



Effect of climate on malarial vector distribution in Monsoon Asia: coupled model for Ecophysiological and Climatological Distribution of mosquito generations (ECD-mg)

Shunji Ohta*, Takumi Kaga

Department of Human Behavior and Environment Sciences, Faculty of Human Sciences, Waseda University, 2-579-15 Mikajima, Tokorozawa, Saitama 359-1192, Japan

ABSTRACT: The relationship between the life cycle and climate conditions of the malaria vector mosquito *Anopheles* was modeled in order to describe its temporal and geographic distribution at a fine resolution. Since the mosquito grows through immature life stages in an aquatic environment, the model was designed to express the surface moisture conditions conducive to the mosquito's growth. The development of the mosquito was estimated using either air or water temperature, depending on the developmental stage of the mosquito's life cycle. To achieve this, the previous model was modified in order to improve the estimation of the water conditions of its habitat. As a result, the modified model was able to predict seasonal patterns of occurrence of *Anopheles* at representative sites with a more reasonable degree of accuracy than the previous model. This model was then applied using simple climate data in order to obtain the geographic distribution of the occurrence of various species of *Anopheles* in Monsoon Asia. The most notable results of the simulated spatio-temporal emergence of the *Anopheles* mosquito is that although the modified model did not include unique parameters of each species, distribution was clearly divided into sub-regions for each dominant species that corresponded to the climate conditions.

KEY WORDS: Climatic resources · Energy balance · Water balance · Life cycle · Malaria vector

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Malaria is considered the most detrimental mosquito-borne disease worldwide. Because of the climate-sensitivity of the mosquito vector, malaria is strongly influenced by climatic factors. Climate variables could play an important role in the geographic distribution and seasonal occurrence of these vector species (Hopp & Foley 2001, Martens & Thomas 2005, Kearney et al. 2009).

The total number of malaria cases has decreased during the past century due to economic development and the disease control measures taken during this period (Hay et al. 2004, Gething et al. 2010). However, malaria is still a serious public

health problem in most developing countries, and the reduced occurrence of malaria during the last century did not correspond to a reduction in the ranges of vector species (WHO 2010). Although the relationship between malaria and climate variables has been assessed in many regions, few studies have addressed the relationship between the vector species and climate variables. In addition, since there are many species of malaria vector mosquitoes in Monsoon Asia—which occurs in various climates, such as cool- and warm-temperate, subtropical and tropical—the relationship between vectors and projected climate conditions is quite complex, depending on the type of species (Paing et al. 1989, Chow 1991, Garros et al. 2008, Manguin et al. 2008,

*Email: shun@waseda.jp

Barik et al. 2009, Ndoen et al. 2010). In particular, little is known about the broad-scale impact of variations in climate on the vector species distributions in these regions.

Recent studies that have mapped vector species have attempted to explain the geographic distribution of *Anopheles* and *Aedes* mosquitoes by analyzing the climate variables of mosquito observation sites using niche-based distribution models (Foley et al. 2008). These studies have generated high-resolution maps of the present distributions of these vectors over large areas using climate data. The ecophysiological and entomological approaches have also been employed in a number of studies to explain the temporal occurrence of vectors, by describing their life cycles and addressing climate factors (Patz et al. 1998, Hopp & Foley 2001, Depinay et al. 2004, Pascual et al. 2006). Apart from simple climatic variables, the activities of the mosquitoes depend on variables related to their native habitats, such as water and soil conditions. Hopp & Foley (2001), for example, expressed the time variation of the surface water balance and soil moisture content using a simple bucket model.

Recently, Kashiwada & Ohta (2010) integrated the ecophysiological model, the energy balance model, and the simple water bucket model to describe the life cycle and the native habitat environments of the *Anopheles* mosquito. Although their model was able to successfully represent the spatio-temporal emergence of the *Anopheles* mosquito, it did not accurately calculate the energy and water balances in the mosquito's habitat, and did not properly take plant cover into account. In particular, it is necessary to more precisely express the soil moisture conditions conducive to the growth of the *Anopheles* mosquito, by modifying the energy and water balance models. The previous model underestimated the occurrence of mosquitoes in subtropical regions (Kashiwada & Ohta 2010).

Therefore, the first purpose of this study is to improve the spatio-temporal distribution model (Kashiwada & Ohta 2010) by reconsidering the description of water conditions in the habitat of mosquito vectors, in order to obtain a map of their distribution on a broad spatial scale. The new calculation method is then used to describe the spatio-temporal distribution of *Anopheles* mosquitoes in Monsoon Asia in terms of the current climate. The obtained simulation results provide insight into the climatic characteristics of the distribution of 5 representative species of *Anopheles* mosquitoes in these regions.

2. METHODS

The water and thermal resources of the habitats of 5 species of mosquitoes were estimated with a 1 d time interval using our modified model and simple climate data of parameters, such as air temperature, precipitation, solar radiation, cloud amount, relative humidity, and wind speed. On the basis of the results obtained, the number of alternations of generations of mosquitoes was estimated.

2.1. Habitat of the *Anopheles* mosquito

The habitats of *Anopheles* at its egg, larval and pupal stages of growth are mainly lowland puddles, which are widely distributed in forests, river basins, coastal areas, swamps, marshes, and man-made water containers. In order to consider the potential distribution of mosquitoes in this study, the availability of a natural water source was assumed and there was no consideration of man-made sources such as ditches and sewerage systems. In order to more precisely estimate the energy and water balance at a site, we simplified our approach by assuming shallow water with growing plants in areas of several 10s m² to be a typical habitat (Fig. 1), though we did not consider the plant cover in the previous model (Kashiwada & Ohta 2010). Such a water body was considered to be the essential habitat to *Anopheles* during immature stages of its development. We described the energy and water exchanges between the water body and soil, and the plants and layers of the atmosphere.

2.2. Description of the mosquito growth model

The first part of the coupled model for Ecophysiological and Climatological Distribution of mosquito generations (ECD-mg) calculates ecophysiological the growth of the mosquito. Numbers ranging from 0 to 4 describe the progression of the mosquito's life cycle from an egg to a mature adult ('*Anopheles* growth model' in Fig. 2). Each stage of development (Δd_k) at the k th day is completed when the accumulated development is 1. The stage of development then proceeds to the next stage. The cumulative development (C_{total}) is expressed as:

$$C_{\text{total}} = \sum_{k=l}^m \Delta d_{\text{egg},k} + \sum_{k=m+1}^n \Delta d_{\text{larva},k} + \sum_{k=n+1}^o \Delta d_{\text{pupa},k} + \sum_{k=o+1}^p \Delta d_{\text{adult},k} \quad (1)$$

where l , $m + 1$, $n + 1$, and $o + 1$ denote the starting day of each developmental stage; m , n , o , and p

