Population Studies of the Filarial Vector *Aedes polynesiensis* (Diptera: Culicidae) in Two Island Settings of French Polynesia

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ABSTRACT A mark–release–recapture study was conducted to estimate the adult population size, migration, and dispersal patterns of male and female *Aedes* (*Stegomyia*) *polynesiensis* (Marks) in a valley of Moorea, a volcanic island, and a motu (islet) on the atoll of Tetiaroa, two settings typical of the Society Islands. *Aedes polynesiensis* recapture rate was high for females and low for males. The distribution of *Aedes* species in the valley was heterogeneous. Marked individuals dispersed to most parts of the motu and over great distances in the valley for some females. The study provides insights into the field dynamics of *Ae. polynesiensis* populations and confirms that more efficient sampling methods are warranted. There was no evidence of active migration between motus on the atoll, suggesting that Tetiaroa is a suitable site for small-scale initial open releases of *Wolbachia* incompatible insect technique and other sterile insect technique-like suppression or replacement strategies.

KEY WORDS *Aedes polynesiensis*, distribution, dispersal, population estimate, xenomonitoring

Aedes mosquitoes transmit a range of pathogens that cause substantial morbidity, mortality, and suffering. *Aedes polynesiensis* is a vector of medical and veterinary importance for the South Pacific. It is the primary vector of *Wuchereria bancrofti* (Cobbold) (Spirurida: Onchocercidae), the causative agent of the diurnally subperiodic lymphatic filariasis (LF) in French Polynesia, and a significant vector of dengue, the most important mosquito-borne viral disease, with an estimated 100 million (WHO 2012) to 390 million (Bhatt et al. 2013) cases per year worldwide. *Ae. polynesiensis* also transmits the dog heartworm, *Dirofilaria immitis* (Leidy) (Nicolas and Scoles 1997, Russell et al. 2005a), a filarial parasite of veterinary importance. Despite sustained mass drug administration (MDA) of prophylactic drugs against *W. bancrofti* over several decades, LF persists in French Polynesia (Esterre et al. 2001, Plichart et al. 2006, Mou et al. 2009). The biology of *Ae. polynesiensis* has been hypothesized to contribute in part to the failure of MDA in certain regions of the Pacific (Pichon 2002). Control of this diurnal exophilic mosquito (Russell 2004) is difficult because it uses a variety of sometimes cryptic, mostly inaccessible, natural and artificial containers such as tree holes, burrows of the land crab *Cardisoma carnifex* Herbst (Decapoda: Gecarcinidae), and rat-chewed coconuts (Bonnet and Chapman 1958, Lardeux et al. 2002). Consequently, supplemental vector control strategies have been advised for areas where *Ae. polynesiensis* is the primary vector of LF (Lardeux et al. 2002, Burkot et al. 2006, Brelsfoard et al. 2008, Bockarie et al. 2009). One such control method is the sterile insect technique (SIT). This technique relies on the release of large numbers of sterile males to seek and mate with wild females, thereby impairing their reproductive capacity. Repeated inundative releases of sterile males lead to population decline and to its eventual collapse, particularly in island settings where the target population is naturally isolated. The method also increases in effectiveness as the size of the target population declines. SIT has been successfully used to suppress or eliminate some major agricultural pest species, including the New World screwworm *Cochliomyia hominivorax* (Coquerel) and the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) (Knipling 1955, Dyck et al. 2005). A first example of successful mosquito elimination was achieved in 1967 against *Culex quinquefasciatus* Say in Myanmar by using the incompatible insect technique (IIT), similar to SIT (Laven 1967). IIT relies on embryonic lethality resulting from cytoplasmic incompatibility, induced by the intracellular bacterium *Wolbachia pipientis* (Werren 1997, Sinkins 2004). Despite some other successful trials (Benedict and Robinson 2003, Dame et al. 2009), SIT has not achieved large-scale application against mosquito vectors, in part because of various technical challenges and insufficient understanding of the population ecology of the target species (Benedict and Robinson 2003, Ferguson et al. 2005). Several technological developments and a better understanding of biological and ecological determinants to male fitness have since improved the quality of mass produced insects, po-

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tentially allowing SIT to become a major new component of integrated vector management (Benedict et al. 2009, Alphey et al. 2010). Genetics-based improvements of this vector control approach are also being developed and tested, which include field trials of genetically modified mosquitoes (Harris et al. 2011, 2012, Lacroix et al. 2012) and *Wolbachia* population replacement (Hoffmann et al. 2011). Recent findings in laboratory (Brelsfoard et al. 2008), semifield (Chambers et al. 2011), and in an open environment (O'Connor et al. 2012) also support the use of IIT for the control of *Ae. polynesiensis.*

Islands of French Polynesia provide relatively isolated *Ae. polynesiensis* populations with limited migration between islands (Shiu et al. 1997, Behbahani et al. 2005, Brelsfoard and Dobson 2012), which are particularly suited to study vector biology and behavioral ecology and for testing novel control technologies on replicated sites. Two sites typical of the high and low island settings of the Society Islands are being considered for open release trials of the self-limiting *Wolbachia*-based suppression strategy: Hotutea, a valley in the district of Afareaitu on Moorea, a volcanic island, and a motu (islet) on the atoll of Tetiaroa (coral island). Moorea is the second most populated island of the Society (Windward) group after Tahiti. The district of Afareaitu, which hosts a public hospital, was recently the focus of an extensive LF survey confirming the persistence of a relatively high disease prevalence, despite decades of rigorous MDA implementation (Gass et al. 2012). The valley of Hotutea extends from the coastal area inland covering a variety of semi-rural to forested habitats. The atoll of Tetiaroa is located 33 miles (54 km) north of Tahiti. Tetiaroa is the site of a future luxury eco-resort currently under development. The considerable nuisance caused by *Ae. polynesiensis* on this and other Pacific islands has generated interest for testing novel control strategies. Dispersal of *Ae. polynesiensis* is influenced by anthropic activities, weather patterns, and natural barriers (Failloux et al. 1997, Brelsfoard and Dobson 2012). The *Ae. polynesiensis* population in the Hotutea valley is surrounded by steep elevated hills, which contribute to a relative isolation of the population.

