stages of *An. albimanus* plus 34 other kinds of animals) were assessed at each site (TABLE 1, TABLE 2). Physical and chemical properties of the water at each site were measured between 10 AM and 2 PM. The pH was measured with colorimetric paper. Temperature, salinity, and conductivity were measured with a YSI meter (Yellow Springs Instrument Co., Yellow Springs, Ohio). Oxygen was measured by the Winkler method (Ruttner 1963).

Terrestrial vegetation was assessed visually as percent ground cover of trees, bushes, flowering plants, or grasses within one meter of the water's edge. Aquatic vegetation was assessed visually as percent cover of submersed, emergent, or floating macrophytes over the entire body of water.

Aquatic fauna, including mosquito larvae and pupae, were collected with a plankton net (120 μm mesh). The mouth of the net was attached to a square frame, 20 cm on a side, which was dragged with a pole through water up to 50 cm in depth. The total distance sampled by the net at each site varied from 10 m to 50 m, depending on the size of the body of water. Wherever possible, the net was dragged along a transect from one side of the water to the other, but it was necessary to drag the net only near the shore if the water was too deep in the middle. Sampling at the largest sites was at intervals along the shore.

Animals collected in the plankton net were preserved in formalin for identification and counting in the laboratory. Counts were by taxonomic groups (TABLE 2); subsamples were counted when animal numbers were large. Mosquito larvae were counted by instar. The large numbers of animals collected by the plankton net provided quantitatively reliable samples of most kinds of animals present at each site, including substantial numbers of mosquito pupae (if present), which we considered to reflect the production of adult mosquitoes. All animal counts, including mosquito larvae and pupae, were expressed as numbers per meter dragged by the plankton net. A log (X+1) transformation was applied to animal counts to bring them closer to a normal distribution before including them in the statistical analysis.

Gut contents of *An. albimanus* larvae were examined under the microscope to assess the quantity of microalgae, bacteria, detritus, and mineral particles. Gut content data were not included in the statistical analyses.

Two kinds of correlations were calculated between the 56 quantitative variables (physical, chemical, floral, and faunal): conventional linear correlation coefficients and nonparametric Spearman rank-order correlation coefficients. A positive correlation between two kinds of plants or animals reflected a tendency for both to be abundant at the same site, as well as scarce or absent at the same sites. A negative correlation reflected a tendency to be present or abundant at different sites. The rank correlations were helpful for identifying associations that were not apparent from conventional correlations because the associations were not linear.

Factor analysis with varimax rotation was applied to the 1,540 conventional correlation coefficients between all physical/chemical, floral, and faunal variables to identify intercorrelated groups of variables. Factors with eigenvalues >2 were considered significant. A variable was considered to be part of the intercorrelated group represented by a particular factor if its factor loading exceeded 0.3.

The factor analysis was repeated with a single juvenile stage (larval instar or pupae) of *An. albimanus*