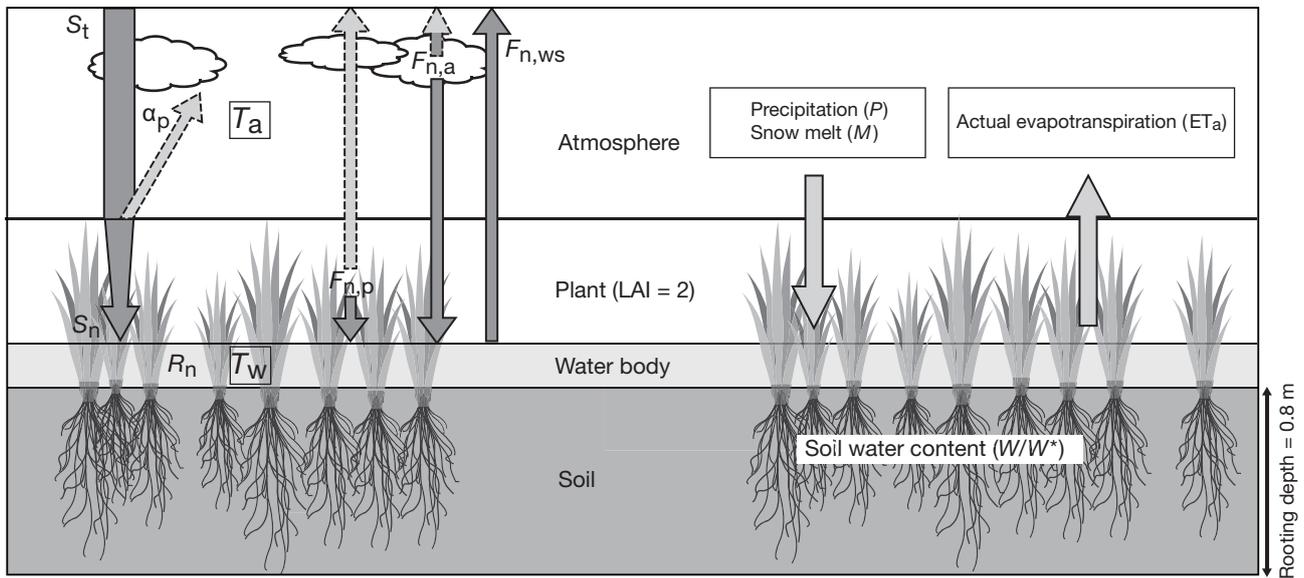


Fig. 1. Energy and water balance in a typical habitat of *Anopheles*. T_a : air temperature; T_w : water temperature; R_n : net radiation; S_t : global solar radiation; S_n : net flux of solar radiation; α_p : albedo of plant layer; $F_{n,p}$: long-wave radiation from plants; $F_{n,a}$: long-wave radiation from air; $F_{n,ws}$: long-wave radiation from water surface; LAI: leaf area index; W : amount of water in soil; W^* : water holding capacity of soil

denote the end day of each stage; and Δd_{egg} , Δd_{larva} , Δd_{pupa} , and Δd_{adult} represent the development of the egg, larva, pupa, and adult mosquito, respectively. Δd_k is expressed as a product of the time unit of development and the inverse of the duration of the completion of each developmental stage at a given constant temperature. The relationships between the temperature threshold and mosquito development at each stage were determined based upon previously published information (Depinay et al. 2004, Kashiwada & Ohta 2010). The rate of development (d^{-1}) was calculated using only water and air temperatures. In the present study, differences among species with regard to this thermal dependence on each stage of development were not considered. The ECD-mg model did not include a unique parameter for the rate of development of each species. The alternation of generations (G ; when $C_{total} > 4$) was counted over a 1 yr period, and the maximum number was described as the potential number of generations (G_{max}) in order to estimate the frequency of occurrence (Yamamura & Kiritani 1998, Kearney et al. 2009, Kashiwada & Ohta 2010).

2.3. Calculation flows of the thermal and water conditions inhabited by mosquitoes

The second part for the ECD-mg model consists of 2 subprocesses that determine the energy balance and

moisture conditions of the mosquito habitat using simple climate data. In order to calculate the growth of mosquitoes using Eq. (1), the values of the parameters of the water temperature and soil moisture content in the assumed habitat (Fig. 1) are needed. The overall flow of the basic calculation is shown in Fig. 2. First, the energy balance of the habitat without plants (leaf area index [LAI] = 0) was calculated using simple climate data (Ohta et al. 1993, 1995) as shown in 'Energy balance model' of Fig. 2. Next, the net radiation without plants obtained at the same time was used to calculate the potential evaporation using the Penman method (Penman 1948), which can get a useful approximation of evaporation at open humid surfaces with simple climate data. Subsequently, the water budget of the soil without the plant cover was estimated tentatively ('Water balance model' in Fig. 2). If the daily soil moisture content was $>15\%$ and the daily mean air temperature was $>5^\circ\text{C}$ (Mintz & Serafini 1992), the energy balance and temperature of the water layer with plants (LAI = 2) were estimated (Ohta & Kimura 2007). Using this value of net radiation of a water body with plants, the reference evapotranspiration (ET_0) and actual evapotranspiration (ET_a) were predicted using the methods of Allen et al. (1998) and Tao et al. (2003). The water budget calculation was conducted again using the ET_a on the k th day obtained from these methods. The detailed calculation processes that take the plant cover into account will be described in next subsections.