In addition to *Ae. polynesiensis*, a dozen mosquito species are reported from the Society Islands (Belkin 1962, Huang 1977, Brunhes and Boussès 2009, Marie and Bossin 2013). Although *Cx. quinquefasciatus* is common and coexists with *Ae. polynesiensis* in various developmental habitats, it is not an important vector of the subperiodic form of *W. bancrofti* circulating in French Polynesia (Iyengar 1965, Lardeux et al. 2002). The peridomestic species *Aedes (Stegomyia) aegypti* (L.), the primary vector of dengue in French Polynesia, is prevalent in urban settings and villages of French Polynesia but less common in more rural areas, where *Ae. polynesiensis* predominates. *Culex annulirostris* Skuse is a vector of Ross River and encephalitis viruses elsewhere (LaPointe 2007) and of nocturnal periodic filariasis in New Guinea (Belkin 1962) but is not competent for the subperiodic form transmitted in the eastern Pacific island region (Lee et al. 1989). Of more recent introduction into French Polynesia, the bromeliad mosquito *Wyeomyia (Wyeomyia) mitchellii* (Theobald) has only been reported in Moorea and Tahiti so far (Marie and Bossin 2013). Little is known about the medical and veterinary importance of this species. Most of the other mosquito species present in the Society Islands are rare endemics with more discrete distributions and unknown vector status. Although it is essential to monitor unintended impact on nontarget species (including disease vectors) during control efforts, these species were not of primary interest in the current study.

Knowledge of the dynamics of adult *Ae. polynesiensis* populations and patterns of mosquito dispersal and migration is fragmented at best (Lardeux et al. 1992). Population size and density estimates in particular are critical to measure efficacy of intervention strategies involving releases of modified or *Wolbachia*-transinfected mosquitoes into the field. Understanding spatial distribution patterns is also vital to optimize release and monitoring effort during implementation of control programs. Mark–release–recapture (MRR) techniques have been successfully applied for the study of *Aedes* mosquito populations in the field. Recent applications have monitored population dynamics of *Aedes albopictus* (Skuse) in relation to Chikungunya virus transmission in Rome, Italy (Marini et al. 2010); *Ae. aegypti* for dengue transmission in Queensland, Australia (Russell et al. 2005b); and the preliminary field testing of genetically engineered sterile males in Pahang, Malaysia (Lacroix et al. 2012). MRR experiments were also recently used with success to study the adult population dynamics of *Ae. polynesiensis* (Mercer et al. 2012b). The Biogents–Sentinel (BGS) trap (Biogents GmbH, Regensburg, Germany) was designed to sample adult *Ae. aegypti* (L.). It is also a practical and effective device for capturing the important filariasis and dengue vector *Ae. polynesiensis* (Schmaedick et al. 2008). BGS traps are a safe and efficient alternative to landing catches and backpack aspirators (Williams et al. 2006, Hapairai et al. 2013). They have been successfully used to estimate the population density of *Ae. aegypti* (Johnson et al. 2012) and *Ae. polynesiensis* (Mercer et al. 2012b).

To facilitate the development and evaluation of novel control strategies, the population size, migration, and dispersal patterns of *Ae. polynesiensis* were examined in the Hotutea valley and a motu (islet) of the Tetiaroa atoll. The frequency of filarial parasites in the Hotutea mosquito population was also investigated to assess the risk of LF transmission in the valley.

Materials and Methods

Study Area and Climate. The climate across the five archipelagoes of French Polynesia is influenced by variations of temperature and precipitation (rain fall), and to a lesser degree by the duration of insolation. Seasonality in the Society Islands is defined by a wet and dry season. The wet season lasts from November to April and the dry season from May to October. However, the period between 2009 and 2011 was in-

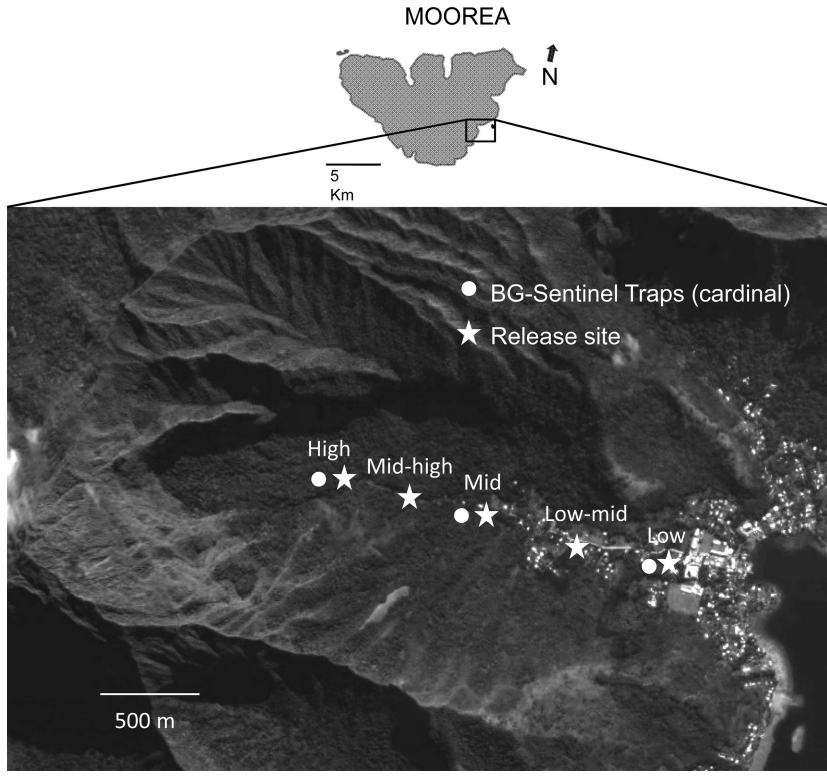

Fig. 1. Aerial view of the Hotutea valley on the east coast of the island of Moorea. Mosquito releases were conducted at five release sites (stars). Release sites are separated by ≈500 m. Mosquito sampling was done at low, mid, and high elevation (circles) by using a set of up to 16 baited BGS traps distributed along the four cardinal directions from the point of mosquito release.