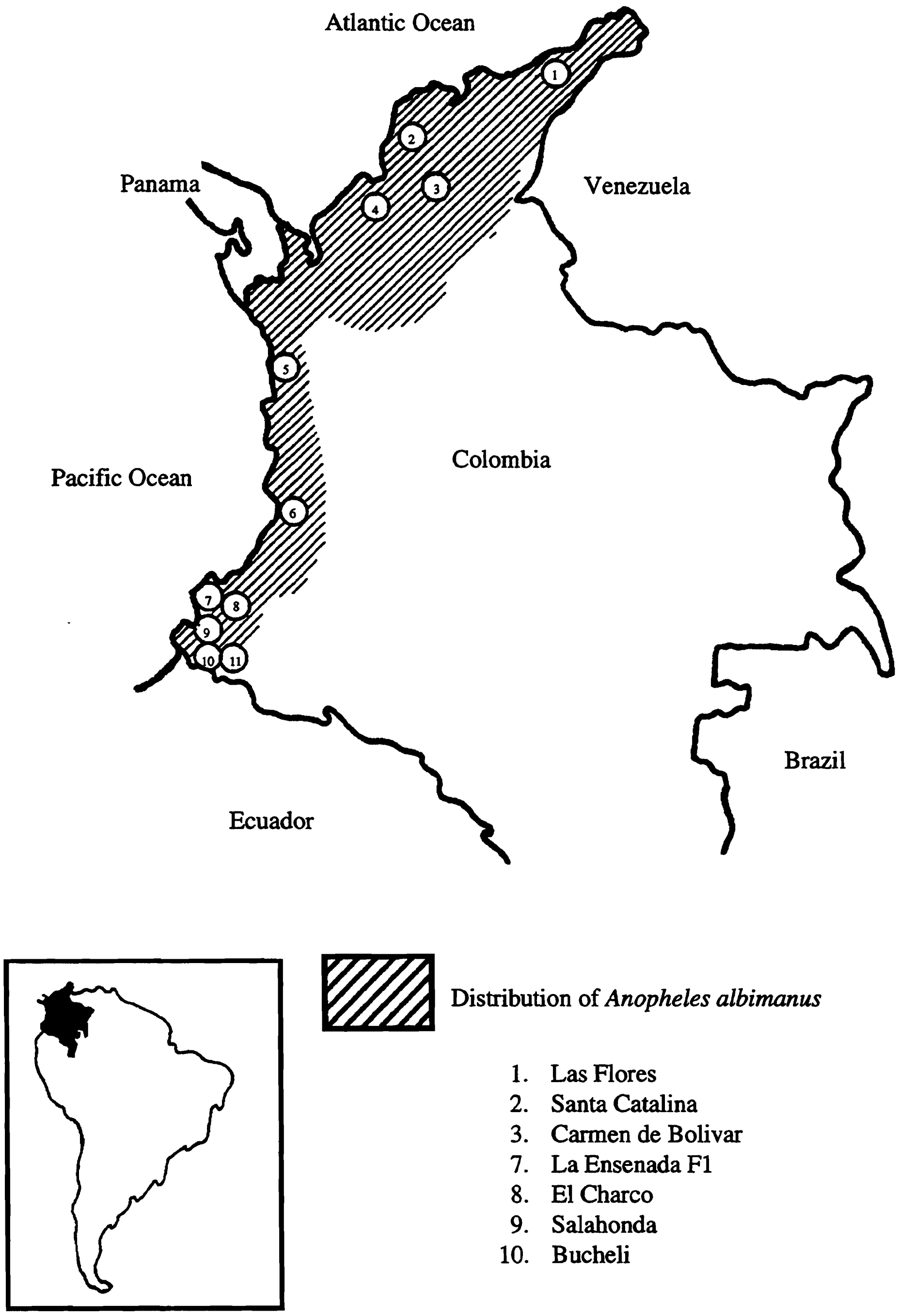

Figure 1. Geographic distribution of *Anopheles albimanus* in Colombia. Sampled sites were at locations 1-3 in the Atlantic region and locations 7-10 in the Pacific region.

TABLE 1. Physical/chemical characteristics evaluated at each sample site.

	Atlantic		Pacific	
	Mean ± SE	Range	Mean ± SE	Range
Area (m^2)[1]	1500±272	144 - 4500	27±6	1 - 150
Depth (m)[1]	1.54±0.10	0.4 - 4.0	0.34±0.04	0.15 - 1.0
Temperature (°C)[2]	29.3±0.3	27.5 - 32	27.7±0.4	24 - 33
Conductivity (mhos)[2]	566±106	80 - 4000	558±252	110 - 7000
Salinity (ppt)[2]	0.10±0.04	0 - 1.5	0.25±0.15	0 - 4.0
Oxygen (ppm)[2]	4.29±0.30	0.5 - 8.0	3.98±0.50	1.0 - 8.5
pH[2]	6.28±0.04	6.0 - 7.0	6.10±0.04	5.8 - 6.4

[1]Area and depth of the sampled water body.
[2]Measured between 10 AM and 2 PM.

TABLE 2. Flora and fauna evaluated at each sample site.

FLORA

Terrestrial vegetation at edge of water. Trees, bushes, flowering plants (Compositae, Verbinaceae), grasses (Gramineae).

Aquatic plants. Submersed plants (e.g., *Chara, Elodea*), emergent plants (e.g., reeds), floating-leaved plants (e.g., *Nuphar, Nymphea, Brasenia*), water hyacinth (*Eichornia*), duckweed (*Lemna*), water lettuce (*Pistia*).

FAUNA

Crustaceans. Cladocera, shrimp (malacostraca), ostracods, large cyclopoid copepods, small cyclopoid copepods, calanoid copepods.