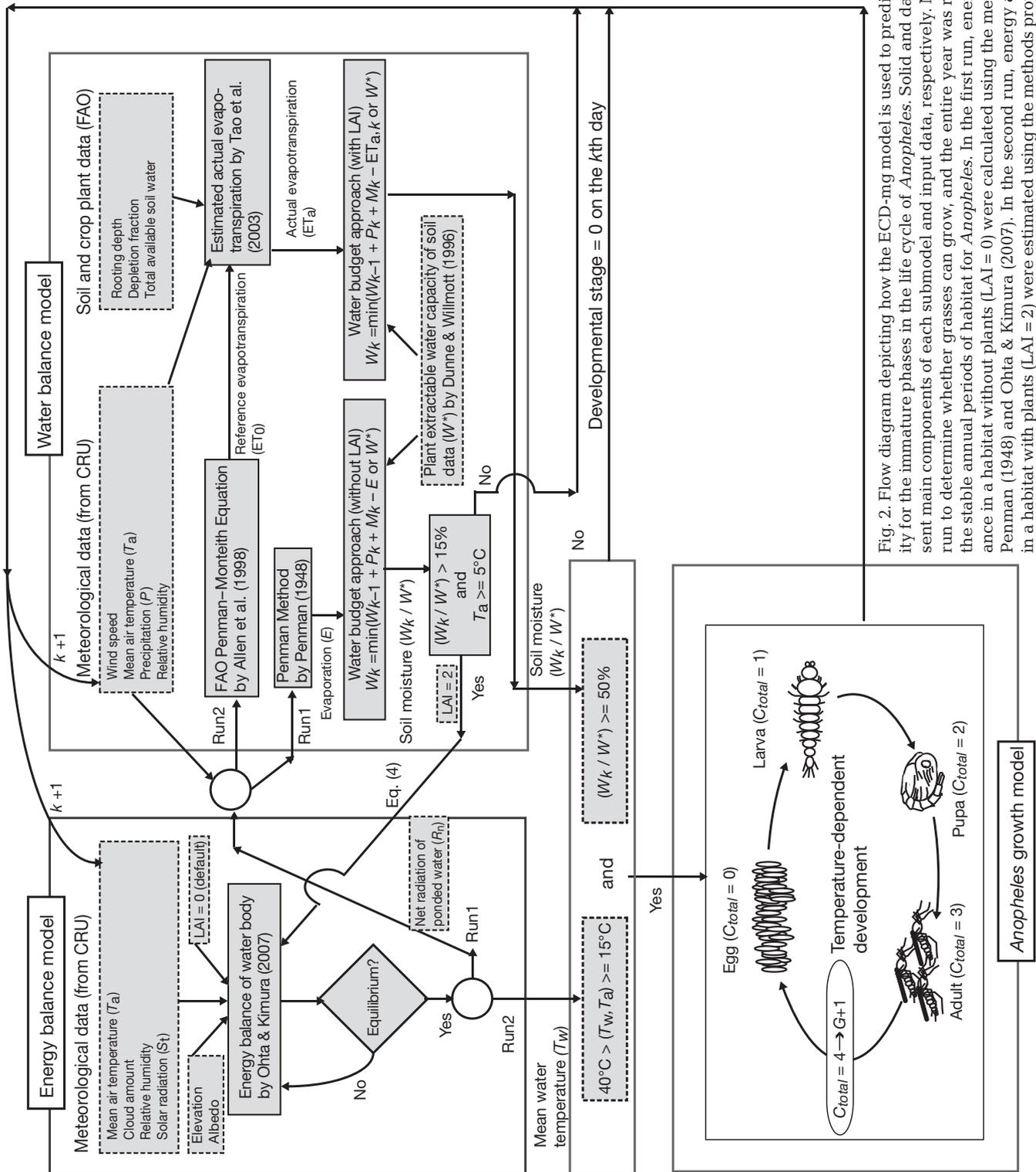


Fig. 2. Flow diagram depicting how the ECD-mg model is used to predict habitat suitability for the immature phases in the life cycle of *Anopheles*. Solid and dashed boxes represent main components of each submodel and input data, respectively. Note each day was run to determine whether grasses can grow, and the entire year was run twice to obtain the stable annual periods of habitat for *Anopheles*. In the first run, energy and water balance in a habitat without plants (LAI = 0) were calculated using the methods proposed by Penman (1948) and Ohta & Kimura (2007). In the second run, energy and water balance in a habitat with plants (LAI = 2) were estimated using the methods proposed by Tao et al. (2003) and Ohta & Kimura (2007). Further details are provided in Sections 2.3 and 2.4

The soil moisture content and water temperature obtained from the abovementioned flow are the main parameters used in the growth model (Fig. 2). Various species of *Anopheles* can develop only in a temperature range from 15 to 40°C and with a soil moisture content that exceeds 50% (Patz et al. 1998).

2.3.1. Calculation of net radiation in habitat with plant cover

For the estimation of evaporation/evapotranspiration or water temperature, it is necessary to accurately calculate the net radiation in the assumed habitat (Fig. 1). The most noteworthy characteristic of the ECD-mg model is that the net radiation during the growing season is determined by the balance of the downward flux of the long-wave radiation emitted from the plant layer and the amount of short-wave radiation that is intercepted by the plant foliage (Ohta & Kimura 2007). Each item of the energy balance of a mosquito habitat with the growth of plants is shown in Fig. 1. To estimate the water temperatures (T_w), we calculated the net radiation at the water surface (R_n ; $W m^{-2}$). When there is a large difference between T_w and air temperature (T_a), the net radiation affecting T_w can be given by:

$$R_n = R_{na} - h_R (T_w - T_a) \quad (2)$$

where R_{na} is the net radiation, which is calculated by assuming that $T_a = T_w$; $h_R (=4\sigma T_a^3)$ is the radiative heat transfer coefficient ($W m^{-2}$); and σ the Stefan-Boltzmann constant ($W m^{-2} K^{-4}$). Then, R_{na} can be represented as follows:

$$R_{na} = S_n + F_{n,p} + F_{n,a} - F_{n,ws} \quad (3)$$

where $F_{n,p}$ is the downward flux of long-wave radiation from the plants ($W m^{-2}$), and $F_{n,a}$ and $F_{n,ws}$ are the downward-directed long-wave radiation from the air and the long-wave radiation emitted by the water surface ($W m^{-2}$), respectively. The calculations of the 3 items of long-wave radiations (F_n) with plant cover were conducted using the method of Ohta & Kimura (2007). S_n is the net flux of solar radiation ($W m^{-2}$), which is reduced by a function of the LAI. Then, S_n can be expressed as:

$$S_n = S_i (1 - \alpha_p) \exp(-K \times LAI) \quad (4)$$

where S_i is the global solar radiation ($W m^{-2}$), α_p is the albedo of the plant layer (0–1), and K is the attenuation coefficient. This calculation method for the net radiation, which considers the plant cover using simple climate data, was valid and was able to provide

precise estimations of the equilibrium water temperature (Ohta & Kimura 2007).

2.3.2. Estimation of the soil moisture content in habitat with plant cover

The soil water content in the mosquito habitat has to be evaluated in order to exclude areas that are too arid for the survival of an immature mosquito. In the present study, the soil water content at the depth of the plant roots was calculated using the water balance approach (Allen et al. 1998, Hopp & Foley 2001, Tao et al. 2003) as illustrated on the right-hand side of Fig. 1. Calculation of the soil water content on the k th day (W_k) was performed using the following equation:

$$W_k = \min(W_{k-1} + P_k + M_k - ET_{a,k} \text{ or } W^*) \quad (5)$$

where W_{k-1} is the soil water content at the end of the previous ($k - 1$) day, P_k is daily precipitation (mm), M_k is daily snow melt on the k th day, and W^* is the holding capacity of soil water (mm), which reflects the types of soil texture and organic content, as obtained from Dunne & Willmott (1996). When W_k obtained from these calculations was larger than W^* , it was assumed that W_k was equal to W^* .

In order to estimate $ET_{a,k}$, a similar procedure proposed by Tao et al. (2003) was adopted. In this method, $ET_{a,k}$ is defined as the ratio of the available water content to the $ET_{0,k}$ calculated using the FAO Penman–Monteith method (Allen et al. 1998). Tao et al. (2003) has determined the soil moisture content by considering the parameters of physical properties of the soil surface and successfully described the geographical distribution of the ET_a in China. Therefore, this method was incorporated into the ECD-mg model.

Using the method of Allen et al. (1998), the value of $ET_{0,k}$ at the surface of a cropland can be estimated without considering parameters such as aerodynamic and canopy resistances and so on, which are difficult to obtain on a broad scale. Further, there is no difference between the vegetation height assumed by Allen et al. (1998) and the vegetation height in the assumed habitat in this study (Fig. 1). Owing to the above 2 reasons, we adopted the method of Allen et al. (1998) to calculate the value of $ET_{0,k}$ at a surface with plants.

