UNIVERSITY OF FLORIDA
EXTENSION
Institute of Food and Agricultural Sciences

ENY70034

Mosquito Control Handbook: Salt Marshes and Mangrove Forests [1]

S.A. Ritchie[2]

In 1992 we celebrated the 500th anniversary of Columbus's discovery of the New World. This event paved the way for the development of western culture and was the beginning of the end for native American civilizations. Incas, Mayans, Aztecs - all fell with amazing speed to the marauding Spaniards with their gunpowder and pathogens. All but one. For although Ponce de Leon thought Florida was the land of the fabled fountain of youth, the rains of summer brought the one native American the Spaniards were no match for: the saltmarsh mosquito. It has only been through the scientific advances of the last 50 years that these "defenders of the Everglades" have been conquered.

Why does Florida produce mosquitoes in numbers thick enough to drive the conquistadors away? Only by understanding Florida's mosquito machine can we devise ways to combat it.

The Salt Marsh Environment

Florida's 1,200 miles of coastline, flat topography and subtropical climate drive its salt marsh mosquito machine. The nearly constant warmth and powerful sunshine provide the energy to make the 1,500 square miles of salt marsh and mangrove swamps a seemingly primordial soup. These are the nursery ground for the multitude of shrimp, crabs and fish that garnish our table as well as the uncountable mosquitoes that dine on us. The flat topography ensures that much of the coastline will be mosquito-producing salt marsh.

Technically, a salt marsh is a bed of rooted vegetation, typically dominated by nonwoody shrubs and grasses, that at some point is inundated by tide. Florida has three general types of salt marshes. North and Panhandle areas feature grass marshes (see Figure 1 a and b). Scrub salt marshes (Figure 2) dominate the east central coast. In south Florida, mangrove swamps dominate (Figure 3). Salt marshes can be further subdivided into high and low marsh,

1. This document is ENY-700-3-4, part of the Mosquito Control Handbook, published cooperatively by the Department of Entomology and Nematology, University of Florida; the Florida Medical Entomology Laboratory, Vero Beach; the Florida Department of Health and Rehabilitative Services, Office of Entomology Services (HRS-ES), Jacksonville; the Florida Mosquito Control Association (FMCS); the St. Lucie County Mosquito Control District; the Indian River Mosquito Control District; the Pasco County Mosquito Control District; Polk County Environmental Services; and the USDA Medical and Veterinary Entomology Research Laboratory, Gainesville, Florida. ENY-700-3-4 was revised December 1992; reviewed March 2000. The electronic edition of the Mosquito Control Handbook is provided by the Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, 32611. Please visit the EDIS Web site at **http://edis.ifas.ufl.edu**.
2. S.A. Ritchie, Worked as entomologist with the Collier Mosquito Control District, Naples, Fla., from 1981 to 1992. Now is a research officer at the Queensland Institute of Medical Research in Brisbane, Queensland, Australia.

each of which has distinctive vegetation. The low marsh is flooded almost daily by tides. Where it intersects the high marsh, a slight levee or berm is formed that prevents daily tidal flooding of the high marsh. Behind this berm the high marsh forms a shallow basin that retains water and is the breeding ground for saltmarsh mosquitoes.

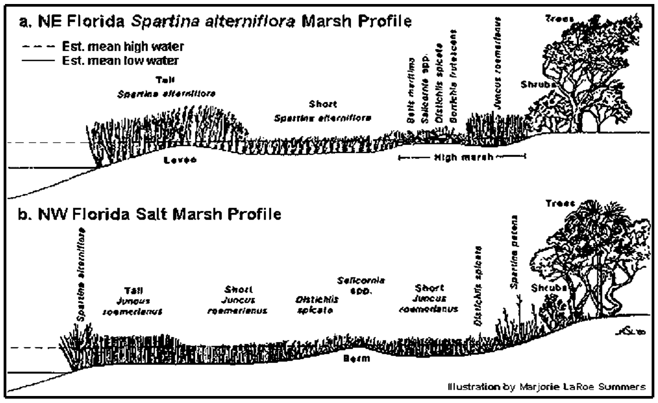


Figure 1. Grass marshes are characterisic of north Florida and the Florida Panhandle.

