

# Impact of climate change on the distribution of *Aedes albopictus* (Diptera: Culicidae) in Northern Japan: Retrospective analyses

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Mogi and Tuno: Climate change impact on the  
*A. albopictus* distribution

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1 **Impact of climate change on the distribution of *Aedes albopictus* (Diptera: Culicidae) in**  
2 **northern Japan: retrospective analyses**

3

4 Motoyoshi Mogi,<sup>1,2</sup> and Nobuko Tuno<sup>3</sup>

**ABSTRACT** The impact of climate change on the distribution of *Aedes albopictus* was analyzed in northern Japan, where chronological distribution records are incomplete. We analyzed local climate data using linear regression of the thermal suitability index (TSI) for the mosquito and mean annual temperature as functions of time. In northern Japan, thermal conditions since the early 20th century have become increasingly suitable for *Ae. albopictus*, more as a result of decreasing coldness in the overwintering season than increasing warmth in the reproductive season. Based on recent discovery records of *Ae. albopictus* in the northern border range, we determined thermal criteria for estimating when its persistent establishment became thermally possible. Retrospective analyses indicated that those criteria were reached in most coastal lowlands of northern Honshu prior to the accelerated temperature increase after the mid-1980s and the first records of this species after 1990; at some sites, temperature criteria were reached during or before the early 20th century. Expansion of the thermally suitable range after 1990 was supported only for inland areas and the northernmost Pacific coast. The estimated expansion rate was ~26 km/decade. Our analyses also demonstrated the importance of local climate heterogeneity (apart from north–south or altitudinal temperature gradients) in determining the expansion pattern.

**KEY WORDS** Culicidae, *Aedes albopictus*, Northern distribution, Climate change, Japan

The mosquito *Aedes albopictus* (Skuse), which is native to East Asia, has spread to North and South America, Europe, and Africa since the end of the 20th century (Benedict et al. 2007). This mosquito is closely associated with humans, using water-filled containers in urban and rural environments as larval habitats and feeding on human blood for ovarian development. Its invasiveness and association with dengue and chikungunya viruses have attracted attention to its northward expansion under anthropogenic climate change.

The impact of future climate change on the distribution of *Ae. albopictus* has been predicted on a global scale (Sutherst 1993), for Japan (Kobayashi et al. 2008a), and for Europe (ECDC 2009, Caminade et al. 2012). Erickson et al. (2012) simulated population dynamics of this mosquito species in North America associated with warming temperatures. All of these studies predicted a severe effect of climate change on the potential distribution range or seasonal dynamics of *Ae. albopictus* within the 21st century.

Effects of past changes in temperature on the distribution of this mosquito provide useful information for future predictions. The past distribution is potentially easier to study in its native range because of its short history (<35 years) in areas where it is invasive and may not yet have reached the climatic limits to its expansion. However, chronological distribution records are less complete in native than in invasive ranges. *Aedes albopictus* populations become discontinuous and sparse and have shortened biting seasons toward the limits of its distribution. Limited locations and frequencies of surveys because of its decreasing medical importance may result in failure to detect this species. Approaches are needed that can compensate for these deficits in data.

The impact of climate change on the native range of *Ae. albopictus* has been studied only for Japan. According to Kobayashi et al. (2002, 2008a), the species, which was limited to south of

37°N until 1950, expanded northward thereafter, most rapidly after 1990. This view is consistent with the increased rates of warming after the mid-1980s in northern Honshu (JMA 2011), and, as such, has been accepted as an example of increasing health risk (MEXT et al. 2009). However, this relies on discovery records and does not include thorough analyses of climate change and its effects on this mosquito's distributions.

Here, we present a case study to evaluate the impact of warming on the native range of *Ae. albopictus* using thermal indices that were shown to be effective for delineating its northern limit (Mogi et al. 2012). Our specific aims were to detect historical trends in thermal conditions for *Ae. albopictus*; determine criteria for estimating when its establishment became thermally possible; and using these criteria, present an alternative view regarding past changes in the distribution of *Ae. albopictus* in northern Japan.