Calculation of the $ET_{0,k}$ requires the data for net radiation discussed in Section 2.3.1, the air temperature, air humidity, and wind speed, along with topographical data such as albedo and altitude (Fig. 2).

Other data needed to perform this calculation method by Tao et al. (2003) are the rooting depth (m) and the soil water-depletion fraction. In the present study, these values were considered to be at the same level as those of grassland and shrubs, and were set to 0.8 and 0.5, respectively (Smith 1992, Canadell et al. 1996).

2.4. Data used for calculation of the model

Data for the Monsoon Asia region (10°S–50°N, 70–150°E) were used in the ECD-mg model (Fig. 3). All meteorological data had a spatial resolution of 0.5° longitude × 0.5° latitude (~50 km). The Climate Research Unit (CRU; University of East Anglia) Global Climate Dataset, which is available through the Data Distribution Center of the Intergovernmental Panel on Climate Change (IPCC; New et al. 1999), was used for the ECD-mg model calculations. The CRU monthly data for air temperature, precipitation, short-wave radiation, vapor pressure, wind speed, and cloud cover were included in the dataset for the 1961–1990 climate normals. If daily data were not available for the ECD-mg model, monthly values were converted to daily values using linear interpolation to ensure that the daily values were consistent with the monthly averages or total values. For the calculation of long-wave radiation, elevation data from GTOPO30 (US Geological Survey, www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html, accessed 25 February 2011) were used in the present study. The elevations in GTOPO30 are regularly at a spatial resolution of 30-arc s, which we averaged and converted to a spatial resolution of 0.5°, excluding the area of the ocean. The monthly albedo of the typical surface and plant layer in each 0.5° longitude × 0.5° latitude resolution (Ohta et al. 1993, Ohta & Kimura 2007) was used. When the air temperature was <0°C, the albedo value was set to 0.7.

Species occurrence data were collected from recent observations in Asia based on molecular identification techniques such as the PCR-assay (Manguin et al. 2008). The current distribution regions of the 5 representative dominant species in all of Monsoon Asia are depicted in the square areas in Fig. 3. *Anopheles sinensis* is an

important vector in the regions of Japan, Korea, and the eastern part of China (Chow 1991); *A. minimus* is the main species to which cattle are exposed in northern Vietnam and southern China (Garros et al. 2006, 2008); *A. culicifacies* has been recorded throughout India, including Kashmir and the high elevations of the Himalayas, but not on the Andaman and Nicobar Islands (Barik et al. 2009); *A. dirus* is an important vector of malaria in Myanmar (Paing et al. 1989); *A. sundaicus* has been reported to be the main vector of malaria in the coastal areas of Southeast Asia (Imai et al. 1988, Ndoen et al. 2010).

3. MODEL EVALUATION

We tested the predictive power of the ECD-mg model by comparing the model estimations to real observational data from many independently published datasets, which ranged from cool-temperate to subtropical or tropical zones (Ho et al. 1965, Yoshida et al. 1974, Dev 1996, Ikemoto 1996, Konradsen et al. 1998, Lee et al. 2002, Toma et al. 2002, Oo 2003, Yeom et al. 2005, Stoops et al. 2009). These data are collected only from seasonal observations of *Anopheles* >1 yr, in order to verify that the ECD-mg model can describe seasonal variations, even though in most developing countries there are very few observations throughout the year (Martens & Thomas 2005). The climate data used for validation of the

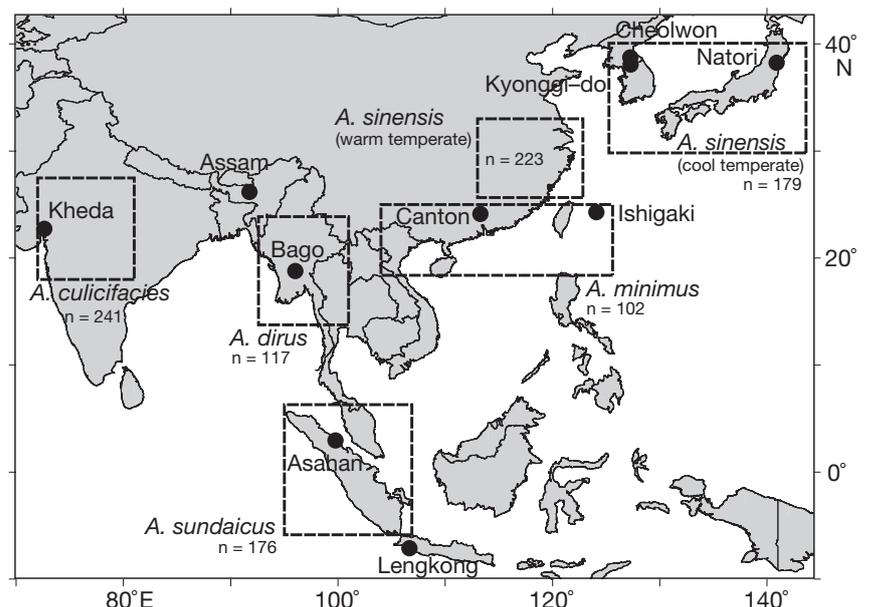


Fig. 3. *Anopheles* spp. Representative observation sites (circles) and the dominant species of *Anopheles* in each selected region (boxes; Manguin et al. 2008). n = number of grids in each square

ECD-mg model were observed simultaneously with the observation of *Anopheles*. If the value of C_{total} calculated from the k th day was >3 , we defined the k th day as the day of mosquito emergence. Since the mosquito could have emerged across different years, the calculation period included 2 yr. The first date of mosquito appearance and the end date were defined as the mosquito emergence date and the mosquito disappearance date, respectively.

The predicted appearance and disappearance dates obtained from the ECD-mg model were concordant with those of the observation data (Fig. 4). The root mean square errors (RMSE) between the observed and modeled values for these dates were ~15 to 20 d. These values were acceptable for a simulation of the potential mosquito distribution, because the mosquito occurrence observations were repeated over periods ranging from several weeks to a few months (Dev 1996, Konradsen et al. 1998). The present model has an improved accuracy that is approximately twice that of the previous model (Kashiwada & Ohta 2010), reflecting the modification of the energy and water balances in the present model. This means that the present model was able to represent well the transient thermal and water state of the habitat of mosquitoes. The appearance and disappearance dates obtained from the ECD-mg model were corroborated by observations at representative sites.

Next, in order to further confirm whether the ECD-mg model can reproduce the temporal patterns of mosquito emergence, the annual temporal changes in the value of C_{total} —which indicates the maximum stage of development—at representative sites are shown in the lower panels of Fig. 5. In addition, the seasonal changes in T_w and soil moisture content (W_k/W^* ; %), which were calculated in the present study, and the period of mosquito occurrence obtained from previous observation data (obs) are shown in the upper panels of Fig. 5.