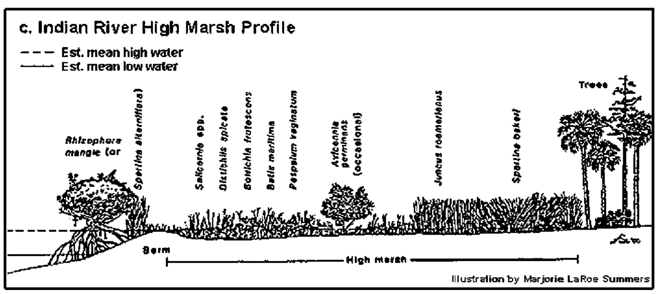


Figure 2. Scrub salt marshes dominate the east central coast of Florida.

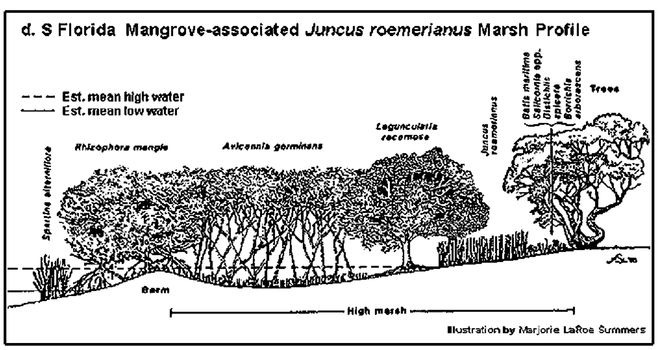


Figure 3. In south Florida, mangrove swamps dominate.

Exceptions to these generalities exist. Slight elevation changes can create high marsh islands within the low marsh. While mangrove basin forests are typically dominated by black mangrove (Avicennia germinans), forests dominated by red mangrove (Rhizophora mangle) and white mangrove (Laguncularia racemosa) can produce saltmarsh mosquitoes.

Types of Saltmarsh Mosquitoes

The high marsh is the home of many species of mosquitoes in Florida. Saltmarsh mosquitoes can by characterized as:

- Residents that are restricted to salt marsh habitat; and
- Transient freshwater species that tolerate brackish water and are occasionally found in the salt marsh.

Resident saltmarsh mosquitoes include the black saltmarsh mosquito (Aedes Taeniorhynchus) and the eastern saltmarsh mosquito (Aedes sollicitans). Aedes sollicitans is predominant in north Florida, especially from fall through spring, and is almost exclusively a grass or scrub marsh mosquito. Interestingly, these mosquitoes are known to breed in inland locations where spray irrigation of phosphate-rich agricultural wastewater occurs. Aedes taeniorhynchus breeds in all three types of salt marshes and is predominant in summer, although this can vary year to year.

Other salt marsh residents include Anopheles atropos, Anopheles barberi, Anopheles bradleyi and Deinocerities cancer. The anophelines, while locally common, do not transmit malaria and are not serious pests. Di. cancer is noteworthy in that it only breeds in holes of the land crab Cartesoma along the southeast coast of Florida. It bites man but is not a major pest. Other pestiferous flies that are salt marsh residents include sand flies, deer flies and horse flies.

Transient saltmarsh mosquitoes are limited to salt marshes rarely flooded by the tide. I have found eggshells and larvae of freshwater mosquitoes such as Aedes atlanticus and Psorophora ciliata in brackish-water mangrove forests. These sites are also an important source of Culex nigripalpus. Occasionally, Culex opisthopus is encountered in south Florida crab holes. No doubt many other freshwater mosquitoes infiltrate the high marsh after heavy rains lower water salinity. Adult Wyeomyia and Aedes mitchellae often reside in the salt marsh despite breeding only in freshwater.

While some saltmarsh mosquitoes (residents) have potential to transmit several arboviruses, none are important vectors in Florida. However, Ae. sollicitans is an important vector of eastern encephalitis in New Jersey, and both saltmarsh Aedes vector dog heartworm.

Saltmarsh Aedes

Life cycle

Aedes sollicitans and Ae. taeniorhynchus, being the most pestiferous saltmarsh mosquitoes, will be the center of discussion regarding saltmarsh mosquito ecology.

Saltmarsh Aedes are floodwater mosquitoes. Eggs are laid on exposed salt marsh soil and following three to seven days of incubation, can hatch when flooded by rain or tide. Hatching rates are over 90 percent in summer but can drop to near zero in cold winter weather. Although eggs can purportedly survive over one year. Most either hatch or are eaten (50 percent die each month in summer). The larvae, feeding on leaf litter and associated microbes, often form dense aggregates, termed balls. Development to adult takes from six to 21 days, depending on temperature.