## Materials and Methods

**Distribution data.** Records of *Ae. albopictus* were compiled from surveys conducted since 1993 by Department of Medical Entomology, the National Institute of Infectious Disease, Japan (Kurihara et al. 1997; Kobayashi et al. 2002, 2004, 2006, 2008a, b, 2012; Satou et al. 2010, 2011) (Fig. 1). Latitude, altitude, climate data used, and chronological *Ae. albopictus* records for each site are presented in Suppl. Table S1. Because most major cities and survey sites were located at altitudes below 200 m, a few higher sites were excluded. Sites from Aomori through Yamagata (no. 2-38) were included in at least one survey. Mutsu (no. 1) is beyond the mosquito's known distribution range. *Aedes albopictus* was first recorded after 1993 at 23 of 24 positive sites (all sites except Sendai, no. 37, with records before 1968) (Fig. 4A).

**Temperature data.** Temperature data were obtained from the Japan Meteorological Agency (JMA; <http://www.jma.go.jp>). To prevent errors resulting from heterogeneity in data quality, we used the periods for which JMA assured the same quality as 2010. Homogenous data from  $\geq 25$  years were available at 13 sites, 10 of which had *Ae. albopictus* records (Suppl. Table S1).

**Analyses of thermal conditions.** Historical trends in thermal conditions at each site were analyzed with a thermal suitability index (TSI) for *Ae. albopictus* calculated from the warmth index (WI), coldness index (CI;  $TSI = WI/CI$ ), and mean annual temperature (MAT). A key assumption of the TSI is that establishment of the species around its northern limits depends on the balance between summer reproduction and overwinter mortality, excluding sites where winter is so cold that hibernating eggs cannot survive. In Mogi et al. (2012), TSI, WI, and CI were calculated from long-term monthly means for a calendar year (Jan.–Dec.) as follows:  $WI = \sum(t - 10)$ , where  $t$  is a monthly mean temperature and the summation is made for  $n$  months with  $t > 10^{\circ}\text{C}$ ; and  $CI = \sum(10 - t)$  where summation is made for  $(12 - n)$  months with  $t < 10^{\circ}\text{C}$ . WI is a simplified index of accumulated warmth  $>10^{\circ}\text{C}$  (reproductive season), while CI represents accumulated coldness  $<10^{\circ}\text{C}$  (overwintering season). Therefore, the TSI is an index of temperature-dependent reproductive success relative to temperature-dependent overwinter mortality, with  $10^{\circ}\text{C}$  as a value dividing the reproductive and overwintering seasons. An advantage of the TSI is that WI and CI can discriminate between continental (hot summer and cold winter) and oceanic climates (mild summer and mild winter) that have the same MAT, and can indicate whether insufficient summer warmth or severe winter coldness is a limiting factor. Details about the assumptions, their bases, and limitations of these indices are provided in Mogi et al. (2012).

To analyze historical trends, TSI, WI, and CI were calculated for ecological years divided by

a monthly mean temperature of 10°C. A single ecological year consisted of 11–13 months including a reproductive season (spring through autumn with monthly mean >10°C) and a succeeding overwintering season (autumn through spring with monthly mean <10°C). MAT is more straightforward than TSI, and was calculated on a calendar-year basis.

The trend of increasing MAT since the late 19th century can be described as a linear function of time for northern Honshu (JMA 2011) and all of Japan (MEXT et al. 2009). We therefore examined historical trends in thermal indices using linear regression analyses.

**Determination of criteria for estimating establishment time.** TSI values >1.0 and MAT >10°C have been shown to be reliable criteria indicating thermal suitability for *Ae. albopictus* in East Asia and North America, based on long-term mean temperatures for periods within 1951–2000 (for Japan 1971–2000) (Mogi et al. 2012). Means for >30 years from a year ending with the digit “1” are regarded as “normal” and are used as conditions most likely to be experienced in a given site (WMO 2007, 2011). The criteria thus derived can be used to evaluate the present suitability using normals available from climatic tables, but do not indicate the conditions when establishment first became possible. We determined criteria for estimating when establishment became thermally possible from the relationship between recent discovery records of *Ae. albopictus* and changes in thermal indices.