Aquatic bugs (nymphs and adults). Hebrids, naucorids, hydrometrids, notonectids, nepids, belostomatids, gerrids, veliids, mesoveliids, corixids, plaeids.

Aquatic beetles (larvae and adults). Dytiscids, hydrophilids, hydraenids, miscellaneous Coleoptera.

Aquatic diptera larvae. *An. albimanus* (each instar and pupae), other *Anopheles*, chironomids, stratiomyids, *Culex* (I/II instars, III/IV instars), miscellaneous Diptera (e.g., ceratopogonids, tipulids)

Odonata nymphs. Mayfly, damselfly, dragonfly.

Other aquatic insects. Collembola.

Aquatic mites. Hydracarina.

Aquatic vertebrates. Fish, tadpoles.

in each run. The reason for not including all stages of *An. albimanus* in the same run was to avoid creating an artificial "*An. albimanus*" factor due to the high correlation between different stages of the same species. The floral/faunal associations identified by the factor analysis were the same regardless of the stage of *An. albimanus* that was included in a particular run.

Stepwise multiple regression analysis was applied to each of the instars (and pupae) of *An. albimanus* as dependent variables, using all floral, faunal and physical/chemical variables as independent variables. Variables were considered significant if the F-value exceeded 4.0 ($P<0.05$).

RESULTS

Atlantic Region

Anopheles albimanus larvae were present at 78% of the sites that were sampled in the Atlantic region. The number of first instars per meter dragged by the plankton net ranged from 0.3 to 55; second instars ranged from 0.1 to 40, third instars ranged from 0.03 to 25, and fourth instars ranged from 0.05 to 12. Only 31% of the sampled sites had *An. albimanus* pupae, ranging from 0.1 to 3.5 pupae per net meter.

The factor analysis did not reveal discrete floral/faunal communities, but it did identify five significant groups of associated flora and fauna (TABLE 3). One (or sometimes two) of the groups was prominently represented at every site we sampled. *Anopheles albimanus* larvae or pupae had a significant positive association with every group except one.

The most distinct floral/faunal group in the Atlantic region (Atlantic Group #1, TABLE 3) was associated with water hyacinth (*Eichornia* sp.). Mid-day water temperatures were relatively low (range: 27.5°-30°C); water temperatures at sites with a heavy cover of hyacinth averaged 2°C less than sites with few or no floating plants. Group #1 contained a diverse and abundant fauna, including *An. albimanus*, *Anopheles pseudopunctipennis* Theobald, *Anopheles triannulatus* (Neiva and Pinto), and *Culex* spp. *Anopheles albimanus* pupae and higher instar larvae were particularly abundant at sites where other animals in Group #1 were also abundant.

Atlantic Group #2 (TABLE 3) consisted of plants and animals associated with sites that had a minimum of bushes or trees at the edge of the water, so the water was fully exposed to the sun. Duckweed (*Lemna* sp.) was often the dominant plant. If the pond was not heavily covered with duckweed, first instar *An. albimanus* larvae were more abundant in association with this floral/faunal group than any other group in the Atlantic region. Other larval instars of *An. albimanus*, as well as pupae, were common as well. However, there were virtually no *An. albimanus* larvae or pupae if the duckweed cover was greater than 85%.

Anopheles albimanus larvae and pupae were a significant part of Atlantic Group #3, which included submersed vegetation and large numbers of aquatic Heteroptera. First instar *An. albimanus* larvae were positively associated with Atlantic Group #4, which included grass at the water's edge and crustaceans such as shrimp and small species of cyclopoid copepods.

TABLE 3. Groups of associated flora and fauna in the Atlantic region, based on factor analysis of all variables in TABLE 1 and TABLE 2.[1]

Group 1 (15.8%).
Dytiscids (.87), plaeids (.82), *Anopheles triannulatus* and *Anopheles pseudopunctipennis* (.80), damselflies (.78), stratiomyids (.74), hydrophilids (.73), *Culex* (all instars) (.70), naucorids (.58), chironomids (.56), water hyacinth (.55), grass at edge of water (-.53), dragonfly nymphs (.52), ***An. albimanus* pupae** (.51), large cyclopoids (.50), temperature (-.50), cladocera (.49), ostracods (.47), **fourth instar *An. albimanus*** (.46), belostomatids (.44), notonectids (.37), **third instar *An. albimanus*** (.36), nepids (.35), mesovelids (.34).

