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Ambient temperature effects on the extrinsic incubation period of *Wuchereria bancrofti* in *Aedes polynesiensis*: implications for filariasis transmission dynamics and distribution in French Polynesia

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Abstract. Temperature effects on development of the human filarial parasite *Wuchereria bancrofti* (Cobbold) (Filaridea: Onchocercidae) in the main Pacific vector *Aedes polynesiensis* Marks (Diptera: Culicidae) are analysed in relation to ambient climatic conditions. A statistical model of the extrinsic cycle duration as a function of temperature is described and used to distinguish three patterns of *W. bancrofti* transmission dynamics: continuous, fluctuating and discontinuous, occurring from north to south geographically among French Polynesian archipelagos. In the northerly Marquesas Islands (8–11° S) filariasis transmission is continuous and very active, facilitated by perennially high temperatures combined with constantly high rates of man–vector contact. In the southerly Australes Islands (21–28° S) filariasis transmission is seasonally discontinuous and, during the cooler months (May–September), the model predicts virtually no transmission because the cycle duration exceeds the life expectancy of the vector. In the Society Islands (16–18° S), between the Marquesas and Australes, transmission is predicted to be intermediate as expected from their latitude, with seasonally fluctuating transmission potential. In the Tuamotu Islands (also geographically intermediate: 14–23° S), with theoretically perennial transmission potential, transmission occurs only intermittently, being limited by other human and environmental factors whereby man–vector contact is confined to seasonal agricultural situations. Generally, among French Polynesian archipelagos where *Aedes polynesiensis* is the vector, the transmission potential for *W. bancrofti* and resulting disease manifestations of lymphatic filariasis in humans are correlated with ambient temperature due to the degree of southern latitude.

Key words. *Aedes polynesiensis*, *Wuchereria bancrofti*, extrinsic cycle, filariasis distribution, humidity, latitude, longevity factor, lymphatic filariasis, mathematical model, temperature, seasonality, transmission potential, vector of filariasis, vectorial capacity, Tahiti, French Polynesia.

Introduction

Wuchereria bancrofti is a filarial nematode parasite transmitted from man to man by mosquito vectors, causing Bancroftian filariasis – one form of lymphatic filariasis (LF) – in most parts of the tropics (Sasa, 1976). Stability of *W. bancrofti* transmission depends on many factors that have been incorporated in mathematical models for vector-borne diseases (Macdonald, 1957; Garret-Jones, 1964; Rochet, 1990; Anderson & May, 1991; Plaisier *et al.*, 1998). Duration of the extrinsic cycle is a key factor in transmission stability. For *W. bancrofti* the mortality rate of larval parasites during their extrinsic development in the mosquito vector appears to be one of the most important determinants of transmission potential. The extrinsic cycle duration and/or parasite mortality rate during the

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extrinsic period (due to larval death or vector mortality) were used by Rochet (1990) and Plaisier *et al.* (1998) to assess filariasis stability. The transmission rate is quite sensitive to changes in biting rates, because the vector has to bite at least twice in order to transmit, and is also sensitive to the daily survival rate of the vector, because the latent period of the parasite in the vector is usually long in relation to the vector life expectancy (Dye, 1992).

In French Polynesia *W. bancrofti* is transmitted by the diurnally active mosquito *Aedes polynesiensis* (Rosen, 1955); factors influencing the extrinsic period and parasite yield are well documented for this vector/parasite combination (Pichon *et al.*, 1974, 1980). The epidemiological concepts of 'limitation, facilitation and proportionality' were introduced for *Ae. polynesiensis* by Pichon (1974) describing the relationship between intake of microfilariae and the resulting number of infective (L3) larvae discharged (Brengues & Bain, 1972; Southgate & Bryan, 1992). Behaviour of *W. bancrofti* infective larvae in *Ae. polynesiensis* was described by Lardeux & Cheffort (1996) in relation to factors affecting L3 transmission to man by the mosquito bite. In the field, environmental factors are of great importance and the role of ambient temperature has been investigated for *W. bancrofti* transmission by various vector species, e.g. *Culex quinquefasciatus* Say in India (Sundar Rao & Iyengar, 1929) and with *Anopheles gambiae* Giles in Madagascar (Brunhes, 1969a, Brunhes, 1969b), *Anopheles funestus* Giles and *An. gambiae* in West Africa (Brengues, 1975) and *Ae. polynesiensis* in French Polynesia (Lardeux & Cheffort, 1997). Temperature and humidity are key factors governing the geographical distribution of Bancroftian filariasis and its seasonal intensity of transmission, as investigated across the Afrotropical Region for example (Brunhes, 1975; Brunhes & Dandoy, 1978; Brengues *et al.*, 1979; Lindsay & Thomas, 2000). At constant temperature with adequate humidity for vector survival, the parasite grows very slowly below 20°C and development is impaired above about 30°C (Basu & Sundar Rao, 1939; Omori, 1958), so that upper and lower threshold temperatures can be defined for extrinsic development of *W. bancrofti* larvae (Lardeux & Cheffort, 1997). Within this range, parasite growth proceeds from microfilaria to L3 infective larva in the vector at rates proportional to temperature, influencing transmission potential. As temperature also influences the daily probability of vector survival to potentially infective age (Macdonald., 1957), the vector may die before completion of filarial parasite development within it.