fluenced by "El Niño" and "La Niña" phenomena affecting seasonal trends of both temperature and precipitation. The first study was conducted in the Hotutea valley (17°33′00.94″ S 149°49′09.07″ W), district of Afareaitu, Moorea (volcanic island). The valley is flanked by steep volcanic hills on the north, south, and west sides (Fig. 1). Likely sources of mosquito immigration would come from the inhabited coastal area directly facing the Hotutea valley. Most human dwellings are found near the coast at low elevation (from shoreline to 60 m above sea level). These dwellings range from small (5 × 5 m) wooden or tin houses to large public buildings (gymnasium). The valley includes 198 households, a stadium, public hospital, schools, grocery stores, and many small annexes. Vegetation in inhabited areas of the valley (low and mid elevation) typically displays mango, breadfruit, and coconut trees, with many ornamental plants. In uninhabited areas (high elevation), the vegetation is typical of subtropical forest found on Pacific high islands (Fig. 1). Water streams are covered by Tahitian Chestnut *Inocarpus fagifer* (S. Parkinson ex Z.) Fosberg, with short *Hibiscus tiliaceus* L. understory. This understory progressively becomes the primary cover further away from the main stream. At higher elevation, the slopes are covered with sword grass *Miscanthus floridulus* (J. J. Labillardière) O. Warburg ex K. M. Schumann & C. A. Lauterbach and ferns. The second study site is the atoll of Tetiaroa (17°00′54.77″ S 149°35′04.00″ W) located 54 km north of Tahiti. This low coral island, which stretches over 2.3 square miles (6 km^2), is divided into 13 motus (islets) of varying surface areas separated by sometimes large stretches of water. One of these islets is motu Auroa located on the north end of Tetiaroa (Fig. 2). This motu is around 165 m in width and 430 m in length for an area of ≈3.2 ha, and its maximum elevation is 3 m above sea level. This motu and its neighboring islets (motu Tauini and motu Hiraanae) were selected for the study. The stretch of water separating Auroa from Tauini (west) and Hiraanae (east) is 77 m and 190 m, respectively (Fig. 2). These motus were similar in vegetation and topography to motu Auroa. Tropical "Alizés" trade winds generally blow from east to west. Vegetation on the north end of the motu is essentially composed of shrubs *Pemphis acidula* (J. R. & G. Forster), with coconut palms *Cocos nucifera* (L.), *Guettarda speciosa* (L.), and *Pisonia umbellifera* (J. R. & G. Forster) Seemann on the rest of the motu.

Mosquitoes. *Ae. polynesiensis* colonies from Hotutea and Tetiaroa were established by collecting adult specimens by using a backpack aspirator (John W. Hock Company, Gainesville, FL). Collected individuals were held in standard 30 by 30 by 30 cm cages

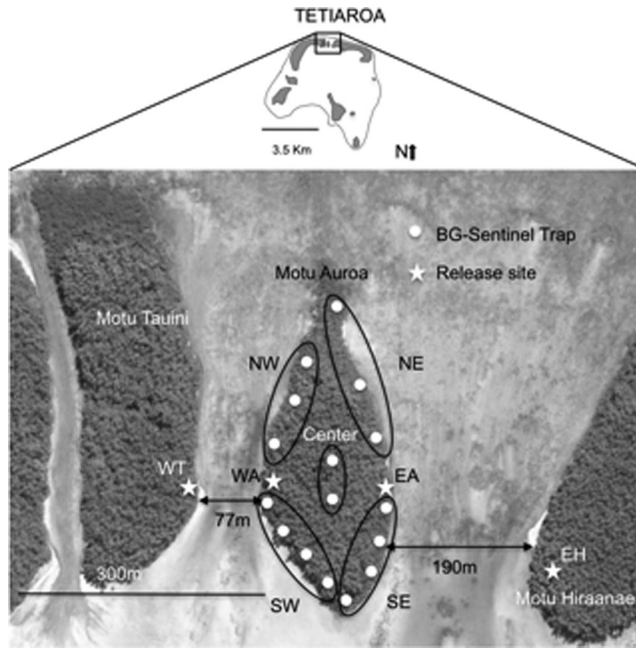

Fig. 2. Aerial view of motu Auroa on the atoll of Tetiaroa. Mosquito releases were conducted at four release sites (stars): one site on each side of motu Auroa (WA and EA), and one site on each shoreline of the islets neighboring motu Auroa (WT and EH). Collection of mosquitoes on the periphery and at the center of motu Auroa was done by using 16 baited BGS traps (white circles) partitioned into four quadrants (NW, NE, SW, and SE) and a center area (black ellipses).

(Bioquip, Rancho Dominguez, CA) with 10% sucrose. Mosquitoes were transferred to the ILM Medical Entomology Research Laboratory, and fed on restrained mice for colony amplification and maintenance. Resulting eggs were hatched under vacuum at each generation. After 48 h, 200 larvae were distributed into each larval pan (30 by 20 by 7 cm) containing 1.5 liter of tap water. Liver powder (MP Biochemicals, Solon, OH) was provided ad libitum (≈600 mg of powder supplied over the entire larval cycle). Sex separation and initial count were done at the pupal stage before emergence.