Group 2 (7.9%).
Veliids (.70), tadpoles (.70), duckweed (.67), **first instar *An. albimanus*** (.63), mesoveliids (.63), calanoids (.53), **second instar *An. albimanus*** (.52), **fourth instar *An. albimanus*** (.49), **third instar *An. albimanus*** (.47), ***An. albimanus* pupae** (.41), hydrophilids (.39), belostomatids (.38), large cyclopoids (-.36), shrimp (-.33), collembola (.33), corixids (.32), trees and bushes (-.30), fish (-.30).

Group 3 (6.9%).
Hebrids (.84), nepids (.72), **third instar *An. albimanus*** (.54), ***An. albimanus* pupae** (.53), dragonfly nymphs (.53), **second instar *An. albimanus*** (.51), belostomatids (.50), **fourth instar *An. albimanus*** (.43), naucorids (.38), submersed plants (.38), chironomids (.38), mayfly nymphs (.34), **first instar *An. albimanus*** (.33), damselfly nymphs (.30).

Group 4 (6.1%).
Shrimp (.83), small cyclopoids (.71), mayfly nymphs (.67), notonectids (.64), pH (.41), grass at edge of water (.36), flowering plants (.34), plaeids (.32), **first instar *An. albimanus*** (.30).

Group 5 (5.9%).
Small cyclopoids (.72), misc. diptera (.67), fish (.56), mites (.56), misc. coleoptera (.52), ostracods (-.51), cladocera (-.45), grass at edge of water (.36).

[1]Percentage of total variation explained by each group is in parentheses after the group number. Factor loadings are in parentheses after each variable. A negative factor loading indicates negative association with the group.

Atlantic Group #5 was characterized by the presence of fish, the presence of small species of cyclopoid copepods (instead of large species), and the absence of ostracods and cladocera (TABLE 3). *Anopheles albimanus* larvae and pupae were not a significant part of Atlantic Group #5.

Results from stepwise multiple regressions (TABLE 4) reflected many of the associations identified by the factor analysis. Each of the positive regression coefficients in TABLE 4 represents a group of intercorrelated variables in TABLE 3. (i.e., most of the variables listed in TABLE 4 are also in TABLE 3, where they have the same relation with *An. albimanus*. The variables selected by multiple regression for TABLE 4 are the best predictors of juvenile *An. albimanus* abundance.)

Faunal variables predominate in TABLE 4; no physical/chemical or floral variables had significant regression coefficients, except for grass at the water's edge. Third/fourth instar *Culex* larvae, veliid or nepid bugs, and grass at the edge of the water were the best predictors of sites with large numbers of *An. albimanus* larvae or pupae. Hydrometrid bugs were a strong negative predictor for all juvenile stages of *An. albimanus*.

All variables with strong negative regression coefficients also had strong negative rank correlations, typically in the range of -0.3 to -0.5. Although fish did not have regression coefficients strong enough to appear in TABLE 4, there was a strong negative rank correlation between fish and *An. albimanus* larvae (r=-.45, P<.01) and pupae (r=-.51, P<.001).

Pacific Region

There were *An. albimanus* larvae at 81% of the sites sampled in the Pacific region. Where larvae were present, the number of first instars per meter dragged by the plankton net ranged from 0.1 to 127, second instars ranged from 0.1 to 31, third instars ranged from 0.03 to 8, and fourth instars ranged from 0.05 to 52. Only 26% of the sampled sites had *An. albimanus* pupae, ranging from 0.1 to 5 pupae per net meter.

The factor analysis revealed five groups of fauna and flora in the Pacific region (TABLE 5). *Anopheles albimanus* larvae or pupae were positively or negatively associated with each of the groups except one.

The faunal composition of Pacific Group #1 (TABLE 5) was similar to Atlantic Group #1 (TABLE 3), except Pacific Group #1 had lower diversity of animals than did Atlantic Group #1. First instar *An. albimanus* larvae were negatively associated with Pacific Group #1, in part because Pacific Group #1 included duckweed, and *An. albimanus* larvae were absent if the

TABLE 4. Results of stepwise multiple regression analysis for the Atlantic region.