Within and between foci of filariasis, the efficiency of transmission is likely to vary seasonally as well as geographically. For French Polynesia, Rivière (1988) assumed that in Tahiti (18° S 149° W) the filariasis vector *Ae. polynesiensis* has a shorter mean life-span (i.e. greater daily mortality rate) during the cooler months (May–September), when development of *W. bancrofti* larvae is slower, reducing the transmission potential, and this seasonal limitation would be generally proportional to the degree of latitude south.

French Polynesia comprises 130 small high volcanic islands and atolls spread over an area equivalent to Europe, spanning 8° to 28°S in the Pacific Ocean. The four main archipelagos of French Polynesia (Fig. 1), from north to south, are the Marquesas (8–11° S), Tuamotu (14–23° S), Society (16–18° S) and Australes (21–28° S). Environmental conditions vary considerably from one island to another, with annual mean temperatures varying from 27°C in the north to 21°C in the south. Globally, the prevalence of LF infection is related to intensity of transmission (Sasa, 1976), with positive correlation between the annual transmission potential (ATP, the number of infective bites/person/year) and the mean microfilaraemia level as well as prevalence of clinical manifestations in communities (Kazura *et al.*, 1997). Independently, Brengues (1975) and Wijers (1977) suggested that prevalence of hydrocoele and elephantiasis tend to be higher where transmission is continuous. Consequently, in areas with more variation in duration of the extrinsic cycle, the prevalence of LF infection and its clinical signs may vary.

In French Polynesia, the prevalence of human infection with *W. bancrofti* has been estimated to range from 30 to 90% in the hottest archipelago, the Marquesas Islands, and 11–20% in the coolest archipelago, the Australes Islands, straddling the Tropic of Capricorn (23°S) where the extrinsic cycle is prolonged by lower temperatures. Microfilaraemia levels ranged from 80 microfilariae (mf) per 20 mm^3 of blood in Tahiti to 16–20 mf/20 mm^3 in the Australes. The prevalence of elephantiasis ranged from >5% in the Marquesas to 'rare' in the Australes (Table 1). The relationship between infection prevalence and environmental temperature warrants investigation.

In the present study, the importance of the extrinsic cycle duration for successful transmission is analysed and illustrated with the pair of *W. bancrofti* and *Ae. polyniesiensis* in French Polynesia. In particular, the role of temperature on the intensity of transmission is discussed. A statistical model for the duration of parasite development within its vector is derived and used to compute extrinsic incubation periods in various localities of different latitudes, i.e. temperature regimes. Results are related to epidemiological patterns of infection and disease in each main archipelago, and stability of transmission is discussed with regard to environmental factors.

Materials and Methods

Estimation of extrinsic cycle duration

For a given temperature T and for complete development of *W. bancrofti* larvae in its vector (i.e. for a microfilaria entering a mosquito and developing to the infective L3 stage), by definition:

$$r(T) \times \Gamma_T = 1 \qquad (1)$$

where Γ_T = mean development time (in days) at temperature T. However, field temperature varies according to a daily cycle that must be taken into account for analysis of population dynamics (Smerage, 1989).

During the 24-h period of each day, the field temperature T may behave according to a sine function oscillating between a minimum (T_{min}) and a maximum (T_{max}) (Allen, 1976; Parton & Logan, 1981) and may be expressed as:

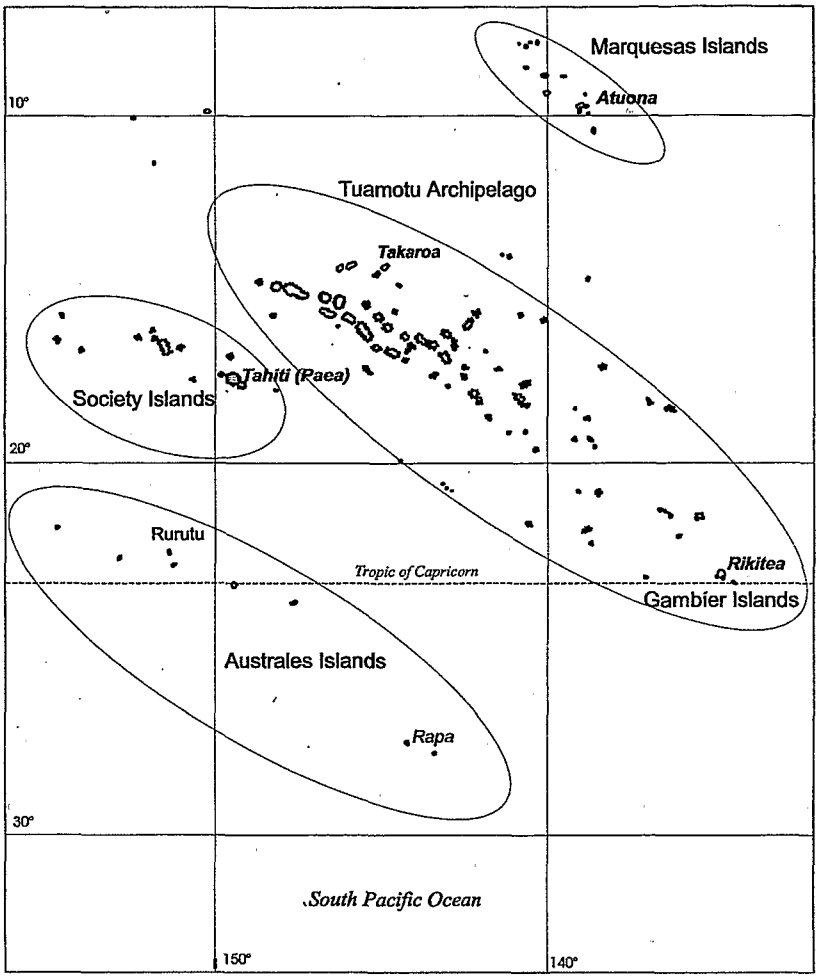

Fig. 1. The four archipelagos of French Polynesia. The Marquesas, Society and Australes are mainly high volcanic islands, whereas Tuamotu are atolls. Bold names are localities where meteorological data were recorded. Australes islands cited in the text are also located.

$$T(t) = a.\sin(t) + b \qquad (2)$$

where a is the amplitude of the sine curve, equal to $(T_{max} - T_{min})/2$, b is the mean of the sine curve, equal to $(T_{max} + T_{min})/2$, and t is the time of the day (in radians, with 1 day = 2π). For field application, T_{max} and T_{min} can be obtained from local weather stations. For each of the 24 h ($H = 0, \ldots 23$) the corresponding temperature can be computed by replacing the time t by $2\pi.H/24 - \pi/2$ in Eq. (2). Because the temperature T is a function of time t (i.e. $T = f(t)$, where f denotes the sine function of Eq. (2)), Eq. (1) can be rewritten for continuous time as:

$$\int_0^a r(T)dt = \int_0^a r(f(t))dt = 1 \qquad (3)$$

where α is the developmental time (i.e. the time for an ingested microfilaria to develop to the L3 infective stage). This time duration is the minimum value of the extrinsic cycle duration of the parasite (maximum values are not straightforward as the vector mosquito can retain the infective larva(e) for several days until a bloodmeal is taken; Lardeux & Cheffort, 1996).

To estimate α, Eq. (3) can be rewritten for discrete time as:

$$\sum_{t=0}^{a} r(f(t))\Delta t \cong 1 \qquad (4)$$

where Δt are periods of constant temperature. In the present study $\Delta t = 1$ h. As a first approximation, these small periods of one hour can be considered as periods where $r(f(t))$ is supposed to stay approximately constant.

Equation (4) can be easily solved iteratively for α. Thus, the minimum extrinsic cycle duration for the parasite (i.e. α days) can be computed using the temperature records of minima and maxima of days following the intake of microfilariae by the vector, stopping the summations when

Table 1. Geographical situation, meteorological characteristics, prevalence of *W. bancrofti* infection and human acute manifestations of filariasis in four archipelagos of French Polynesia. [1]Data from 1949–1955, before mass treatment with diethylcarbamazine for filariasis control. Mean duration of parasite extrinsic cycle based on mean annual temperature.

Archipelago (from north to south)	Latitude	Absolute humidity (mg/m^3)	Mean annual rainfall (mm)	Mean annual temperature (°C)	Mean duration of extrinsic cycle (days)	Prevalence of *W. bancrofti* infection in humans (%)[1]	Prevalence of elephantiasis (%)[1]
Marquesas	7.5–10.35° S	20	470–800	27	11.1	30–90	>5
Tuamotu	14–24° S	18.2	1350–1720	24.8	13.1	1–18	0.80
Society	15–18° S	18.7	1720–2350	25.8	12	23–32	6
Australes	21–28° S	15	1720–2350	21	22.2	11–23	Rare

$$\sum_{t=0}^{a} r(f(t))\Delta t \cong 1$$

For each temperature $T = f(t)$, the corresponding value $r(T)$ can be computed using the function of Lactin *et al.* (1995):

$$r(T) = \exp(\rho T) - \exp\left[\rho T_m - \frac{(T_m - T)}{A}\right] + \lambda \qquad (5)$$

This function adequately describes the development of *W. bancrofti* larvae in *Ae. polynesiensis* (Lardeux & Cheffort, 1997). In Eq. (5), T_m is the thermal maximum, i.e. the 'lethal' temperature at which life processes cannot be sustained by this mosquito–parasite pair, A is the temperature range over which 'thermal breakdown' becomes the over-riding influence, and ρ can be interpreted as a composite value for critical enzyme-catalysed biochemical reactions. The parameter λ is the value of $r(T_m)$ (i.e. when $T = T_m$) and allows the curve to intersect the abscissa at suboptimal temperatures, permitting estimation of the base temperature (i.e. the temperature below which development stops) by allowing $r(T) = 0$ to be solved for particular parameter values. For the combination *W. bancrofti* +*Ae. polynesiensis*, the parameters and their standard error (SE) were $\lambda = -1.179$ (0.189), $A = 10.98$ (1.28), $\rho = 0.0126$ (0.0005) and $T_m = 56.72$ (0.51).