Mark or Release. Laboratory-reared male and female mosquitoes were allowed to emerge into respective cages (30 by 30 by 30 cm), each containing ≈700 individuals. Once emerged, adults were provided a 10% sucrose solution as energy source and the cages were placed in 25–30°C and 65–80% relative humidity (RH) holding conditions. Adult cages were covered and transported to each study site. To mark mosquitoes, fluorescent powders (Day Glo, Switzer Brothers, Cleveland OH) of various colors were applied by using a 250-ml polyethylene wash bottle (Thermo Fisher, Pittsburg, PA) covered with a 100-μm mesh cloth. Fluorescent powder was applied through the cage screen by brief squeezes of the wash bottle and mosquitoes were released within minutes. Mosquitoes were 3–4 d old and sugar-fed at time of release (host seeking). Marked and nonmarked male and female specimens were held for control in separate cages under laboratory conditions, and survival was recorded for 12 d.

For Hotutea, cohorts marked with fluorescent powders of different colors were released at stations each separated by 500 m, selected along an altitudinal transect (Fig. 1; Table 1). The low elevation (17°33′3.74″ S 149°47′45.28″ W) was at 18 m above sea level 500 m away from the coastal line, low-mid elevation (17°32′59.90″ S 149°48′2.49″ W) at 30 m, mid elevation (17°32′56.64″ S 149°48′17.00″ W) at 65 m, mid-high elevation (17°32′51.90″ S 149°48′34.94″ W) at 110 m, and the high elevation (17°32′48.33″ S 149°48′52.49″ W) at 215 m. Males were marked and released at all five points over a 2-hour period. Females were released similarly, with the exception of the lower two release sites considered too close to human dwellings for female releases (Table 1).

For Tetiaroa, mark and release was done on motu Auroa to measure intra-motu dispersal and on the shorelines of its two neighboring islets motu Tauini and motu Hiraanae to investigate the potential for inter-islet mosquito migration (Fig. 2). Powders of different fluorescent colors were used to distinguish between four release sites: one site on the west shoreline of motu Tauini (WT), one on the east shoreline of motu Hiraanae (EH), and two release sites along the west and east shorelines of motu Auroa (WA and EA, respectively).

Recapture. One day after release, mosquitoes were sampled daily for 5 consecutive days by using BGS traps baited with BG-Lure (Biogents, Regensburg, Germany). Traps were powered by 12-V (7-amp) nonspillable batteries, charged in parallel in groups of four at 24-h intervals (Lacroix et al. 2009).

Table 1. Results of *Ae. polynesiensis* mosquito mark–release–recapture experiments conducted in Moorea (Hotutea valley) and Tetiaroa atoll, French Polynesia

Site	Sex	Location	Elevation	Released	No. BGS	Recaptured	% recaptured	Unmarked *Ae. polynesiensis*	*Ae. aegypti*	*Cx. quinquefasciatus*
Hotutea	♂	Low	18 m	2,149	15	5	0.23	16a	48a	5a
		Low-mid*	30 m	1,615	0	0	0	N/A	N/A	N/A
		Mid	65 m	902	16	0	0	95b	0a	5a
		Mid-high*	110 m	1,207	0	0	0	N/A	N/A	N/A
		High	215 m	1,132	14	7	0.62	64ab	0a	0a
	♀	Low	18 m	0	15	N/A	N/A	79a	61a	14a
		Low-mid	30 m	0	0	N/A	N/A	N/A	N/A	N/A
		Mid	65 m	1,919	16	133	6.93	277b	5b	7a
		Mid-high*	110 m	1,860	0	10†	0.54	N/A	N/A	N/A
		High	215 m	1,903	14	58	3.05	53a	0	0
Tetiaroa	♂	West Auroa	Sea level	460	16	3	0.65	143	0	0
		East Auroa	Sea level	405		4	0.99			
		Motu Tauini	Sea level	667	0	0	0	N/A	0	0
		Motu Hiraanae	Sea level	754	0	0	0	N/A	0	0
	♀	West Auroa	Sea level	448	16	42	9.38	617	0	0
		East Auroa	Sea level	435		213	48.97			
		Motu Tauini	Sea level	442	0	0	0	N/A	0	0
		Motu Hiraanae	Sea level	406	0	0	0	N/A	0	0

* Mark–release only.

† Specimens recaptured at mid and high elevation.

a,b: For each species, means in the same column followed by the same letter are not significantly different (Tukey's multiple comparison test, $P = 0.05$ on Log10$(x + 1)$-transformed trap catches).

Trapping Routine. Mosquitoes were collected at three of the five release sites (1,000 m apart) in the Hotutea valley at low, mid, and high elevations (Fig. 1). Up to 16 BG sentinel traps were placed at each of the three sampling elevations: four traps along each cardinal direction (north, south, east, and west) at 25, 50, 100, and 250 m away from the point of release (Fig. 3). Hence, the Mid50E sampling refers to BGS trap located 50 m east of the mid elevation release point. The approximate sampling area was of 1.9 ha for low and mid and only 1.0 ha for high elevation because the 250-m sampling locations on the north and west were inaccessible (cliffs). In total, 3 sampling zones and 46 BGS traps were used in the Hotutea experiment. This release–recapture design allowed measuring potential dispersal at distances up to 2,000 m from the release point. For Tetiaroa, recapture was done by using 16 BGS traps distributed across motu Auroa (Fig. 2). The mean distance between release (WA, EA) and recapture (BGS traps) sites was measured to check the significance of distance differences. There was no significant difference in the mean distance ($t = 0.3199$; df = 30; $P = 0.751$) separating WA (119.7 m, SEM ± 13.01 m) and EA (125.3 m, SEM ± 11.83 m) from the BGS traps.

Xenomonitoring. The presence of LF in the mosquito population was assessed only in the Hotutea valley, as there are no human hosts living on motu Auroa and, therefore, no expected parasite transmission. DNA from pools of female *Ae. polynesiensis* collected in this valley was extracted by using the Qiagen DNeasy kit protocol (Qiagen, Hilden, Germany). The purified DNA was used in a real-time polymerase chain reaction (PCR) with the ligase detection reaction primers (Rao et al. 2006) mixed with SYBR Green (Bio-Rad, Hercules, CA) by using the iCycler (model 170-8731, Bio-Rad) by using a protocol similar to Chambers et al. (2009).