Stage[1]		Significant independent variables[2]
1st instar ($R^2 = .74$)[3]	Positive:	*Culex*[4] (.50±.10)
		veliids (.34±.09),
		water depth (.32±.09)
		tadpoles (.26±.10)
		small cyclopoids (.20±.09)
	Negative:	large cyclopoids (-.39±.11)
		hydrometrids (-.25±.09)
2nd instar ($R^2 = .75$)[3]	Positive:	veliids (.35±.11)
		nepids (.35±.09)
		Culex[4] (.32±.09)
		grass at edge of water (.28±.11)
		small cyclopoids (.26±.09)
	Negative:	hydrometrids (-.21±.09)
3rd instar ($R^2 = .92$)[3]	Positive:	veliids (.45±.07)
		nepids (.43±.06)
		Culex[4] (.41±.06)
		area of water body (.35±.07)
		small cyclopoids (.23±.06)
		grass at edge of water (.19±.07)
	Negative:	salinity (-.27±.07)
		hydrometrids (-.26±.05)
4th instar ($R^2 = .95$)[3]	Positive:	veliids (.44±.05)
		nepids (.42±.05)
		Culex[4] (.41±.06)
		dytiscids (.32±.07)
		grass at edge of water (.30±.06)
	Negative:	salinity (-.47±.06)
		hydrometrids (-.34±.07)
		misc. beetles (-.27±.05)
Pupae ($R^2 = .77$)[3]	Positive:	nepids (.46±.09)
		Culex[4] (.43±.09)
		small cyclopoids (.41±.09)
		grass at edge of water (.27±.09)
	Negative:	hydrometrids (-.28±.09)
		mayfly nymphs (-.27±.10)

[1]Dependent variables are each juvenile stage of *An. albimanus*.

[2]Significant independent variables (P<0.05). Normalized partial regression coefficients and their standard errors are shown in parentheses.

[3]R^2 = percent of total variation in the dependent variable explained by the listed independent variables.

[4]III/IV instars.

cover of duckweed was complete. Mid-day oxygen was relatively low (0.5-1.7 ppm), and pH was low (5.8-5.9). Water hyacinth was not part of Pacific Group #1. No hyacinth was found at the sites sampled in the Pacific region.

Pacific Group #2 (TABLE 5) was associated with small, shallow bodies of water fully exposed to the sun. Mid-day water temperatures (27°-30°C) and dissolved oxygen (3.5-8.5 ppm) were higher than at other sites. There were seldom fish, and there were large numbers of *Culex* larvae. Early instar *An. albimanus* larvae were more positively associated with Pacific Group #2 than any other group.

Pacific Group #3 (TABLE 5) was associated with floating-leafed plants, as well as flowering plants along the shore. Tadpoles were usually abundant. *Anopheles albimanus* larvae and pupae were neither positively nor negatively associated with Pacific Group #3.

Pacific Group #4 (TABLE 5) was associated with bushes or trees at the edge of the water. The water was shaded, so mid-day water temperatures (24°-26°C) and oxygen (0.8-2.5 ppm) were relatively low. First instar *An. albimanus* larvae were conspicuously absent from Group #4, but *Anopheles punctimacula* Dyar and Knab larvae were a major part of this group.

Pacific Group #5 (TABLE 5) was associated with small water bodies that lacked aquatic plants such as reeds and floating-leafed plants. Group #5 had an abundance of zooplankton (clacoderans and small species of cyclopoid copepods), which were not a prominent part of the other floral/faunal group associated with small water bodies (Pacific Group #2). *Anopheles albimanus* pupae and higher instar larvae were more abundant in association with Group #5 than any other floral/faunal group in the Pacific region.

In stepwise multiple regressions for the Pacific region (TABLE 6), third/fourth instar *Culex* larvae and cladocera were the best predictors of the abundance of late-instar *An. albimanus* larvae and pupae. Dytiscid beetle larvae were the best negative predictors of *An. albimanus* larvae and pupae.

As in the Atlantic region, rank correlations for the Pacific region were in agreement with negative regression coefficients. In addition, malacostracan shrimp had significant negative rank correlations with *An. albimanus* larvae ($r=-.42$, $P<.01$) and pupae ($r=-.32$, $P<.01$) in the Pacific region.

TABLE 5. Groups of associated flora and fauna in the Pacific region, based on factor analysis of all variables in TABLE 1 and TABLE 2.[1]

Group 1 (13.0%).
Misc. coleoptera (.93), plaeids (.87), misc. diptera (.86), duckweed (.79), hydrometrids (.55), mayfly nymphs (.52), shrimp (.51), pH (-.45), notonectids (.45), chironomids (.45), dytiscids (.40), veliids (.36), **first instar *An. albimanus*** (-.30).