Another value of interest is the upper threshold, T_{upper}, which is the value of T for which $r(T)$ is maximum (i.e. the first derivative $r'(T)$ is equated to zero and solved for (T).

$$T_{upper} = \frac{TLn(A\rho)}{(1 - A\rho)} + T_{max} \qquad (6)$$

Validation of Lactin et al. *(1995) function estimates under varying temperature conditions*

Experimental infection of *Ae. polynesiensis* with *W. bancrofti* followed procedures described by Lardeux & Cheffort (1996). Parameters of the function $r(T)$ (i.e. Eq. (5)) describing the developmental rate of *W. bancrofti* larvae were estimated by Lardeux & Cheffort (1997) under laboratory conditions with various constant rearing temperatures and relative humidity (RH) fixed at ~80%. In some cases, such a function may not be adequate under variable temperature conditions (Stinner *et al.*, 1974), so computation of the development time in field conditions (based on Eq. (4)) would be inaccurate. Therefore, the function $r(T)$ was tested with variable temperatures. The same experiment was undertaken as in Lardeux & Cheffort (1997) but, instead of keeping infected mosquitoes at a range of constant temperatures in environmental chambers, temperatures were changed between 22.5 and 30°C on a daily basis, following a sinusoid pattern. Thus, infected mosquitoes were held at 22.5°C just after infection (day 0 = 1/2 day), at 25°C during day 1, at 27.5°C during day 2, at 30°C during day 3, at 27.5°C during day 4, at 25°C during day 5, at 22.5°C on day 6, at 25°C on day 7 and so on, with constant RH 80%. Each day, a sample of the mosquitoes were dissected and their *W. bancrofti* larvae identified by stages and counted. As previously described in Lardeux & Cheffort (1997), the non-parametric procedure of Pontius *et al.* (1989) was used to estimate the mean time of L3 appearance. This value, corresponding to the observed real time to L3 stage, was compared to the development time computed from Eq. (4) in order to validate the accuracy of the function estimates under field conditions with varying temperature.

Field data

Daily field temperature minimum and maximum (recorded under cover, 1 m above ground level, complete records from 1985 to 1994) were obtained from National Meteorological stations in representative localities of the four archipelagos: Atuona (139°3′ W 9°47′ S) in the Marquesas; Takaroa (145° W 14°5′ S) in the Tuamotu Archipelago; Paea (149°35′ W 17°42′ S) in the Society Islands, and Rikitea (135° W 23° S) in the Gambier islands (on the Tropic of Capricorn and climatically equivalent to the Australes; Fig. 1). These localities exemplify the various environmental conditions where filariasis transmission occurs in French Polynesia (Table 1). According to the Litinsky classification (ORSTOM, 1992), French Polynesia has a humid or subhumid maritime tropical climate. Annual mean air temperatures are >20°C

Table 3. Theoretical mean proportion of *Ae. polynesiensis* females surviving and their residual life expectancy (longevity factor, in days) after completion of parasite extrinsic cycle, based on 1993 temperature data. Human prevalence of *W. bancrofti* and mean microfilaria rate (blood smear measurement) at the four localities under study (based on Rivière, 1988)

Locality (N to S)	Archipelago	Proportion of *Ae. polynesiensis* females after parasite cycle completion (%)				Residual life expectancy				*W. bancrofti* human prevalence (%)	Microfilariae per 20 mm^3 blood
		Mean	SD	Min	Max.	Longevity factor (days)	SD	Min.	Max.		
Atuona	Marquesas	21.9	1.1	19.8	23.9	1.7	0.08	1.6	1.9	50	?
Takaroa	Tuamotu	24.8	1.2	22.1	26.9	1.9	0.09	1.7	2.1	9	20
Paea	Society	17.9	3.1	11.6	23.5	1.4	0.2	0.9	1.8	30	81.7
Rikitea	Gambier (Australes)	10.9	6.8	1.7	22.0	0.8	0.5	0.1	1.7	26	16

throughout the Territory: <22.7°C in the southern area, 22.7–25°C in the southern Tuamotuan atolls and >25°C in the Society Islands, northern Tuamotu and Marquesas Islands (Fig. 1). Mean temperature decreases by 1°C each 220 km in latitude from north to south. Precipitation increases across a gradient from N–E to S-W with mean annual rainfall <1000 mm in the Marquesas and >2000 mm in southern Australes. RH averages ~80% with little variation from north to south in French Polynesia.