In cool- and warm-temperate regions, adult mosquitoes occurred from the middle of June to the end of September, a period in which there is a high enough temperature for them to grow to maturity. In subtropical regions, adult mosquitoes occurred from March to the middle of November, except for 3 mo when T_w decreased slightly and W_k/W^* was $<50\%$. In dry tropical regions, the period of occurrence of adult mosquitoes ranged from August to September, and the other seasons were severely limited by W_k/W^* . In the same way, the occurrence of adult mosquitoes in tropical regions was limited by W_k/W^* . In a comparison of observation data from representative sites (obs), the present ECD-mg model was able to estimate seasonal patterns of the occurrence of mosquitoes (lower panels of Fig. 5) with a more reasonable degree of accuracy than the previous model (Kashiwada & Ohta 2010).

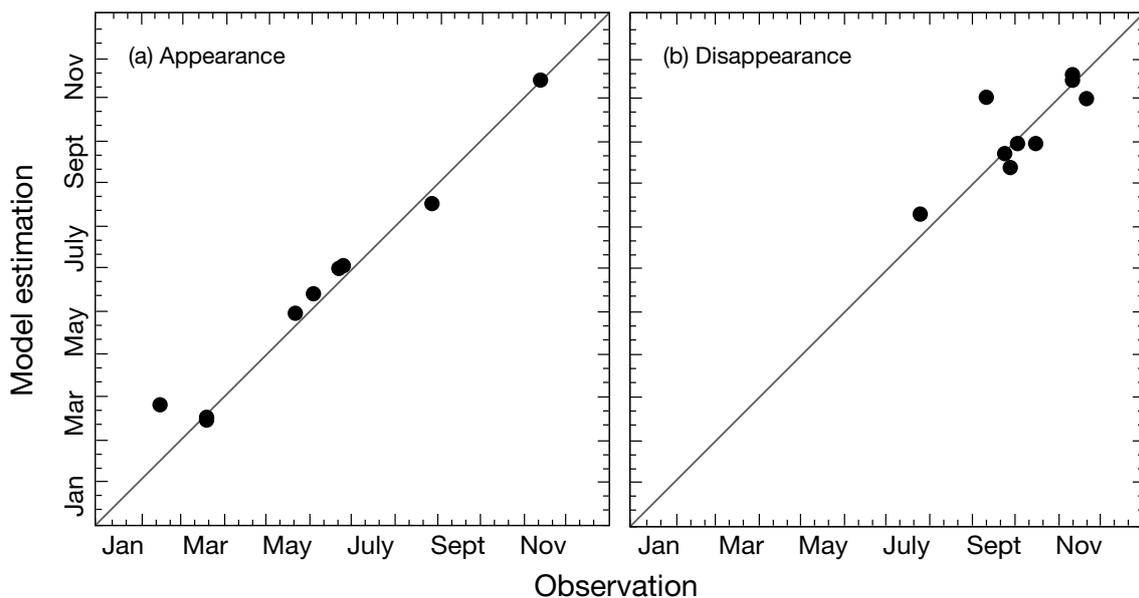


Fig. 4. *Anopheles* spp. Relationships between observed values and values estimated from the modified model for the dates of (a) appearance and (b) disappearance of the *Anopheles* mosquito at representative sites (see Fig. 3). A time lag for the average time from egg to adult mosquito was included in the calculation of the ECD-mg model. Data from Asahan was excluded because of the appearance of mosquitoes all year round. RMSE values for start and end dates were 15.2 ($p < 0.001$) and 20.8 d ($p < 0.01$), respectively

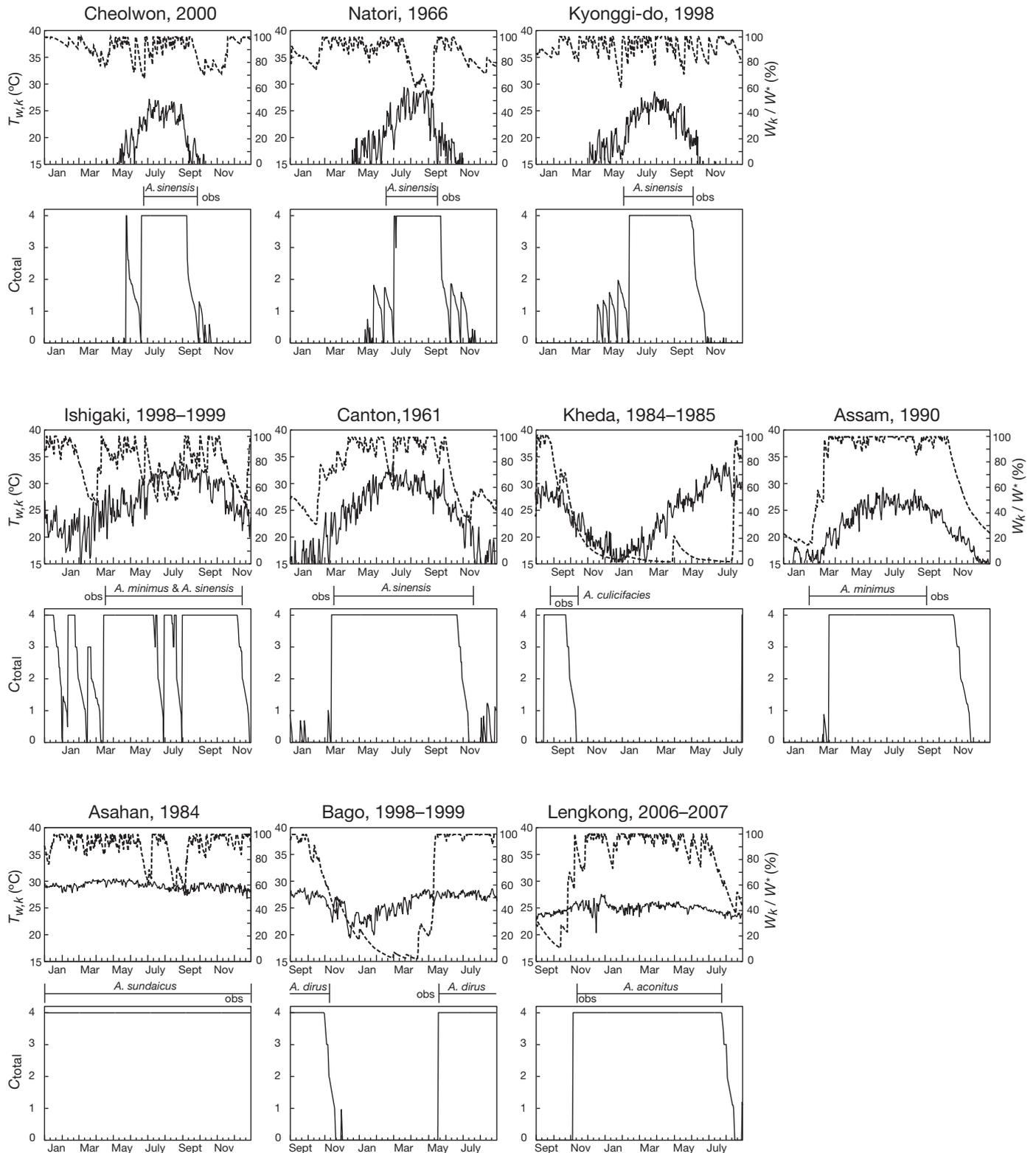


Fig. 5. *Anopheles* spp. Temporal variations in appearance of mosquitoes as obtained from the ECD-mg model and observation data (obs) for representative sites. Upper panels: seasonal variations in water temperature ($T_{w,k}$, solid line) and soil moisture content (W_k/W^* , dashed line) used in calculations for growth. Lower panels: cumulative development (C_{total}) of *Anopheles* using the ECD-mg model. Observed time varies from 1961 to 2007, depending upon the research paper used. Due to the local characteristics of the study sites, the dominant species observed in some sites are different from those in Fig. 3