Group 2 (9.9%).
Culex (all instars) (.85), dragonfly nymphs (.77), **first instar *An. albimanus*** (.76), **second instar *An. albimanus*** (.67), water temperature (.66), chironomids (.66), oxygen (.52), water depth (-.49), fish (-.33), area(-.30).

Group 3 (9.4%).
Belostomatids (.81), tadpoles (.80), mesoveliids (.76), damselfly nymphs (.62), floating-leaved plants (.59), flowering plants (.42), pH (.37).

Group 4 (9.3%).
Anopheles punctimacula (.91), hydraenids (.81), grass at edge of water (-.74), dytiscids (.68), oxygen (-.50), trees and bushes (.50), **first instar *An. albimanus*** (-.30), water temperature (-.30).

Group 5 (6.7%).
Emergent plants (-.74), cladocera (.67), **third instar *An. albimanus*** (.66), **fourth instar *An. albimanus*** (.63), ***An. albimanus* pupae** (.56), area of water body (-.63), small cyclopoids (.56), mites (.50), pH (.34), oxygen (-.33), floating-leaved plants (-.32), collembola (.30).

[1]Percentage of total variation explained by each group is in parentheses after the group number. Factor loadings are in parentheses after each variable. A negative factor loading indicates negative association with the group.

TABLE 6. Results of stepwise multiple regression analysis for the Pacific region.

Stage[1]		Significant independent variables[2]
1st instar (R^2 = .45)[3]	Positive:	temperature (.51±.15)
		collembola (.50±.15)
	Negative:	(no significant variables)
2nd instar (R^2 = .44)[3]	Positive:	*Culex*[4] (.67±.17)
	Negative:	dytiscids (-.51±.17)
3rd instar (R^2 = .88)[3]	Positive:	*Culex*[4] (.94±.11)
		cladocera (.50±.09)
		grass at edge of water (.24±.09)
		small cyclopoids (.20±.09)
	Negative:	dytiscids (-.41±.11)
		dragonfly nymphs (-.50±.15)
		hydraenids (-.31±.10)
4th instar (R^2 = .89)[3]	Positive:	*Culex*[4] (1.15±.11)
		cladocera (.72±.10)
		belostomatids ((.24±.09)
	Negative:	dytiscids (-.69±.11)
		dragonfly nymphs (-.37±.10)
Pupae (R^2 = .89)[3]	Positive:	cladocera (.87±.10)
		Culex[4] (.72±.10)
		duckweed (.72±.10)
		stratiomyids (.31±.10)
		belostomatids (.27±.09)
	Negative:	dytiscids (-.75±.12)
		large cyclopoids (-.45±.11)
		hydrometrids (-.35±.09)

[1]Dependent variables are each juvenile stage of *An. albimanus*.

[2]Significant independent variables (P<0.05). Normalized partial regression coefficients and their standard errors are shown in parentheses.

[3]R^2 = percent of total variation in the dependent variable explained by the listed independent variables.

[4]III/IV instars.

DISCUSSION

Ideally, it would be desirable to identify discrete floral/faunal communities, some of which include *An. albimanus* and others of which do not. Dominant vegetation or other flora/faunal indicators in each community could facilitate prediction of the magnitude of *Anopheles* production.

Although we did not find biological communities that were completely distinct from one another, we did find consistent associations among many of the aquatic plants and animals. *Anopheles albimanus* larvae and pupae had a discernable relation (positive or negative) with most of these floral/faunal groups, the connection generally being stronger with the fauna than with the flora. Among the physical/chemical factors that we measured, only salinity appeared to be of consequence to the distribution of *An. albimanus* larvae.

Although there were similarities between the floral/faunal groups in the Pacific and Atlantic regions (particularly Group #1 in each region), the floral/faunal groups in the two regions were far from identical. This is not surprising, considering the physical differences between aquatic habitats of the two regions. We found a greater diversity of flora and fauna in the Atlantic region, apparently because many of the water bodies that served as larval habitat for *An. albimanus* in the Atlantic region were larger than those in the Pacific region.