Considering Bancroftian filariasis disease manifestations and transmission patterns among indigenous human populations of the various archipelagos and localities under study, Tables 1 and 3 summarize prevalence of *W. bancrofti* microfilaraemia and elephantiasis symptoms from the period before any mass chemotherapeutic treatments were given (Rosen, 1954, 1955; Iyengar, 1965; Rivière, 1988).

Results

Aedes polynesiensis infected with *W. bancrofti* and maintained at variable temperature were dissected and examined for the stages and numbers of developing filarial larvae up to day 18 post-infection when the last batch of mosquitoes was dissected. Developing larvae reached L3 stage from day 12 onwards and the procedure of Pontius *et al.* (1989) gave a mean time of 12.58 days (variance = 0.21) for appearance of the L3 stage. Computation of developmental time using Eq. (4) gave 12.04 days. As these two values were not significantly different, the developmental function $r(T)$ can be used to represent field conditions of temperature fluctuation.

For each of the 3650 days from 1 January 1985 until 12 December 1994 the extrinsic cycle duration for *W. bancrofti* was computed for the study localities representing the four archipelagos. The annual pattern of extrinsic cycle duration was found to follow an equivalent pattern in the four study localities (Fig. 2), with much amplitude variation between the archipelagos, lasting longer during austral winter months (June–October) when temperatures are cooler. This pattern fluctuates most in the Australes (Fig. 2D), less in the Society Islands (Fig. 2C) and least in the Marquesas (Fig. 2B) and Tuamotu archipelago (Fig. 2A), where temperatures are constantly warmer throughout the year. Table 2 shows the basic statistics of extrinsic cycle duration for each locality. Mean duration of extrinsic cycle, computed for the period 1985–94, lasts 11.0 days in the Tuamotus (Takaroa), 12.1 days in the Marquesas (Atuona), 13.4 days in the Societies (Paea) and 18.2 days in the Australes (Rikitea). In the Marquesas and Tuamotu archipelago, higher temperatures reduce the extrinsic cycle duration to ~10 days during the summer months (December–March). This duration approaches to the minimum possible value (Lardeux & Cheffort, 1997): at T_{upper} = 31.5°C the extrinsic cycle lasts only 9.7 days.

Populations of *Ae. polynesiensis* adult females have high daily mortality rates in French Polynesia. Rivière (1988) reported that nearly all the female mosquitoes die within 2 weeks in the field: among 8139 captured the oldest female