Adult emergence is complete in two to three days. A strong migratory drive, especially in Ae. taeniorhynchus, can result in the sudden appearance of millions of mosquitoes in urban areas many miles from breeding sites. Migrations have been dense enough to confound radar signals and force drivers to use their windshield wipers. Adults mate within 48 hours of emergence, then females seek a blood meal. In south Florida, most females are autogenous, laying a small egg batch (about 25 eggs) without a bloodmeal. A bloodmeal (typically from mammals, although birds and even sea turtles are a source) enables her to lay 50 to 200 eggs. Adult females are relatively long-lived, with an estimated summer survival of 80 percent per day; thus, after two weeks, 4 percent of a brood is still alive.

Why the high marsh?

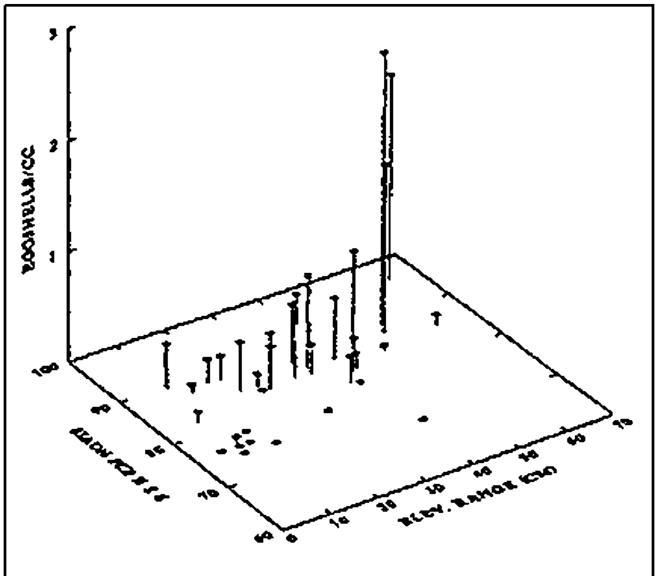
Why is mosquito production limited to the high marsh? This question is best answered in reverse: Why aren't mosquitoes produced in the low marsh? Mosquito larvae, like humans, share the basic needs of a home that offers food and security. Literally speaking, larvae need water with a rich nutrient source and security from predators, namely fish. In this respect, the low marsh fails. Low marshes are typically sloped toward the ocean and thus don't hold water long enough for larval development. Even low marshes with basins and ponds that retain water are poor larval habitat because frequent tidal flooding prevents oviposition, flushes nutrients and introduces fish.

Why is Florida so prone to saltmarsh Aedes?

History clearly shows that Florida is unique. Coastal areas of the United States north of Florida, despite mosquito-infested salt marsh, developed many thriving ports of commerce. While not totally responsible for this, the magnitude of Florida's mosquito problems no doubt played a role in reducing urban development. In south Florida, the subtropical climate allows for year-round salt marsh Aedes production, and the extensive coastline and flat topography create a disproportionate area of salt marsh. And Florida's low latitude location creates the perfect tide regime for the creation of high marsh.

Tidal range (height difference between high and low tide) is greatest in middle latitudes due to intense Coriolis force, culminating in the 40-foot tidal ranges in the Bay of Fundy in New Brunswick (45 degrees N). Maurice Provost, former director of the Florida Medical Entomology Lab in Vero Beach, recognized that the relative area of high marsh increased as tidal range decreased. Why? Consider two salt marshes of equal slope. A storm tide of 3 feet would represent an increase of 30 percent for a tidal range of 10 feet versus a 150 percent increase for a salt marsh with a 2-foot tidal range. Thus these annual high tides (be they storm or astronomical) cover disproportionately more area in low latitude, low tidal range salt marshes. Is it any wonder that the Florida Keys (Flamingo) with a tidal range of 2 feet, produce so many salt marsh mosquitoes?