One of the most important findings of the survey was that some sites had large numbers of all larval instars of *An. albimanus* as well as pupae, while other sites had large numbers of early instar larvae but no pupae. Most sites without pupae also lacked fourth instar larvae. Sites that have large numbers of larvae because they are attractive to oviposition are not necessarily the best sites for larval survival and the production of adult mosquitoes.

Despite differences between the floral/faunal groups of the Pacific and Atlantic regions, the relation of *An. albimanus* larvae and pupae to floral/faunal groups was similar in both regions. In both regions first instar *An. albimanus* larvae (which we consider to reflect oviposition) were associated with sun-exposed sites, particularly sites with grass at the edge of the water. Sites that were shaded by trees or bushes at the edge of the water, or completely covered with floating plants such as duckweed, were least favored for oviposition.

Anopheles albimanus pupae (and presumably the production of adult mosquitoes) were associated with two ecological factors. First was food supply, as indicated by the abundance of *An. albimanus* pupae at sites with an abundance of animals (e.g., *Culex* larvae or cladocera) that feed on algae. Sites with large numbers of these animals had abundant phytoplankton (or submersed vegetation covered with periphyton), and the guts of *An. albimanus* larvae at these sites contained large quantities of microalgae. The hypothesis that microalgae are a key resource for *An. albimanus* production is compatible with the observation of Savage et al. (1990) and Rejmankova et al. (1993) that *An. albimanus* larvae were associated with planktonic algae and periphyton in Mexico and cyanobacterial mats in Belize.

Predation was the second factor of importance to the abundance of *An. albimanus* pupae in our survey. Curiously, most predators of mosquito larvae were positively associated with *An. albimanus* larvae and pupae, apparently reflecting a positive response of all fauna, whether predator or prey, to sites with a high level of biological productivity. Only two kinds of predators—fish and hydrometrid nymphs—had a consistent negative association with *An. albimanus* larvae and pupae in both Atlantic and Pacific regions. The negative association with hydrometrids was most striking. No *An. albimanus* pupae were observed at any sites in the Pacific or Atlantic regions where hydrometrids were present, though *An. albimanus* pupae were found at 44% of the sites without hydrometrids (contingency table chi-square=7.07, df=1, P<.01). Dytiscid larvae and dragonfly nymphs were negatively associated with *An. albimanus* in the Pacific region.

Marten et al. (1989) reported a strong negative association between large cyclopoid copepods and juvenile *An. albimanus* from the first 42 sites sampled in this study. After all 69 sites were sampled, large cyclopoids had negative rank correlations with *An. albimanus* larvae and pupae ranging from -.24 to -.28. It appears the full magnitude of negative association between the most effective cyclopoid predators and *An. albimanus* was obscured by grouping all larger cyclopoid species for the statistical analyses reported here; large cyclopoids included *Mesocyclops longisetus* (a more effective predator) and *Mesocyclops venezolanus* (a less effective predator).

What are the implications of this study's findings for control of *An. albimanus*? While water hyacinth was identified as an indicator of *An. albimanus* production, the study did not identify other macrophytes to signal production at sites without water hyacinth. However, some plants appear to be reliable as indicators of sites that do not produce *An. albimanus*. Production was low from sites that were completely shaded by trees, and a complete cover of small floating plants such as duckweed excluded *An. albimanus* larvae from a site. It might be practical to plant shade trees around small water bodies that would otherwise produce *An. albimanus*. Small floating plants (e.g., duckweed or *Salvinia*) might be used to render breeding sites unsuitable (Hobbs and Molina 1983; Margaret Dix, personal communication).

Planktonic, epiphytic, and benthic microalgae appear to be the most reliable indicators of a site's capacity to produce *An. albimanus*. The practical significance of microalgae for *An. albimanus* control requires further study, which should be specific with regard to the kind of algae, because some algae are nutritious for *An. albimanus* larvae and others are not (Marten 1986). It is possible that *An. albimanus* production could be reduced if microalgae were suppressed by chemical or biological means or if nutritious algae were replaced by algae that are not nutritious.

Results from the survey point to specific predators of possible use for biological control: fish, hydrometrid nymphs, large cyclopoid copepods, and dytiscid larvae. While fish are in common use, copepods have been used for *Anopheles* control only in field trials (Marten et al. 1994). Dytiscids and hydrometrids are known to prey on mosquito larvae (Mijares and Broche 1985; G. G. Marten, personal observation), but they have not been used for operational mosquito control.

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