4. RESULTS AND DISCUSSION

4.1. Potential number of generations for the spatial distribution of *Anopheles*

The number of consecutive completions of the life cycle (generation) was summed across the year for each grid, thus representing the climate's suitability for mosquitoes. Fig. 6 depicts the spatial distribution of the value of G_{\max} of *Anopheles* mosquitoes. The many areas with >20 generations of G_{\max} were frequently found in the lower latitudes. The value of G_{\max} dwindled in terms of the thermal gradient with increasing latitudes. In addition, in the lower latitudes, where there is a shortage of soil moisture content, the value of G_{\max} was <10 generations.

The current northern limit of the regions where group malarial infections by insect vectors have been reported is in the Korean peninsula (Chai 1999). The value of G_{\max} in this region, as obtained from the ECD-mg model, was 4 to 5 generations. The value of G_{\max} in northeastern China and Japan, where group infections were reported decades earlier (Hay et al. 2004), was also 4 to 5 generations. Therefore, the potential geographical distribution of the northern limit of the vector mosquitoes in Monsoon Asia, where there is fear of malarial infection, could represent the isolines of 4 to 5 generations.

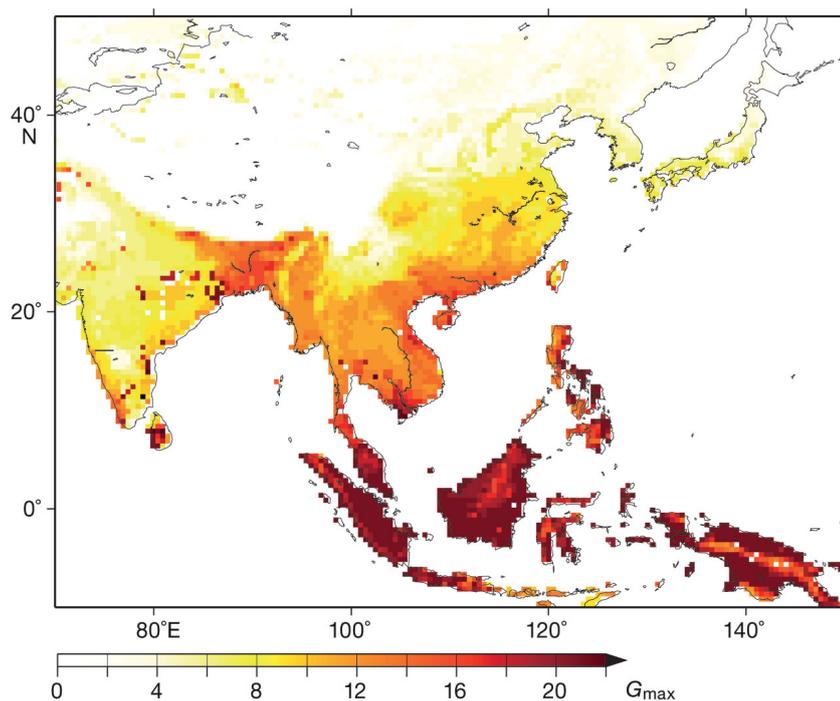


Fig. 6. *Anopheles* spp. Geographical distribution of potential number of generations (G_{\max})

The value of G_{\max} in Thailand, which has an intense dry season, was ~ 12 generations, which coincides with the results estimated from the number of malaria cases (Chareonviriyaphap et al. 2000). Previous methods (Kashiwada & Ohta 2010) underestimated the G_{\max} value in Thailand, determining a value of 0 to 1 generations, due to insufficient methods for the calculation of the soil moisture content. The modified ECD-mg model eliminates this problem and improves the reproducibility of potential distribution of the vector mosquito in Monsoon Asia.

A notable feature in Fig. 6 is that the G_{\max} value in India (~ 6 generations) was appreciably less than it was in other areas in tropical or subtropical regions. Indeed, this G_{\max} value in India was almost equal to that found in temperate regions. Notwithstanding this, many cases of malaria are reported in India, and these account for 65% of the total cases in Southeast Asia (WHO 2010).

4.2. Factors limiting the distribution of each *Anopheles* species

To explore the reason for such a discrepancy of the G_{\max} value in India, 5 species that are dominant in each region were selected (Fig. 3), and the species data on each grid was plotted on 2 axes: the annual mean water temperatures ($T_{w, \text{annual}}$) and soil moisture content (W_{annual}/W^* ; %) of the habitat (Fig. 7a). The most distinctive feature learned from this analysis is that the plots are densely distributed in a relatively narrow range for each species of *Anopheles*. Then, in order to clarify the factor limiting the growth of each species, the values of the minimum/maximum $T_{w,k}$ and W_k/W^* were connected by a straight line for each species (Fig. 7b). The crossover point of each species represents the average values of daily $T_{w,k}$ and W_k/W^* . Because the daily growth of mosquitoes begins when $T_{w,k}$ is $>15^\circ\text{C}$ and W_k/W^* is $>50\%$ in the present model, the range of the upper left quadrant of Fig. 7 shows the circumstances that are conducive to the growth of *Anopheles*.

The average values of *Anopheles dirus* and *A. culicifacies* were in a dry area (lower left quadrant) in Fig. 7b, and there were clearly a number of