Mosquito production, as measured by the number of eggs, in the high marsh is affected by topography as well as tides. My work with mangrove basin forests demonstrated that mosquito production increases exponentially with berm height (and thus tidal flooding frequency) and elevation range (Figure 4). As suggested earlier, mosquito production at tidally flushed sites would be low. But why would a mangrove forest flooded by less than 5 percent of the tides be the greatest mosquito producer? The key may be that these sites, almost exclusively flooded by rain, contain few fish. Mosquitoes (Anopheles punctipennis) have been shown to avoid ovipositing on water containing fish and tadpoles. This would explain why Ae. taeniorhynchus oviposits on exposed soil in a partially flooded site only if it is relatively fish-free. Finally, the association of elevation range with increased mosquito production reflects the propensity for ponds and potholes to produce more salt marsh Aedes than the surrounding salt marsh.



Relationship of eggshell concentration to the basin spillover elevation (BSE) and elevational range in mangrove basin forests. The BSE is the berm height and reflects tidal flooding frequency. In this case, the eggshell threshold occurs at a BSE of 75 cm or a tidal flooding frequency of 14 percent.

Figure 4. Mosquito production increases exponentially with berm height (and thus tidal flooding frequency) and elevation range.

The Annual Saltmarsh Mosquito Cycle

We can use these relationships to understand the saltmarsh Aedes annual cycle, based on the distinctive wet-dry season of south Florida mangroves. Mangrove basin forests can be grouped as follows:

- **Type I:** Low-bermed, low elevation, tidally flooded
- **Type II:** High-bermed, low elevation, rain-flooded with ponds and potholes
- **Type III:** High-bermed, high elevation, rain-flooded with no deep ponds

Starting in late winter and early spring, low tides and the lack of rain dry the mangrove swamps, killing fish and exposing the area for oviposition. Monthly high tides and infrequent frontal rains hatch small broods in types I and II mangrove forests, while a low water table limits oviposition and hatching in Type III sites.

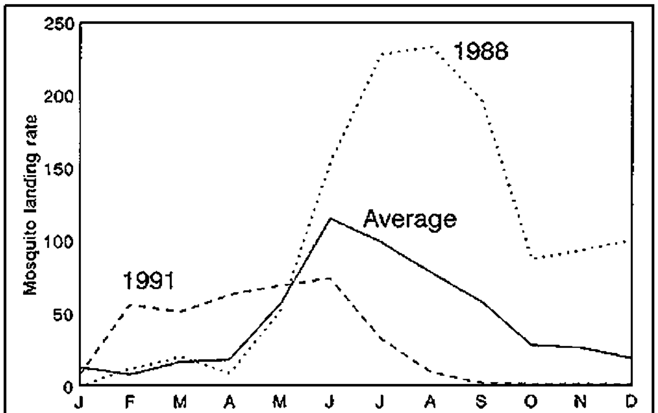
As spring arrives, warmer weather and higher tides hatch additional broods, of which the relative number and size increase with each tidal flooding. A computer simulation that assumes 50 percent larval mortality for each brood estimates that egg populations increase eight fold with each successive brood. By late spring, a considerable eggbank has accumulated, especially in Type II sites.

The initial rains of the rainy season result in widespread flooding, hatching tremendous broods. If rains are scattered or intermittent, further "cycling" can result in even larger broods. Eventually, Type II mangrove swamps become submerged, fish such as Gambusia gain access, and mosquito production ceases. Gravid females, searching far and wide for the few remaining oviposition sites (Type III), are subject to increased mortality. Saltmarsh Aedes populations dwindle to a small fraction of their earlier level.

Fall brings an end to the rainy season, and broods emerge only occasionally from sites previously dry or containing few fish. These mosquitoes serve to carry over the population into winter.

Significant changes in the geographical or weather pattern can dramatically impact saltmarsh mosquito production. Sanibel Island, off the coast of Fort Myers, Fla., Lee County, once featured a perimeter of relic beach dunes that surrounded a large inland slough dominated by cordgrass (Spartina bakeri). This slough was a giant Type III salt marsh, serving as the oviposition site for broods hatched at the start of the rainy season in the mangroves. Later, rains would hatch this giant eggbank of up to half a billion eggs per acre, producing the enormous late summer/early fall population of Ae. taeniorhynchus that Sanibel was famous for prior to water management practices.

Weather patterns also alter saltmarsh mosquito production. The summer drought of 1988 delayed the rainy season for one month in Naples, Fla., allowing one extra tidal brood in June and additional eggbank deposits. The subsequent heavy rains of July hatched a huge brood that killed cattle and confounded the Miami radar. Conversely, it is little wonder that 1991 saltmarsh mosquito populations petered out early, considering the wet winter and early rainy season. (Figure 5)



The annual cycle of Ae. taenioryhnchus as depicted by Marco Island, Fla, landing rate counts. The average cycle peaks sharply in June, then slowly declines as the water table rises, inundating breeding sites. A delay in the rainy season (1988) dramatically increased and prolonged populations while a wet January, coupled with an early rainy season, reduced production.