Geographic and Climatic Measurements. All climatic data were recorded by using an automated weather station (model U30 Hobo, Pocasset, MA). Global positioning system locations were measured by using a Garmin 78S model (Garmin International, Inc., Olathe KS). Elevation data were cross-referenced to Google maps.

Data Analysis. Statistical analysis was done by using GraphPad Prism version 5.0 (GraphPad Software Inc., LA Jolla CA). Comparisons between numbers of captured mosquitoes were transformed as $\mathrm{Log}_{10}(x + 1)$ to correct for lack of normality and unequal variances in the raw data. Treatments were compared with each other by using analysis of variance and mean separation by the Tukey's multiple comparison test. Pairwise comparisons of dispersal distance between elevations for males and females were calculated by using Student's *t*-tests. Population estimates in Hotutea valley were calculated by using the revised Jackson's positive method assuming open population by using the equation $y_i = (R_i * 100 * 100) / (M_c * C_i)$ (Trpis et al. 1995, Silver 2008). The recapture rate is the proportion (percent) of marked mosquitoes recaptured over the total number of marked mosquitoes released. The number of unmarked (U) and recaptured (R) female mosquito was used to calculate the corrected recaptures (y) and total captured (T). The adjustment of marked recaptured (M) for each day was calculated by subtracting the total captured of previous collection. Data were computed into the equation $Po = (100*100)/ao\text{-}M$, with $ao = 1.25$ for males at low elevation and 1.73 and 2.29 for females at mid and high elevations, respectively. Estimates of LF prevalence through xenomonitoring was calculated by using the

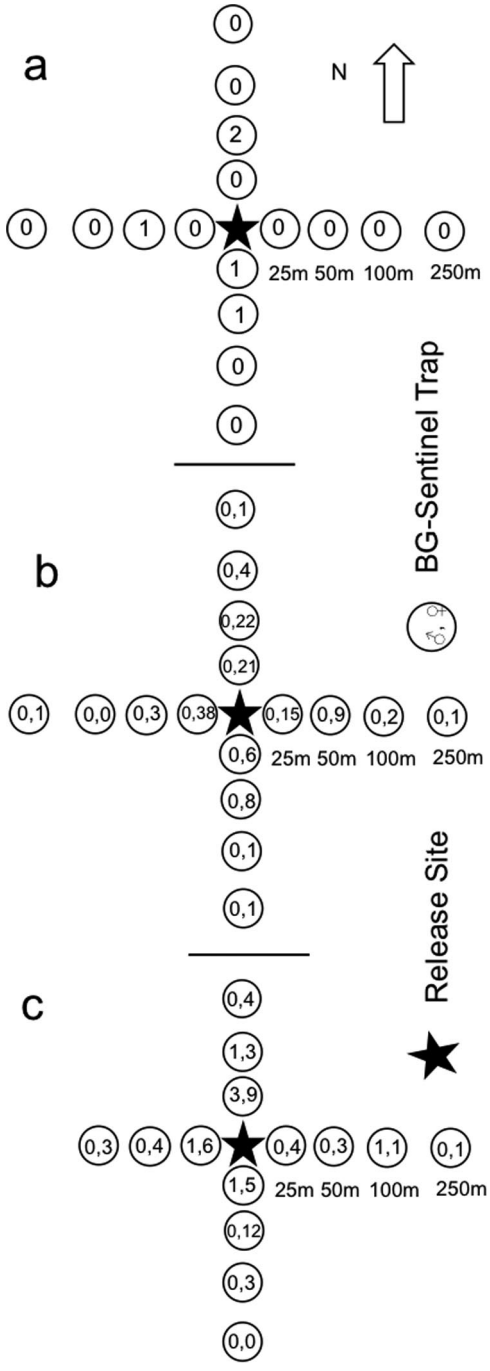

Fig. 3. Distribution of traps and numbers of marked and released *Ae. polynesiensis* specimens recaptured in the Hotutea valley: (a) low elevation, (18 m), (b) mid elevation (65 m), and (c) high elevation (215 m). Stars indicate release points and circles sampling locations. Values in meters refer to the distance of each sampling location to the release point. The numbers separated by a comma in the circles indicate the number of marked and recaptured males and females, respectively. At low elevation, only recaptured marked males are indicated, as no females were released at this site.

PoolScreen (v. 2.02) software (Department of Biostatistics and Division of Geographic Medicine, University of Alabama at Birmingham), which provided maximum likelihood estimates with 95% CIs based on likelihood ratio method.

On Tetiaroa, population aggregation was analyzed by allocating traps to quadrants: NW and NE (three traps each), SW and SE (four traps each), and two traps at the center. Population estimates were calculated by using the Lincoln–Peterson index with subtraction of marked mosquitoes released and its variance by using the equations $P = (an/r)\text{-}a$ and $varP = [a^2n(n\text{-}r)]/r^3$ (Lincoln 1930, Silver 2008). The standard error was calculated as the square root of the variance (Costantini et al. 1996).

Results

Weather Data. High precipitation was observed in the Hotutea valley, with >160 mm during the 5 d of the MMR study (4–9 May 2011). This resulted in low insolation (54.97 W/m^2) and high relative humidity (93.21%). The average temperature recorded in this valley during the study was 22.67°C, with prevailing south-west winds blowing from the coast into the valley. During the course of the MRR study in Tetiaroa (12–17 April 2011), weather records indicated a higher average temperature (27.63°C), greater insolation (159.69 W/m^2), and lower relative humidity (77.11%) and precipitation (7 mm). The trade winds (Alizés) pattern typical of the dry season in the tropics came from the east.