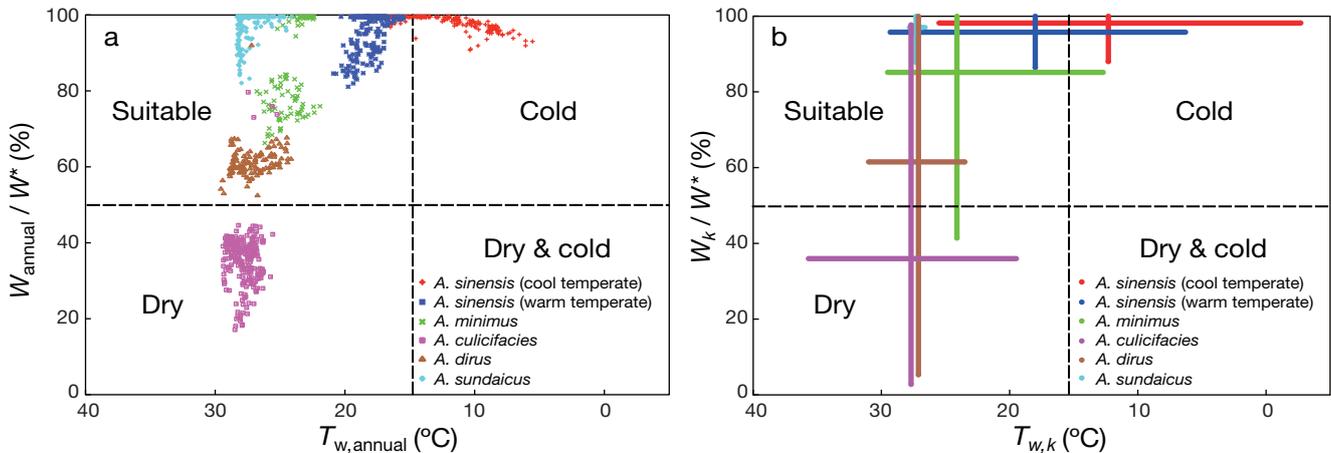


Fig. 7. *Anopheles* spp. Soil moisture content (W/W^*) and water temperature (T_w) of habitat for each species: (a) annual mean and (b) annual maximum to minimum of daily (k th day) values (lines). Note the x-axis scales run from right to left

periods in which their habitat experienced severe climate conditions and were thus too dry to permit their growth. The seasonal larva densities of the 2 species correlated positively with the number of days of rainfall (Oo et al. 2003, Barik et al. 2009). The average value of *A. sinensis* in temperate regions was in a cold area (upper right quadrant) of Fig. 7b, showing that the factor limiting the growth of *A. sinensis* was the thermal resources. This finding agrees well with the observation that hibernating *A. sinensis* mosquitoes flew out from the grass within a few minutes when the temperature increased by 15°C (Ree 2005). On the other hand, although $T_{w,k}$ and W_k/W^* of the habitat of *A. minimus* changed seasonally, the species can grow during most periods. The limiting factors for the growth of *A. minimus* for 2 or 3 mo was both the thermal and water resources (Fig. 7b). Throughout almost the entire year, there were conditions conducive to the growth of *A. sundaicus*, without seasonal changes in $T_{w,k}$ and W_k/W^* . According to the observation data (Collins et al. 1979), in the south part of Sulawesi Island, *A. sundaicus* can survive throughout the year, though the peak density of its growing period is at the beginning of the rainy season due to the low level of salinity in the water the larvae inhabit (Imai et al. 1988, Dusfour et al. 2004). The limiting factor for the growth for *Anopheles* depends on the characteristics of each species, and the dominant species in each region are different and various.

4.3. The need for further improvement of the ECD-mg model

The tendencies of the aggregated distribution of each species that can be identified in Fig. 7a could be

caused by climate factors because the ECD-mg model did not include the unique parameter of the developmental rate of each species, as described in Section 2. The abovementioned climate-species analysis suggests that there is a distinct relationship between climate factors and the regional distribution of each species in Monsoon Asia. Although the present modified procedure is not a niche-based model (e.g. Foley et al. 2008), but rather, is an established mechanistic model of growth for mosquitoes, the climatic niche of *Anopheles* could be roughly expressed.

However, because there was insufficient gridded data on the species, the relationships at the overlapping boundaries of multiple species could not be studied in sufficient depth. The climate niche will be able to be clarified by application of the present ECD-mg model to a small-scale and local evaluation using more accurate species data.

5. CONCLUDING REMARKS

Using the ECD-mg model, we calculated the spatio-temporal distribution of various species of vector mosquitoes in Monsoon Asia. The simulation results were superimposed on the distribution of 5 representative species on the basis of previous observations. This study found that there is a distinct relationship between climatic factors and the regional distribution of each *Anopheles* species in Monsoon Asia.

The ECD-mg model, which is driven by the various climate factors, can also be applied to predict changes in the distribution of each species on a broad scale under future climatic conditions, as has been

done by Yamamura & Kiritani (1998) and Pascual et al. (2006). Kearney et al. (2009) also clarified the changes in G_{\max} of *Aedes aegypti* in Australia under future climatic conditions. However, the G_{\max} obtained from the ECD-mg model represents an calculated potential, and the actual number of generations will vary significantly, depending upon human structures and activities such as ditches, sewerage systems, irrigation, changes in land use, etc. (Kearney et al. 2009). Further study is required that would take into account the impacts of these factors. Moreover, the growth parameters of each species must be included in the ECD-mg model in order to predict the vector distribution more accurately than the present model does. Also, it is difficult to know the magnitude and dynamics of the *Anopheles* population from the potential number of generations indicated by the present study. Therefore, a population dynamics model would be more suitable for the evaluation of the risk of malarial infection than a growth model that determines the potential number of generations.

Acknowledgements. This study was funded in part by the Ministry of Education, Science and Culture of Japan (Grant-in-Aid for Scientific Research C-21510022) and a Waseda University Grant for Special Research Projects (2010A-088, 2011A-079).