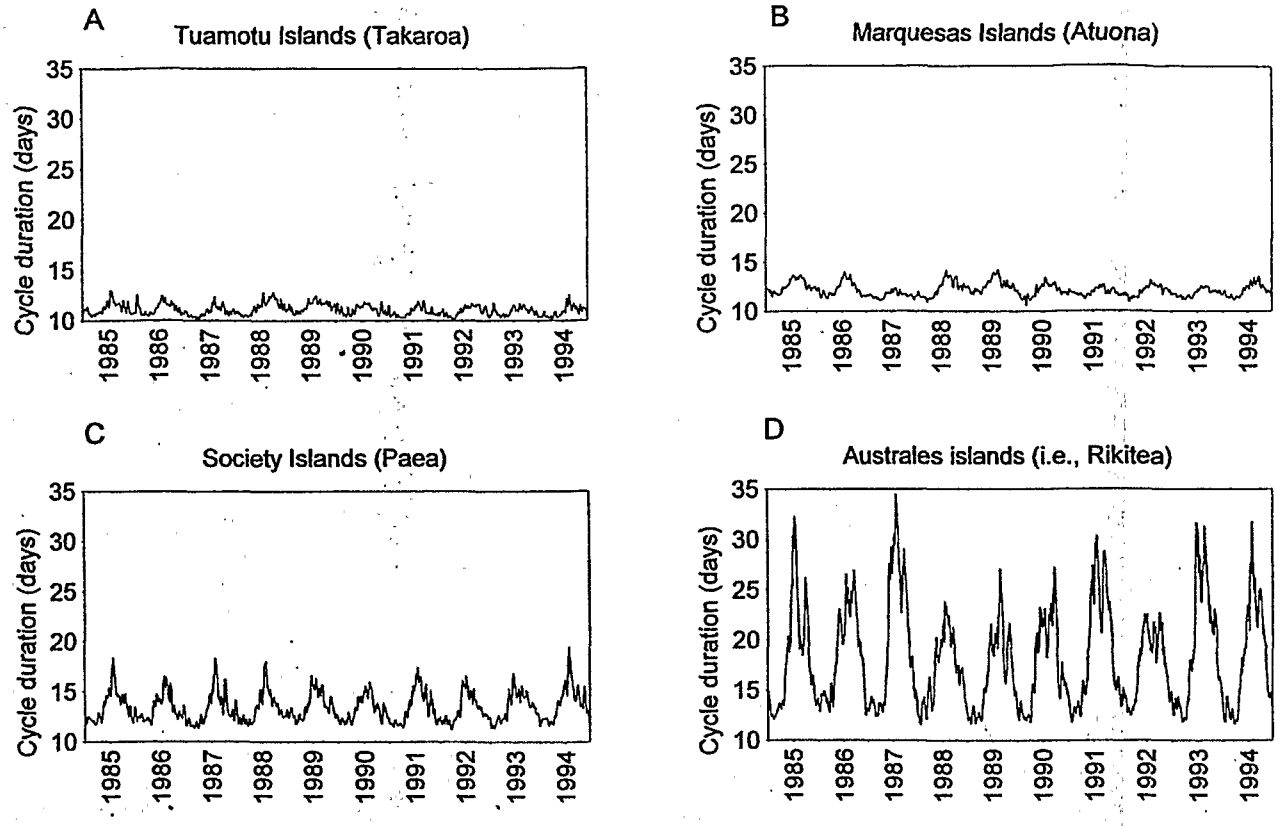

Fig. 2. Extrinsic cycle duration (in days) of *Wuchereria bancrofti* in *Aedes polynesiensis* in four localities representing French Polynesian archipelagos: (A) Tuamotu Islands; (B) Marquesas Islands; (C) Society Islands; and (D) Australes Islands. Data from 1 January 1985 to 12 December 1994.

Table 2. Statistical characteristics of the extrinsic cycle duration of *W. bancrofti* in *Ae. polynesiensis* in four archipelagos of French Polynesia, based on 1985–1994 data.

Locality (north to south)	Archipelago	Mean extrinsic cycle duration (days)	SD	Minimum duration (days)	Maximum duration (days)	% of days in year when extrinsic cycle duration <16 days	% of days in year when extrinsic cycle duration <15 days
Atuona	Marquesas	12.1	0.66	10.6	14.2	100	100
Takaroa	Tuamotu	11	0.54	10.1	13	100	100
Paea	Society	13.4	1.46	11.2	19.5	94.1	83.7
Rikitea	Gambier (Australes)	18.2	5.07	11.5	34.5	37.8	44

was estimated to be 15–16 days old, which may be taken to represent the maximum longevity of *Ae. polynesiensis*. Considering that the extrinsic cycle of *W. bancrofti* takes a minimum of 10 days in this vector, the probability of transmission will be very low – even for a 15–16-day-old mosquito, as their first bloodmeal is taken when nulliparous females are a few days old. For the period 1985–94, the proportion of days when duration of the extrinsic parasite cycle was < 15 or < 16 days was computed for each of the four localities under study (Table 2). Results show an extrinsic cycle no longer than 13 or 14 days in the northern archipelagos, Marquesas and Tuamotus, so that transmission could occur throughout the year. In the Society islands the extrinsic cycle lasts < 15–16 days during 84–94% of the year, so transmission would be expected to occur during all but the coldest month or two (during the period June–August, see Fig. 3). At the southerly latitude of the Australes, the cycle is completed within < 15–16 days only during 38–44% of the

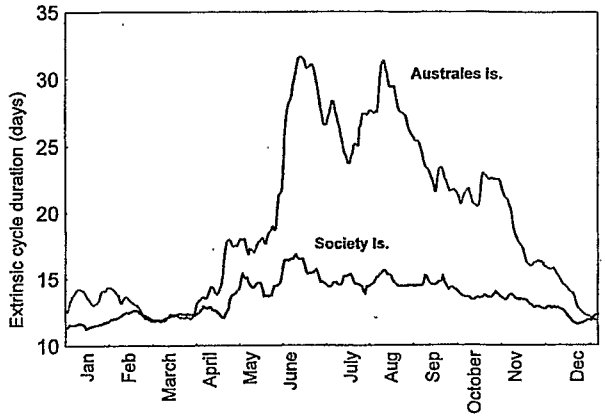

Fig. 3. Extrinsic cycle duration (in days) of *Wuchereria bancrofti* in *Aedes polynesiensis* at Paea, in Tahiti, the main Society Island, and in Rikitea, Gambier Islands, representing climatic conditions of the Australes Islands, during 1993. In each case the extrinsic cycle duration is longer from June to September, the cooler season in French Polynesia.

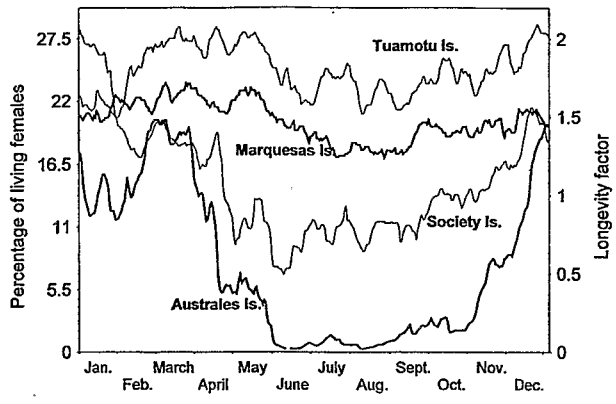

Fig. 4. Theoretical maximum proportion of female *Aedes polynesiensis* still alive after completion of *W.bancrofti* extrinsic cycle (left abscissa) and 'longevity factor' in days (right abscissa), i.e. remaining life expectancy after completion of extrinsic parasite cycle, in the four named archipelagos, based on 1993 temperature records, assuming that all females take a first infective bloodmeal on day 2 and their mean daily survival rate is 0.88.

year (Table 2), so transmission is unlikely to occur during most months (Fig. 3).