Abundance and Distribution. In total, 7,005 male and 5,682 female *Ae. polynesiensis* were marked and released at five locations in the Hotutea valley (Fig. 1; Table 1). There was no significant difference in survival between marked and nonmarked mosquitoes held in control cages (log-rank, $P = 0.25$). Mosquitoes were collected at three of the five release sites at low, mid, and high elevations (Fig. 3a–c). In total, 175 male and 409 female *Ae. polynesiensis* (including 12 marked males and 191 marked females), 48 male and 66 female *Ae. aegypti*, and seven male and 21 female *Cx. quinquefasciatus* were collected from all three sampled elevations. There were significant differences in the number of both male ($F = 5.114$; df = 2; $P = 0.010$) and female ($F = 8.440$; df = 2; $P < 0.001$) *Ae. polynesiensis* at each of the three elevations. Pairwise comparisons for *Ae. polynesiensis* showed that the number of males at mid-elevation was significantly higher than at low elevation ($P < 0.05$); other comparisons were not significantly different (Table 1). Pairwise comparisons showed that there was significantly more female *Ae. polynesiensis* at mid elevation than at low or high elevation ($P < 0.05$). There was no difference in the number of female *Ae. polynesiensis* between low and high elevation. Male *Ae. aegypti* were collected only at low elevation, whereas female *Ae. aegypti* were collected at both low and mid elevation; no *Ae. aegypti* were collected at high elevation. Comparisons for female *Ae. aegypti* showed that low and mid elevation collections were significantly different ($t = 4.863$; df =

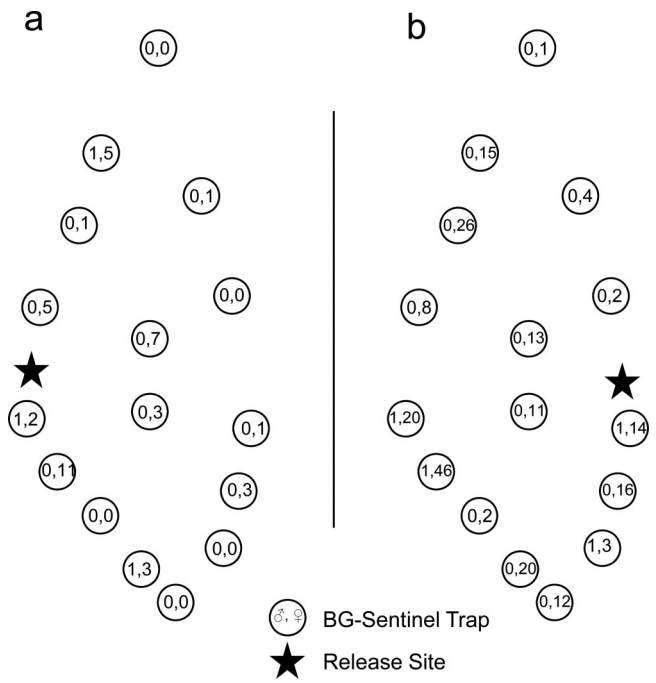

Fig. 4. Distribution of traps and numbers of marked and released *Ae. polynesiensis* specimens recaptured on motu Auroa: (a) mosquitoes marked with yellow fluorescent powder, released on the west shore and recaptured throughout the motu, and (b) mosquitoes marked with orange fluorescent powder, released on the east shore and recaptured throughout the motu. Stars indicate release points and circles sampling locations. The numbers separated by a comma in the circles indicate the number of marked and recaptured males and females, respectively.

30; $P < 0.0001$). *Cx. quinquefasciatus* was not collected at high elevation. Comparison for *Cx. quinquefasciatus* at low and mid elevation was not significant for either male ($t = 1.118$; df = 29; $P = 0.27$) nor female ($t = 0.998$; df = 29; $P = 0.32$).

On the Tetiaroa atoll, 2,286 male and 1,731 female *Ae. polynesiensis* were marked and released (Table 1). Mosquitoes marked and released on WA and EA (Fig. 4a and b, respectively) of motu Auroa were recaptured by using 16 BGS traps. In total, 150 male and 872 female *Ae. polynesiensis* were collected on this motu, including 7 marked males and 255 marked females. None of the mosquitoes marked and released on the shores of the neighboring Tauini and Hiraanae islets were recaptured on motu Auroa. There were significant differences in the number of males captured ($F = 8.204$; df = 4; $P = 0.0026$) in each of the five sampling sections (i.e., four quadrants and center), but these differences may be attributed to the overall low number of captures. There were no significant differences in the number of females between the five sampling sections ($F = 2.976$; df = 4; $P = 0.068$).

Dispersal. In the Hotutea valley, the average distance of dispersal for males at low and high elevation was 45.0 m (SEM ± 5 m) and 39.28 m (SEM ± 10.7 m), respectively, with no significant difference between the two elevations ($t = 0.430$; df = 10; $P = 0.6812$). Average distance of dispersal for females at mid and high elevation was 43.6 m (SEM ± 3.55 m) and 52.58 m (SEM ± 4.98 m), respectively, also with no significant difference ($t = 1.422$; df = 189; $P = 0.1566$). Ten of the 191 recaptured females (5% of total) released at the mid-high elevation were caught at significantly greater distances: two females at mid50E (640 m), two females at mid100E (690 m), one female at mid100N (570 m), one female mid250N (530 m), one female at high250E (200 m), and three females at high50S (490 m). Average distance of dispersal of these 10 females was 534 m (SEM ± 45.82 m).

On motu Auroa, the average dispersal distance of mosquitoes marked and released on WA was 106.6 m (SEM ± 61.5 m) for males and 122.5 m (SEM ± 18.9 m) for females. From EA, the average dispersal distance was 108.75 m (SEM ± 54.37 m) for males and 125.23 m (SEM ± 8.58 m) for females. There was no significant difference in the dispersal of males released from either shores ($t = 0.044$; df = 5; $P = 0.96$). However, difference in distance of dispersal was significant for females ($t = 5.244$; df = 252; $P < 0.0001$).