Figure 5. 1991 saltmarsh mosquito populations petered out early, considering the wet winter and early rainy season.

The 10,000 islands of southwest Florida contain yet another type of mangrove basin forest that may be the most prolific producer of Ae. taeniorhynchus. The hanging or perched mangrove forest features an exceptionally high berm that prevents tidal inundation by all but storm tides. These sites are flooded primarily by rain and lack the high populations of fish associated with tidally flooded sites. Interestingly, these sites are exclusively subjected to Ae. taeniorhynchus oviposition even when submerged, with eggs being laid on adjacent upland soil. Thus, perched mangrove forests serve as refuge for mosquitoes when other sites are flooded and cannot be used for oviposition. Because these forests often contain deep ponds, they have the potential to produce Ae. taeniorhynchus throughout the year, with winter and spring broods serving as "seed broods" for other mangrove forests.

Mortality

Mortality of saltmarsh mosquitoes is caused by a number of factors. Eggs are preyed on by a number of invertebrates, including ants, beetles, isopods, amphipods and snails. Larvae fall victim to aquatic insects and especially fish. Larval diseases are caused by fungal, protozoan, nematode and viral agents, although only rarely do they have much impact (Table 1). Stranding due to drought or flushing by extreme tides can decimate broods, as can starvation due to overcrowding. Adults are subject to predation on the wing by dragonflies, birds and bats. Predation of resting mosquitoes is little-studied but could be significant; I have seen ants feeding on emerging adults and pupae in a recently dried-out swamp. Adult disease is little-understood but could be a promising biocontrol agent. Mortality due to weather (freezes, drought and storms) could also be significant.

Surveillance

Eggs

Control of saltmarsh mosquitoes utilizes many of the methods used for other mosquitoes. Before control can be initiated, mosquitoes must be detected by surveillance. Egg surveillance is generally labor-intensive and therefore unpopular. Salt marsh soil can be sampled with a mason's trowel or golf hole corer. Thick detrital soils of mangrove forests can be sampled by grabbing a handful of moist leaf litter. Samples are commonly stored in plastic deli cups or Ziplokr bags.

Soil is processed for eggs by sieving, then isolating eggs with bleach, or by floating in a saturated salt or sugar solution. The easiest method is to incubate the soil sample for three to seven days, flood with dilute yeast solution to hatch the eggs, and count larvae 24 to 48 hours later. Eggshell sampling is a new method used to identify oviposition sites and relative mosquito production based on the concentration of eggshells (shells from previously hatched eggs) in the soil. A soil corer made from a plastic syringe is used to take 10 to 20 soil cores that are then sieved and processed for eggshells. The advantages of eggshell sampling include:

- the soil can be sampled anytime, even if flooded;
- small sample volume and number;
- a site need be sampled only once;
- it will detect an oviposition site in the absence of larvae or live eggs.

Larvae

Larval sampling is primarily done using a 300 ml white plastic dipper. Numerous sampling regimes exist, with most applicable to research. The most underrated surveillance method is observation. Careful observation of marsh water can detect larvae where random dipping would not; this is especially true of low density populations. Also, larval balls and pupal rafts create a shimmering water surface that can be seen at a great distance.

Adults

Adult surveillance is done using landing rates and various traps. Landing rates are effective due to the daytime aggressiveness of salt marsh mosquitoes. Although variations exist, landing rates consist of counting the mosquitoes that land on a particular body part over a specified time period. Traps commonly employed to monitor saltmarsh mosquitoes include New Jersey and CDC light traps and suction traps. Often these are baited with CO2 and or octenol, which is particularly attractive to Ae. Taeniorhynchus. Saltmarsh mosquitoes are also monitored indirectly by service requests and intuition (e.g., expect an increase in mosquitoes one to two weeks after a large rain).