LITERATURE CITED

- Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration: guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper 56. Food and Agriculture Organization [FAO] of the United Nations, Rome
- Barik TK, Sahu B, Swain V (2009) A review on *Anopheles culicifacies*: from bionomics to control with special reference to Indian subcontinent. *Acta Trop* 109:87–97
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) Maximum rooting depth of vegetation type at the global scale. *Oecologia* 108:583–595
- Chai JY (1999) Re-emerging *Plasmodium vivax* malaria in the Republic of Korea. *Korean J Parasitol* 37:129–143
- Chareonviriyaphap T, Bangs MJ, Ratanatham S (2000) Status of malaria in Thailand. *Southeast Asian J Trop Med Public Health* 31:225–237
- Chow CY (1991) Malaria vectors in China. *Chin J Entomol Spec Publ* 6:67–79
- Collins RT, Jung RK, Anoez H, Sutrisno RH, Putut D (1979) A study of the coastal malaria vectors, *Anopheles sundaicus* (Rodenwaldt) and *Anopheles subpictus* Grassi, in south Sulawesi, Sulawesi, Indonesia. WHO/Mal 79, World Health Organization, Geneva
- Depinay JMO, Mbogo CM, Killeen G, Knols B and others (2004) A simulation model of African *Anopheles* ecology and population dynamics for the analysis of malaria transmission. *Malar J* 3:29
- Dev V (1996) *Anopheles minimus*: its bionomics and role in the transmission of malaria in Assam, India. *Bull World Health Organ* 74:61–66
- Dunne KA, Willmott CJ (1996) Global distribution of plant-extractable water capacity of soil. *Int J Climatol* 16: 841–859
- Dusfour I, Harbach RE, Manguin S (2004) Bionomics and systematics of the oriental *Anopheles sundaicus* complex in relation to malaria transmission and vector control. *Am J Trop Med Hyg* 71:518–524
- Foley DH, Rueda LM, Peterson AT, Wilkerson RC (2008) Potential distribution of two species in the medically important *Anopheles minimus* complex (Diptera: Culicidae). *J Med Entomol* 45:852–860
- Garros C, Van Bortel W, Trung HD, Coosemans M, Manguin S (2006) Review of the Minimus Complex of *Anopheles*, main malaria vector in Southeast Asia: from taxonomic issues to vector control strategies. *Trop Med Int Health* 11:102–114
- Garros C, Van Nguyen C, Trung HD, Van Bortel W, Coosemans M, Manguin S (2008) Distribution of *Anopheles* in Vietnam, with particular attention to malaria vectors of the *Anopheles minimus* complex. *Malar J* 7:11
- Gething PW, Smith DL, Patil AP, Tatem AJ, Snow RW, Hay SI (2010) Climate change and the global malaria recession. *Nature* 465:342–345
- Hay SI, Guerra CA, Tatem AJ, Noor AM, Snow RW (2004) The global distribution and population at risk of malaria: past, present, and future. *Lancet Infect Dis* 4:327–336
- Ho KM, Jung K, Ko HL (1965) The physiological age of *Anopheles hyrcanus sinensis* in the Canton area. *Acta Entomol Sin* 14:46–52 (in Chinese)
- Hopp MJ, Foley JA (2001) Global-scale relationships between climate and the dengue fever vector *Aedes aegypti*. *Clim Change* 48:441–463
- Ikemoto T (1996) Ecological diversities of *Anopheles sundaicus* as a vector mosquito of malaria. *Med Entomol Zool* 47:1–13 (in Japanese)
- Imai C, Ikemoto T, Takagi M, Yamugi H and others (1988) Ecological study of *Anopheles sundaicus* larvae in a coastal village of North Sumatra, Indonesia. I. Topography, land use, and larval breeding. *Jap J Sanit Zool* 39:293–300
- Kashiwada M, Ohta S (2010) Modeling the spatio-temporal distribution of the *Anopheles* mosquito based on life history and surface water conditions. *Open Ecol J* 3:29–40
- Kearney M, Porter WP, Williams C, Ritchie S, Hoffmann AA (2009) Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Funct Ecol* 23:528–538
- Konradsen F, Stobberup KA, Sharma SK, Gulati OT, van der Hoek W (1998) Irrigation water releases and *Anopheles culicifacies* abundance in Gujarat, India. *Acta Trop* 71: 195–197
- Lee JS, Lee WJ, Cho SH, Ree HI (2002) Outbreak of *vivax* malaria in areas adjacent to the demilitarized zone, South Korea, 1998. *Am J Trop Med Hyg* 66:13–17
- Manguin S, Garros C, Dusfour I, Harbach RE, Coosemans M (2008) Bionomics, taxonomy, and distribution of the major malaria vector taxa of *Anopheles* subgenus *Cellia* in Southeast Asia: an updated review. *Infect Genet Evol* 8:489–503
- Martens P, Thomas C (2005) Climate change and malaria risk: complexity and scaling. In: Takken W, Martens P, Bogers RJ (eds) *Environmental change and malaria risk: global and local implications*. Springer, Dordrecht, p 3–14

- Mintz Y, Serafini YV (1992) A global monthly climatology of soil moisture and water balance. *Clim Dyn* 8:13–27
- Ndoen E, Wild C, Dale P, Sipe N, Dale M (2010) Relationships between anopheline mosquitoes and topography in West Timor and Java, Indonesia. *Malar J* 9:242
- New M, Hulme M, Jones P (1999) Representing twentieth-century space-time climate variability. 1. Development of a 1961–90 mean monthly terrestrial climatology. *J Clim* 12:829–856
- Ohta S, Kimura A (2007) Impacts of climate changes on the temperature of paddy waters and suitable land for rice cultivation in Japan. *Agric For Meteorol* 147:186–198
- Ohta S, Uchijima Z, Seino H, Oshima Y (1993) Probable effects of CO₂-induced climatic warming on the thermal environment of ponded shallow water. *Clim Change* 23: 69–90
- Ohta S, Uchijima Z, Oshima Y (1995) Effect of 2 × CO₂ climatic warming on water temperature and agricultural potential in China. *J Biogeogr* 22:649–655
- Oo TT (2003) The biology and vector competence of the Anopheline mosquitoes of Myanmar with special consideration of *Anopheles dirus*. PhD thesis, University of Heidelberg
- Oo TT, Storch V, Becker N (2003) *Anopheles dirus* and its role in malaria transmission in Myanmar. *J Vector Ecol* 28:175–183
- Paing M, Sebastian AA, Lin T (1989) Anopheline mosquitoes of Myanmar. 1. *Anopheles (Cellia) dirus* Peyton and Harrison, 1979. *Myanmar Health Sci Res J* 1:122–129
- Pascual M, Ahumada JA, Chaves LF, Rodó X, Bouma M (2006) Malaria resurgence in the East African highlands: temperature trends revisited. *Proc Natl Acad Sci USA* 103:5829–5834
- Patz JA, Strzepek K, Lele S, Hedden M and others (1998) Predicting key malaria transmission factors, biting and entomological inoculation rates, using modeled soil moisture in Kenya. *Trop Med Int Health* 3:818–827
- Penman HL (1948) Natural evaporation from open water, bare soil and grass. *Science* 193:120–145
- Ree HI (2005) Studies on *Anopheles sinensis*, the vector species of vivax malaria in Korea. *Korean J Parasitol* 43: 75–92
- Smith M (1992) CROPWAT: a computer program for irrigation planning and management. FAO Irrigation and Drainage Paper 46. FAO, Rome
- Stoops CA, Rusmiarto S, Susapto D, Munif A, Andris H, Barbara KA, Sukowati S (2009) Bionomics of *Anopheles* spp. (Diptera: Culicidae) in a malaria endemic region of Sukabumi, West Java, Indonesia. *J Vector Ecol* 34: 200–207
- Tao F, Yokozawa M, Hayashi Y, Lin E (2003) Future climate change, the agricultural water cycle, and agricultural production in China. *Agric Ecosyst Environ* 95:203–215
- Toma T, Miyagi I, Malenganisho WLM, Murakami H, Nerome H, Yonamine M (2002) Distribution and seasonal occurrence of *Anopheles minimus* in Ishigaki Island, Ryukyu Archipelago, Japan, 1998–1999. *Med Entomol Zool* 53:29–42
- WHO (World Health Organization) (2010) World Malaria Report 2010. World Health Organization, Geneva
- Yamamura K, Kiritani K (1998) A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Appl Entomol Zool (Jpn)* 33:289–298
- Yeom JS, Ryu SH, Oh S, Lee WJ and others (2005) Status of *Plasodium vivax* malaria in the Republic of Korea during 2001–2003. *Am J Trop Med Hyg* 73:604–608
- Yoshida S, Watanabe T, Yajima T (1974) Seasonal changes of the mosquito population collected with the pig baited trap and the dry ice baited trap in a paddy field area during three years: 1965, 1966 and 1967. *Med Entomol Zool* 24:241–248 (in Japanese)

Editorial responsibility: Mauricio Lima, Santiago, Chile

Submitted: August 23, 2011; Accepted: January 24, 2012
 Proofs received from author(s): May 7, 2012