**Estimation of past ranges.** Using regression equations, we estimated the years in which TSI and MAT reached the establishment criteria at each site. As a simple indicator of reliability, early and late limits of the estimates were calculated from the 95% confidence limit (CL) of the slope of each equation.

**Calculation.** We used SPSS Base 10.0 (SPSS 1999) for the regression analyses. Other statistical procedures followed Sokal and Rohlf (1981). The TSI for serial years was expressed as

a geometric mean because overall reproductive success is a product of yearly population performance.

## Results

**Historical trends in thermal indices.** The results of the regression analyses are compiled in Suppl. Table S2; detected trends are summarized in Table 1. Slopes of TSI, CI, and MAT were significant except for Shinjou (no. 32), which had the shortest period of available data (25 years), indicating increasing thermal suitability throughout northern Honshu from the early 20th century onward. For the nine sites in which both WI and CI were significant, the absolute values of the slopes were larger for CI, except in Sakata (no. 30). In northern Honshu, the decrease in coldness during the mosquito's overwintering season was more widespread and generally more rapid than the increase in warmth during the reproductive season. Shinjou was excluded from the following analyses.

**Determination of criteria for estimating establishment time.** Of eight sites in which the first *Ae. albopictus* records were later than 1993, thermal indices exceeded the long-term establishment criteria (TSI = 1.0 and MAT = 10°C) after 1980 only in Hachinohe (no. 7) and Morioka (no. 12) (Table 2). The relationship between discovery records and thermal indices was then examined for these sites. *Ae. albopictus* was first recorded in 2010 in Hachinohe and 2003 in Morioka, after the regression lines reached or approached TSI = 1.1 and MAT = 10.5°C (Fig. 2). This was consistent with trends in 5-year moving averages. In Hachinohe, the 5-year geometric mean (5GM) of TSI first significantly exceeded 1.1 for 2006–2010 [5GM (SE range) = 1.18 (1.14–1.22); lower 95% CL for one-tailed test = 1.11]. In Morioka, the 5GM of TSI exceeded 1.1



twice, during 1997–2001 [1.15 (1.13–1.17), 1.12] and in 2006–2010 [1.17 (1.14–1.20), 1.12].

Five-year annual means also had historical maxima exceeding 10.5°C (but not significantly) for 2006–2010 in Hachinohe (mean  $\pm$  SE = 10.6°C  $\pm$  0.1, lower 95% CL for one-tailed test = 10.3) and Morioka (10.6  $\pm$  0.1, 10.4).

Using the relationship between TSI and MAT in Hachinohe [ $TSI = 0.0953\exp(0.2346MAT)$ ,  $r^2 = 0.79$ ] and Morioka [ $TSI = 0.1252\exp(0.207MAT)$ ,  $r^2 = 0.73$ ], MAT of 10.5°C corresponds to TSI = 1.12 and 1.10, respectively, indicating that 10.5°C and TSI = 1.1 are almost equivalent. We adopted 1.1 and 10.5°C in regressions with positive slopes as criteria for estimating when establishment of *Ae. albopictus* became thermally possible.

**Estimation of past ranges.** For the past, late estimate limits (the latest year by which establishment became possible) are useful for avoiding overestimation of warming effects. Five- to 20-year differences between estimates and late limits existed for TSI (median = 12,  $n = 11$ ), with 5–62-year differences for MAT (median = 13,  $n = 11$ ) (Table 3). The extreme value (62 years, whereas the others were  $\leq 22$ ) in Miyako resulted from the gentlest slope at the lower 95% CL (0.000338, compared to the other slopes of 0.00102–0.0258).