Control

Control of saltmarsh mosquitoes is largely dictated by the salt marsh habitat (see chapters on control techniques for greater detail). Pesticide use may be restricted or illegal. Historically, source reduction by filling, ditching and impounding have had great success in controlling saltmarsh Aedes. This represents one of the few instances where the egg stage (specifically oviposition) has been targeted. Although not practical in Florida, fire has been shown to effectively kill saltmarsh Aedes eggs in South Carolina. Larval control is primarily done using insecticides, although oil was once commonly used. Organophosphates such as temephos (Abater) and the insect growth regulator methoprene (Altosidr) are commonly used. Bacillus thuringiensis israliensis (B.t.i.) is also popular, although Bacillus sphaericus is not effective. Fish populations are augmented by ditching and establishment of refuge ponds.

Fenthion (Baytexr), malathion and naled (Dibrom ULVr) are effective against saltmarsh mosquitoes using ground or aerial equipment. There is some resistance to malathion in certain populations.

Speculations on the Future

The future will undoubtedly hold many saltmarsh mosquitoes in Florida. However, two of the headliner issues, habitat loss by development and global warming, may have a silver lining for mosquito control. Many of the mangrove areas near Naples, despite state regulations, are being converted into upland asphalt ecosystems. Global warming, if delivered as promised, will raise the sea level, destroying the marshes. Because much of the upland area adjacent to salt marshes is developed, we have a net loss of salt marsh and its mosquitoes.

Future surveillance and control will increasingly center on techniques that utilize computer technology while minimizing pesticide use. Eggshell surveys can be used to pinpoint breeding sites. Larval surveillance may rely on telemetried tide and rain data from remote gauges and radar. Models could be used to anticipate broods based on hydrologic inputs. Climatic indicators, such as winter rainfall, could be used to make long-range mosquito forecasts. Solar-powered larval or adult traps and sensors could transmit data directly into your field computer.

Control efforts will increasingly focus on biocontrol and spot treatment. Common marsh organisms such as algae may be bioengineered to produce larval toxins. Baits and pheromones might be used to control adults by disrupting mating, removal trapping or attracting mosquitoes away from people. New insecticides may be used as a barrier against migrating adults. No doubt many other new techniques will evolve. But application of new technology depends on affordability, foresight and adaptability.

References

Florida Salt Marshes and Mangroves

Myers, R.L. and J.J. Ewel. 1990. Ecosystems of Florida. Univ. Central Florida Press, Orlando.

Provost, M.W. 1973. Mean high water mark and use of tidelands in Florida. Fla. Scientist 36: 50-66.

Provost, M.W. 1976. Tidal datum planes circumscribing salt marshes. Bull. Mar. Sci. 26: 558-563.

Saltmarsh Mosquitoes

Addison, D.S., S.A. Ritchie, L. A. Webber and F. Van Essen. 1992. Eggshells as an index of aedine mosquito production: II. the relationship of Aedes taeniorhynchus eggshell density to larval production. J. Amer. Mosq. Control Assoc. 8: 38-43.

Nayar, J.K., ed. 1985. Bionomics and physiology of Aedes taeniorhynchus and Aedes sollicitans, the saltmarsh mosquitoes of Florida (summary chapters on physiology, ecology and control). Institute for Food and Agricultural Sciences, University of Florida, Gainesville, Fla.

O'Meara, G.F. 1976. Saltmarsh mosquitoes (Diptera: Culicidae) pp. 303-333. In L. Cheng, ed., Marine Insects. North-Holland, Amsterdam.

O'Meara, G.F. and D.G. Evans. 1973. Blood feeding requirements of the mosquito: geographical variation in Aedes taeniorhynchus. Science 180: 1291-1293.

Petranka, J.W. and K. Fakhoury. 1991. Evidence of a chemically mediated avoidance response of ovipositing insects to bluegills and green frog tadpoles. Copeia 1991: 234-239.

Provost, M.W. 1951. The occurrence of saltmarsh mosquitoes in the interior of Florida. Fla. Entomol. 48-53.

Provost, M.W. 1969. Man, mosquitoes and birds. Fla. Naturalist 42:63-67.

Ritchie, S.A. 1984. Record winter rains and the minimal populations of Aedes taeniorhynchus (Wiedemann): cause and effect? J. Fla. Anti-mosq. Assoc. 55: 14-21.

Ritchie, S.A. and D.S. Addison. 1992. Oviposition preferences of Aedes taeniorhynchus (Diptera: Culicidae) in Florida mangrove forests. Env. Entomol. 21:1.