Population Estimates. For the Hotutea valley, population estimates were calculated by using recaptured marked specimens across 5 sampling days by using the Jackson's positive method (Mercer et al. 2012b). The estimate of population size (*Po*) for males at high elevation was 6,859 (6,800 males/ha). For females, the population size estimate was 3,870 (2,000 females/ha) at mid elevation and 2,457 (2,400 females/ha) at high elevation (Table 2).

For motu Auroa, the Lincoln–Peterson index, which subtracts marked individuals over time, was used to

Table 2. Data for calculation of population estimate in Hotutea valley using Jackson's positive method

Location	Day released	Adjustment of marked recaptured (*M*)	Total recaptured (*T*)	Unmarked captured (*U*)	Marked recaptured (*R*)	Corrected recaptured(*y*)
♂ High	0	1,132	—	—	—	—
	1	1,132	49	46	3	0.541
	2	1,129	2	2	0	0.000
	3	1,129	4	2	2	4.429
	4	1,127	3	2	1	2.958
	5	1,126	13	12	1	0.683
♀ Mid	0	1,919	—	—	—	—
	1	1,919	152	116	36	1.234
	2	1,883	96	47	49	2.711
	3	1,834	94	59	35	2.030
	4	1,799	62	51	11	0.986
	5	1,788	6	4	2	1.864
♀ High	0	1,903	—	—	—	—
	1	1,903	34	22	12	1.855
	2	1,891	13	4	9	3.661
	3	1,882	24	11	13	2.878
	4	1,869	32	13	19	3.177
	5	1,850	10	3	7	3.784

estimate the size of the closed population (Mercer et al. 2012b). Two estimates were calculated for the male and female population by using release–recapture data. The total male population was estimated at 21,926 individuals (SEM ± 12,791; 6,852 males/ha) and 14,478 individuals (SEM ± 7,340; 4,524 males/ha) from WA and EA, respectively. Total female population estimates were 6,581 individuals (SEM ± 1,050; 2,056 females/ha) and 1,260 individuals (SEM ± 100; 394 females/ha) from WA and EA, respectively (Table 3). The female population estimates for the motu differed by ≈5.2× between the two cohorts.

Xenomonitoring. In total, 63 pools of female mosquitoes were analyzed by PCR: 14 pools collected at the low elevation ($n = 79$), 36 pools at the mid elevation ($n = 268$, nine females were removed because of missing body parts), and 14 pools at the high elevation ($n = 53$). Three pools turned out positive by PCR for *W. bancrofti*, one from the low elevation and two from the mid elevation. Pool screen estimates indicated a maximum likelihood of infection in the Hotutea vector population of 0.77% (0.15–2.23%).

Discussion

Our study provides a better understanding of the population dynamics, migration, and dispersion patterns of the medically important *Ae. polynesiensis* mosquito species at two island settings typical of the Society Islands in French Polynesia. MRR experiments have previously been used with success to study the population dynamics of *Ae. polynesiensis* on a motu in the lagoon of Raiatea in the Society Islands (Mercer et al. 2012b). Dusting did not appear to be detrimental to either male or female *Ae. polynesiensis* in view of the high initial flight out of the cage, survival of controls, and rapid dispersal across the release area (valley and motu). Survival of marked and unmarked control individuals was satisfactory. Marked females were recaptured from all cardinal directions at both sites, suggesting mixing with the field population. Although males accounted for a comparatively low, but significant, proportion of trap catches relative to females, marked males were poorly recovered compared with marked females. Recapture rates of marked males on Auroa were comparable with those reported on Toamaro (Mercer et al. 2012b). Together these data suggest a) that male *Ae. polynesiensis* are relatively short-lived in the field and b) that a more efficient male trapping system is warranted. Lincoln–Petersen female population estimates varied greatly for motu Auroa. In nature, reported parity rates are high for *Ae. polynesiensis* (Russell et al. 2005a), with ≈80% parous females caught in BGS traps (Mercer et al. 2012b). Moreover, it is estimated that a relatively high proportion of females are actively seeking a bloodmeal at any given time (Mercer et al. 2012b). Under these assumptions, the female population estimates for the Hotutea valley and motu Auroa should, conservatively, be doubled. Population estimates for males calculated for both study sites may not be accurate owing to the low recapture rate.

Table 3. Lincoln–Peterson Index with approximate density of mosquitoes on motu Auroa

Side released	Sex	Lincoln–Peterson index[a]	SEM	Approximate density[b]
West Auroa	♂	21,926	12791	6852
East Auroa		14,478	7340	4524
West Auroa	♀	6,581	1050	2056
East Auroa		1,260	100	394

[a] Lincoln–Peterson index with a subtraction of the no. marked mosquitoes.
[b] Estimated no. mosquitoes per hectare.

Not surprisingly, *Ae. aegypti* was more abundant closer to the costal area in the Hotutea valley, where most of the urbanization occurs. Its presence rapidly decreased inside the valley, whereas that of *Ae. polynesiensis*, a comparatively highly exophilic species, increased sharply. Overall, the presence of *Aedes* vectors throughout the valley sustains the risk of exposure to potentially infectious bites across the area. Although

the BGS traps were primarily positioned for the purpose of measuring dispersal with most traps away from houses and other likely sites of LF transmission, this risk was well substantiated through our xenomonitoring investigation with the collection of several LF-positive *Ae. polynesiensis* pools in the valley. Taken together, our observations suggest that population replacement strategies (Hoffmann et al. 2011) could be successful, as potential for gene transfer is high, thus encouraging the development of disease-refractory *Ae. polynesiensis* lines.