Trends in TSI were distinct among the three northernmost coastal sites (Fig. 3). In Mutsu (no. 1), the 5GM remained  $\leq 1.0$  throughout the period of analysis. In Aomori (no. 2), TSI rose rapidly after the mid-1980s, and 5GM first significantly exceeded 1.1 in 1988–1992. In contrast, 5GM in Fukaura (no. 4) first significantly exceeded 1.1 in the 1940s and TSI values were mostly  $>1.1$  thereafter. This pattern was similar to that in Miyako (no. 13, a Pacific site with *Ae. albopictus* records south of Hachinohe) where 5GM was first significantly  $>1.1$  in the 1950s. The slopes of the regression equations were gentlest in Fukaura and Miyako, indicating a more rapid increase in TSI at the other sites (Suppl. Table S2). *Aedes albopictus* has not been recorded in Aomori or

Fukaura (Fig. 1) despite satisfaction of the TSI criterion.

The estimated suitable range (Fig. 4B, C) indicated northward expansion of *Ae. albopictus* earlier than previously thought based on collection records (Fig. 4A). The range estimated by the TSI included Fukaura on the west coast and Miyako on the east coast prior to 1950 (Fig. 4B). MAT indicated slightly slower rates of expansion but the range still included Fukaura prior to 1960 and Miyako prior to 1980 (Fig. 4C). Differences between estimates made using TSI and MAT were <10 years except for Fukaura and Miyako. Both indices indicated that Ishinomaki (no. 35) and Yamagata (no. 38) were thermally suitable at the beginning of the 20th century or earlier.

We conclude that the thermal range that allows establishment of *Ae. albopictus* has expanded northward continuously since the early 20th century, and encompassed the Honshu lowlands prior to the recent rapid warming, except for inland areas (e.g., Morioka) and the northernmost Pacific coast (e.g., Hachinohe). The latitudinal distance between Yamagata and Hachinohe is ~260 km. Assuming this advance occurred over 100 years, the northward expansion rate was ~26 km/decade.

## Discussion

**Adequacy of analyses.** Prerequisites for our analyses are homogeneity of long-term temperature data and reliability of thermal establishment criteria. We used time periods for which homogeneity with 2010 data was assured. The establishment criteria were determined based on recent discovery records for *Ae. albopictus*. Persistence of this species in Hachinohe (no. 7) and Morioka (no. 12) has yet to be confirmed, but TSI is rising more rapidly in these areas than in Fukaura (no. 4) and Miyako (no. 13), where TSI was mostly >1.1 once the criteria were met.

Absence of this mosquito from Aomori and Fukaura, if confirmed, is probably a result of factors other than temperature that have delayed its introduction and establishment.

A flaw in our method is that the variability of estimates is sometimes large. Variations in slope cause regression lines to rotate around data means (Sokal and Rohlf 1981); therefore, the range of variability widens as estimated years depart from mean values. The variability also depends on the steepness of the slope of the regression, as seen for Miyako (no. 13). Despite this flaw, our conclusion regarding the expansion of thermally suitable ranges earlier than the first discoveries of *Ae. albopictus* after 1990 remains valid.

To clarify the attributes of the new criteria, values above the criteria in respective years do not necessarily indicate a risk of persistent establishment, and they are not independent of environmental variables other than temperature. For example, environments that are more favorable to summer reproduction than the present environment may facilitate establishment and lower the thermal criteria. The latter aspect is important for *Ae. albopictus* that occupies habitats subject to rapid anthropogenic change.

**Impact of warming.** Our results support the previous view that warming has favored the northward expansion of *Ae. albopictus* (Kobayashi et al. 2002, 2008a). A larger contribution of decreasing coldness during the overwintering season than increasing warmth in the reproductive season agrees with the more rapid temperature increase in winter than in summer in northern Japan (MEXT et al. 2009). However, the previous emphasis on rapid and extensive *Ae. albopictus* range expansion after 1990 in northern Honshu (Kobayashi et al. 2002, 2008a) was supported only for inland areas and the northernmost Pacific coast.