Control

Chapman, H.C. 1985. Biological control of mosquitoes. Bull No. 6 Amer. Mosq. Control Assoc. Fresno, Calif.

Beidler, E.J. and G.D. Dodd. 1985. Control of larvae. Ch. 11 in J.K. Nayar, ed. Bionomics and physiology of Aedes taeniorhynchus and Aedes sollicitans, the saltmarsh mosquitoes of Florida. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Fla.

Rathburn, C.B., Jr. 1985. Control of adults. Ch. 12. In J.K. Nayar, ed. Bionomics and physiology of Aedes taeniorhynchus and Aedes sollicitans, the saltmarsh mosquitoes. Florida Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Fla.

Roberts, D.W., R.A. Daoust and S.P. Wraight. 1983. Bibliography on pathogens of medically important arthropods. 1991. W.H.O. Bull. VBC/83.1, Geneva.

Wallace, F.L., M.A. Tidwell, D.C. Williams and K.A. Jackson. 1990. Effects of controlled burning on Aedes taeniorhynchus eggs in an abandoned rice impoundment in South Carolina. J. Amer. Mosq. Control Assoc. 6: 528-529.

Sampling

Bidlingmayer, W.L. 1985. The measurement of adult mosquito population changes - some considerations. J. Amer. Mosq. Control Assoc. 1: 328-348.

Horsfall, W.R. 1956. A method for making a survey of floodwater mosquitoes. Mosq. News 16: 66-71.

Kline, D.L., J.R. Wood and J.A. Cornell. 1991. Interactive effects of 1-octen-3-ol and carbon dioxide on mosquito surveillance and control. J. Med. Entomol. 28: 254-258.

Morris, C.D. and K.B. Clanton. 1989. Significant associations between mosquito control service requests and mosquito populations. J. Amer. Mosq. Control Assoc. 5: 36-41.

Ritchie, S.A. and D.S. Addison. 1991. Collection and separation of Aedes taeniorhynchus eggshells from mangrove soil. J. Amer. Mosquito Control Assoc. 7: 113-115.

Ritchie, S.A., D.S. Addison and F. Van Essen. 1992. Eggshells as an index of aedine mosquito production: II. the distribution, movement and sampling of Aedes taeniorhynchus eggshells. J. Amer. Mosq. Control Assoc. 8: 32-37.

Ritchie, S.A. and E.S. Johnson. 1989. The use of sodium hypochlorite to detect aedine mosquito eggs in mangrove soils and insect feces. J. Amer. Mosq. Control Assoc. 5: 612-613.

Ritchie, S.A. and E.S. Johnson. 1991. Distribution and sampling of Aedes taeniorhynchus (Diptera: Culicidae) eggs in a Florida mangrove forest. J. Med. Entomol. 28: 270-274.

Service, M.W. 1976. Mosquito ecology. Halstead Press Book, John Wiley & Sons, New York.

Scotton, G.L. and R.C. Axtell. 1979. Aedes taeniorhynchus and Aedes sollicitans (Diptera: Culicidae) oviposition on coastal dredge spoil. (Photographs differentiate eggs.) Mosq. News 39: 97-110.

Table 1. Pathogens of *Aedes solicitans* (AS) and *Ae. Taeniorhynchus* (AT). Notes refer to larvae unless noted. (From Chapman 1985 and Roberts et al. 1983).

Pathogenic agent	Species	Notes
VIRUSES		
regular iridovirus (RMIV)	AT	iridescent orange, lethargic
turquoise iridovirus (TMIV)	AT	iridescent turquoise, lethargic
nuclear polyhedrosis (NPV)	AS, AT	stunted, lethargic
cytoplasmic polyhedrosis (CPV)	AT	
BACTERIA		
Bacillus thuringiensis (B.t.i.)	AS, AT	lab and field inoculations
Bacillus sphaericus	AT	field inoculations
PROTOZOA		
Microsporidia	AT	little overt pathology
Amblyospora polykara	AT	infects eggs and adult females
Nosema algerae	AT	
Vavraia culicis	AT	
CILIATA		
Tetrahymena pyriformis	AT	lab-infected pupae
FUNGI		
Coelomomyces psorophorae	AS, AT	yellow-rusty, lethargic
Lagenidium giganteum	AS, AT	lab-infected larvae in freshwater only
Metarhizium anixopliae	AS	lab-infected larvae
Nematode		
Perutilmermis culcis	AS	develops in adults