In Tahiti, Rivière (1988) estimated the mean daily survival rate of female *Ae. polynesiensis* to be $s = 0.88$. Based on this value, the vector mosquito mortality rate is $m = -\mathrm{Ln}(0.88) = 0.128$ per day, so the maximum proportion P of mosquito females surviving long enough for potential transmission of the parasite can be estimated by $P = 100e^{[-0.128t]}$, where t = duration of the parasite extrinsic cycle. This proportion is a rough approximation because it assumes that the probability of vector survival is not influenced by other factors such as temperature, mosquito age or infection, that probably have some effects. Even so, this approximation demonstrates the annual pattern of potential transmission months, as illustrated with 1993 data in Fig. 4. Considering the whole year for the Marquesas and Tuamotu archipelagos, respectively, 20–24% and 22–27% of *Ae. polynesiensis* females survive to the potentially infective age (Table 3). In Tahiti, this proportion varies from >23% during summer to <12% during cooler months. In the Australes, there is practically no vector potential from June to October, but transmission is possible during December–March when the proportion of females reaching potentially infective age ranges from 10 to 22%. Correspondence between annual vector potential and prevalence of human infection at each locality is shown in Table 3, although for Takaroa the observed prevalence of *W. bancrofi* is lower than might be expected from the vector potential.

The most important factor is the infective life expectancy of the vector, i.e. mosquito survival probability after completion of the extrinsic cycle of the parasite, which may be called the residual expectation of vector life. Assuming that the daily mortality rate m of vectors is constant, the life expectancy is $1/m$. With the above estimate of $m = 0.128$, the mean life expectancy is 7.8 days, showing that relatively few *Ae. polynesieinsis* females reach the age of potential infectivity (minimum ~10 days). The residual expectation of life (in days) when transmission is possible was defined by Garret-Jones (1964) as the 'longevity factor' (Table 3, Fig. 4). For the warmer archipelagos of French Polynesia, the longevity factor fluctuates between ~1.5–2 days in the Tuamotus and 1.2–1.7 days in the Marquesas. At Paea, representing Tahiti in the less tropical Society Islands, the longevity factor stays below one day during the cool season and reaches 2 days in January. At Rikitea, climatically similar to the Australes, the longevity factor is below 0.5 days from April to October, almost zero during June–August, and longer than 1 day during the first quarter of 1993.

Discussion

The statistical model developed here to compute duration of the extrinsic cycle for *W. bancrofti* gave results in agreement with observations on the vector *Ae. polynesiensis* in Fiji (Symes, 1960) and Samoa (Samarawickrema *et al.*, 1980) where the cycle duration was found to be 12–13 days at about 24°C. To be realistic, our model includes daily temperature variations (minimum and maximum) for correspondence with vector density and survival rate and man–vector contact (biting rate) to assess transmission dynamics. Although vector longevity may also be correlated with temperature (Rivière, 1988), no such quantitative data were available so mortality was assumed to be constant. Data for experimental infection of *Ae. polynesiensis* with *W. bancrofti* were based on Lardeux & Cheffort (1996). The relationship between development of the parasite and longevity of the vector was then simplified, but not

described quantitatively as by Takaoka (1982) for the similar pair *Onchocerca volvulus* with *Simulium ochraceum*.

For *Ae. polynesiensis* the maximum theoretical 'longevity factor' (i.e. remaining life expectancy of females after development of parasite larvae to L3 infective stage) was estimated to be ~2.3 days, assuming a daily survival rate of 0.88 and the shortest possible extrinsic cycle duration of 9.7 days for the parasite at the optimal temperatures prevailing in the Tuamotu archipelago (Fig. 4). Despite theoretically perennial transmission potential, however, *W. bancrofti* prevalence is generally low in the Tuamotu atolls and completely absent from some. This deficiency may be explained by the limitation of man–vector contact as a major component of vectorial capacity (Birley & Charlwood, 1986; Dye, 1986; Rochet, 1990). The filariasis vector *Ae. polynesiensis* is far outnumbered by the refractory non-vector *Aedes aegypti* (L.) in most Tuamotu villages, despite implementation of mosquito control activities (Lardeux, 1992), whereas *Ae. polynesiensis* predominates among coconut groves (breeding prolifically in coconut shells) where people are bitten intensively by *Ae. polynesiensis* with transient risks of filariasis transmission only during the copra harvest season (Lardeux *et al.*, 1992). Another reason why transmission rates are lower than expected in the Tuamotus could be through reduction of vector longevity by the windy conditions with low rainfall on most atolls. Local confounding factors therefore make our model inapplicable to the conditions limiting filariasis transmission on some Tuamotu atolls.