Dispersal patterns among *Aedes* mosquito species may influence disease transmission dynamics. Dispersal is influenced by local variables such as availability of suitable habitats for development, exposure to wind, and vegetation. As observed in the current study, the conditions in the valley and on the motu influenced dispersal in different ways. The average dispersal distance measured for both males and females was significantly greater on the motu than in the valley. Maximum dispersal distances were undoubtedly constrained by the relatively limited dimensions of the motu. Dispersal on the motu may have been influenced by additional factors, including the type and density of vegetation, and the more direct exposure to prevailing winds compared with the valley. Distance of dispersal on the motu was consistent with the dry season dispersal pattern of female *Ae. polynesiensis* on motu Toamaro (Mercer et al. 2012b). Although host-seeking female *Ae. polynesiensis* occasionally venture on the shoreline of highly infested motus to secure a bloodmeal (unpublished data), *Ae. polynesiensis* is not thought to frequently cross open spaces, preferring to disperse through the vegetation instead. None of the individuals released on the shorelines of either islets flanking motu Auroa were recaptured on Auroa, thus supporting this hypothesis. Similarly, those females that dispersed over significantly greater distances in the Hotutea valley did so through the relatively thick vegetation present between the mid and high release/sampling zones. Early field ecology studies estimated the *Ae. polynesiensis* dispersal range at 100 yards (92 m) (Jachowski 1954). Our present measurements indicate a greater dispersal capacity (690 m).

Baited BGS traps collected systematically lower numbers of males compared with females, with total males accounting for 29.9 and 14.6% of all *Ae. polynesiensis* catches in the Hotutea valley and motu Auroa, respectively. A similar male proportion (18.2%) was observed during a 2-yr (March 2009 through March 2011) mosquito monitoring study involving nonbaited BGS traps on the island of Tahiti (unpublished data). Although they represent, on average, only a quarter of collected females, these numbers contrast sharply with the much fewer males collected during another MRR study (1.3% of all *Ae. polynesiensis* specimens collected) conducted on motu Toamaro (Mercer et al. 2012b). A similarly low male proportion (0.9%) was encountered in BGS traps during a 2-yr study involving Toamaro and three other relatively isolated neighboring populations (Mercer et al. 2012a). These data highlight important differences of male population densities between typical sites of the Society Islands. Higher host-seeking female catches in BGS traps are generally attributed to the lower survival rate of males. On motu Auroa, the population of males was sufficiently abundant to observe mating events around the field operators. No such observation was made on Toamaro, which is consistent with the drastically lower male population density recorded on this motu. Environmental conditions met on motus were generally less favorable for male mosquito survival than in the Hotutea valley, with greater exposure to prevailing winds and lower relative humidity. However, the presence of numerous coconuts chewed by an abundant rat population (Russell et al. 2011) in Tetiaroa may provide sufficient larval habitats compensating to some degree for the shorter male lifespan. By comparison, on motus like Toamaro, where rats are much less abundant, the male mosquito population is extremely low, possibly indicating a strong correlation between rat and mosquito population densities on motus covered with unexploited coconut groves.

During the current study, the proportion of total male *Ae. polynesiensis* collected in BGS traps was lower than that of *Ae. aegypti*. Male captures of *Ae. polynesiensis* usually contrast with the greater proportions of males in trap catches for other *Stegomyia* species. In French Polynesia, male *Ae. aegypti* typically account for up to three quarters of *Ae. aegypti* catches when BGS traps are set in areas where the species is abundant (unpublished data). This relatively low male capture inevitably affected the recovery of marked and released male *Ae. polynesiensis*. In the current study, the recapture rate of marked males was low at both study sites (Table 1). By contrast, >18% of marked male *Ae. aegypti* were recaptured by using BGS traps during an indoor MRR study in suburban Cairns, Queensland (Johnson et al. 2012), and up to 16% marked male *Ae. albopictus* were recaptured in an outdoor MRR in La Réunion (Lacroix et al. 2009). Comparatively, a much greater recapture rate of marked female *Ae. polynesiensis* was observed on motu Auroa. Although field operators do their best to optimize sampling by placing the BGS traps in a likely harborage area for *Ae. polynesiensis*, certain features of the study sites, including the topography of the terrain (high vs low elevation, steep vs flat terrain), level of shade provided by the vegetation cover, local weather and microclimate conditions, or trap visibility, might have influenced *Ae. polynesiensis* behavior, thus impacting trap captures.

It is apparent that the mosquito population on motu Auroa is isolated from neighboring islets by a natural barrier (a stretch of water) that greatly reduces mosquito emigration and immigration between islets, as demonstrated by the absence of recaptured marked mosquitoes from the neighboring islets.

A critical parameter worth measuring in anticipation of release program is the dispersal capacity of a target mosquito population to assess likely invasive pressures (Hendrichs et al. 2005). On one hand, mosquitoes displaying a highly dispersive behavior are

advantageous for control strategies involving release of sterile or refractory mosquitoes, as this characteristic will increase their chances of finding and mating with their female counterparts in the field. However, the greater the dispersal capacity, the greater the risk of immigration to and recolonization of treated areas (Lance and McInnis 2005). In the Hotutea valley, immigration could potentially come from, and be limited to, the low elevation zone near the coastal area. The rest of the valley is surrounded by steep hills with characteristics (lower temperature, low vegetation cover, and direct exposure to winds) that are less suitable for *Ae. polynesiensis* population sustenance. To overcome immigration issues from costal areas, a "barrier zone" could be prescribed by using traditional control methods (Curtis et al. 1982) or by increasing the release rate of sterilizing males if an SIT strategy is to be conducted (Benedict and Robinson 2003).

Beyond the logistical challenges associated with an area-wide intervention, the success of a genetics-based control strategy will rely largely on the ability to accurately measure population suppression, that is, entomological end points. The results presented here are relevant to the design and implementation of small-scale open releases as part of an incremental stepwise approach for testing and scale-up of a self-limiting *Wolbachia*-based suppression strategy. The present findings highlight the importance of establishing baseline population dynamics data before area-wide control strategies to minimize the risk of and appropriately manage potential reinfestation events after strategy implementation. Naturally contained populations typically found in island settings are better suited for initial release trials to minimize the interference of migration into the treated area. Our data suggest that motus of Tetiaroa are suitable sites for initial releases of cytoplasmically incompatible males for a suppression or replacement strategy, as there is little evidence of migration between motus.

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