The usual goal of vector control is to prevent transmission by reducing the vector life expectancy below that required for the parasite extrinsic cycle to reach infectivity (Macdonald, 1957). This is the main objective of malaria vector control operations based on house-spraying with residual insecticides, or the use of pyrethroid-impregnated bednets, which also provide more immediate personal protection through reduction of man–vector contact. Vector density in relation to man (another key component of vectorial capacity, *sensu* Garrett-Jones, 1964) and the proportion of infective bites are two very variable factors that may be combined to measure transmission potential. Among wild populations of *Ae. polynesiensis* in French Polynesia, the proportion of infective females is usually $<2\%$ (Rivière, 1988; Cartel *et al.*, 1992; Lardeux *et al.*, 1995), so the annual biting rate (ABR) provides a ready index of transmission risk.

In the Marquesas, the hottest and most northerly islands of French Polynesia, the extrinsic cycle duration is consistently short (mean 11.1–12.1, range 10.6–14.2 days) and people are exposed to perennially high biting rates of *Ae. polynesiensis* (Lardeux, unpublished data) reinforcing the continuous transmission potential. Hence, the human prevalence of *W. bancrofti* infection is high and clinical manifestations are often severe in the Marquesas. In the geographically and climatically intermediate Society Islands, the extrinsic cycle duration fluctuates markedly between summer and winter as demonstrated by our model (Fig. 4). Near Paea on Tahiti Island, Rivière (1988) found the monthly transmission potential (MTP, number of infective bites/person/month) ranged from MTP > 100 during summer (October–March) down to MTP < 12) during the cooler months, with perennial transmission.

In the more southerly island groups, Australes and Gambiers, due to prevailing lower temperatures the extrinsic cycle duration of *W. bancrofti* larvae is longer than *Ae. polyensiensis* life expectancy except during December–March. The proportion of female vectors surviving to potentially infective age is close to zero during five consecutive months (June–October) and peaks during warmest months of February and March. This very seasonal filariasis transmission contrasts with perennial transmission potential and generally higher levels of Bancroftian filariasis endemicity northwards in French Polynesia, allowing for local variations of ecology and epidemiology as mentioned above and summarized by Sasa (1976). Consequently, the computation of ATP should allow for climatic seasonality, especially southwards in French Polynesia, so we recommend the computation of ATP by summing MTPs, particularly for islands with marked seasonal fluctuations in transmission potential, i.e. Australes, Gambiers and the Society Islands including Tahiti. Although lacking the full power of vectorial capacity analysis, simple ATP and ABR values appear to be useful comparative indicators of the risks of exposure to vector-borne infections. Since the 1970s these criteria have proved to be a reliable basis for evaluating results of vector control in the Onchocerciasis Control Programme (OCP) in West Africa (WHO, 1994). ATPs are routinely computed on a monthly basis for OCP to guide vector control activities, sometimes on a weekly basis to monitor seasonal influences on vector longevity or extrinsic development of the filarial parasite *Onchocerca volvulus* in blackflies of the *Simulium damnosum* complex.

Based on the temperature effect, the present results show how *W. bancrofti* transmission by *Ae. polynesiensis* in French Polynesia can be classified into three main strata corresponding with latitude. From north to south these strata are: perennial high level transmission in the Marquesas Islands, continuous transmission with fluctuating intensity in the Society Islands and intermittent seasonal low rates of transmission in the Australes and Gambier Islands. Among atolls of the Tuamotu archipelago, the filariasis situation departs from temperature-based expectations of the model, apparently because of limited man–vector contact and reduced longevity of the vector due to environmentally unfavourable conditions. Our results indicate that, where no other factors interfere, the prevalence of Bancroftian filariasis depends mainly on ambient temperature in southern French Polynesia, where the Tropic of Capricorn coincides with the southern limit of *W. bancrofti* distribution, as in Africa (Brengues *et al.*, 1979). Moreover, the usual vector *Ae. polynesiensis* is absent from Rapa, the most southerly island of the Australes (Belkin, 1962). In these boundary regions, the disease is less stable and it is likely that the basic reproduction ratio R_o of the parasite is very close to 1. Filariasis was relatively easily eradicated from Rurutu, one of the Australes Islands, with diethylcarbamazine prophylactic mass treatment, which has not been accomplished elsewhere in Polynesia (Sasa, 1976; Rivière, 1988). Above the tropic of Capricorn, environmental conditions are conducive to intense transmission perennially in the northern archipelagos of

Tuamotu and the Marquesas, more seasonally in Tahiti and the other Society islands. Precipitation and evapotranspiration were used by Lindsay & Thomas (2000) to map the probability of Bancroftian filariasis presence in Africa, but these criteria seem to be of less influence on filariasis endemicity in French Polynesian islands, although we recognize the limiting influence of low rainfall in drier Tuamotu atolls. As demonstrated by our model corresponding with the observed levels of filariasis endemicity and transmission in four representative localities, temperature determination of the parasite extrinsic period accounts for most differences in filariasis clinical manifestations and infection risks between climatically contrasted Polynesian archipelagos.

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