Thermal suitability does not necessarily indicate actual establishment. However, various facts support or are consistent with the view that *Ae. albopictus* has moved northward following the

expansion of a thermally suitable range. First, precipitation does not limit its distribution in Japan, with year-round rain and annual totals rarely <1000 mm and usually much higher. ECDC (2009) assumes maximal suitability for *Ae. albopictus* when annual precipitation exceeds 800 mm. No increasing or decreasing trend for summer precipitation in northern Honshu has been noted (JMA 2011). In addition, northern Japan (especially the western part) receives abundant snowfall, which could benefit overwintering eggs (Hanson and Craig 1995). For example, the temperature of the ground surface covered with 13 cm of snow was 0.7°C when the air temperature was -13°C (Noshiro and Sakai 1974). Larval habitats and blood-meal hosts were more readily available in towns in the past than they are at present. Before the prevalence of city water, water was stored in containers for consumption and fire prevention. Buddhist temples had plenty of water-filled containers, and people were more exposed to mosquito bites because of the absence of screen windows, air conditioners, and modern insecticides. Towns and transportation systems have been established for centuries. Many towns on Japan's west coast (e.g., Fukaura, no. 4; Akita, no. 11; Sakata, no. 30) prospered as ports for cargo ships and were the primary centers for trade between northern and southern Japan until the late 19th century (major railways in northern Honshu were opened by the early 20th century). The rapid photoperiodic adaptation of *Ae. albopictus* to local climates in its invasion range (Urbansky et al. 2012) suggests that its expansion was probably not hindered by genetic constraints. The estimated expansion rate (26 km/decade) is comparable to that of other insects in Japan (Kiritani 2011, Kitahara et al. 2001) and falls within the highest frequency range of poleward shifts of isotherms (Barrows et al. 2011). Finally, mosquito surveys in northern Honshu were insufficient. LaCasse and Yamaguti (1950), who provided the basis for the 37°N limit until 1950 (Kobayashi et al. 2002, 2008a), surveyed mosquitoes only in Sendai (no. 37), while Tanaka et al. (1979) conducted one survey in Aomori

Prefecture. Not unexpectedly, *Ae. albopictus* remained unrecorded until increased attention was paid to its northern limit.

Differences in TSI trends among the latitudinally close northernmost sites reflect complex climatic zonation around the strait between Honshu and Hokkaido. Differing from other northern Honshu sites classified as Köppen's Cfa (temperate, humid climate with hot summer), Mutsu (no. 1) is classified as Cfb (temperate, humid climate with warm summer) (Miyamoto 2009) and cooler than a few sites in southern Hokkaido (JMA; <http://www.jma.go.jp>). Fukaura (no. 4) is warmer than Aomori (no. 2) and Hachinohe (no. 7) because of a warm ocean current along the west coast (JMA 2011). Climatic heterogeneity (in addition to the north–south or altitudinal temperature gradient) can influence the northward expansion pattern of *Ae. albopictus*.

**Limitations of our method.** The relative significance of thermal suitability declines in regions that are drier than Japan. Multifactor climatic-niche models based on distribution data or physiological requirements of *Ae. albopictus* (e.g., Sutherst 1993, ECDC 2009) would be useful for such cases. One ECDC model indicated a recent decrease in suitability in parts of Europe due to increasing dryness that accompanied warming trends (Caminade et al. 2012).

Direct evidence is absent, or at best fragmentary, for past distributions of mosquitoes in their native ranges. Changes in the direction and extent of distribution ranges are highly variable among species for a given degree of temperature increase (Chen et al. 2011). Effects of anthropogenic environmental changes (other than temperature) can be either suppressive or facilitative for *Ae. albopictus*. Range changes estimated from thermal indices should be supported as much as circumstantial evidence. Mechanistic population models that run on a given set of conditions could provide a useful tool for estimating past and future ranges of mosquitoes inhabiting water-filled containers (Kearney et al. 2009).

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### **Footnotes to the first page**

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**Table 1. Regression slopes (+, positive; –, negative) for thermal indices in northern Honshu, Japan.**

| Index | Significant <sup>1</sup> |    | ns <sup>1</sup> |
|-------|--------------------------|----|-----------------|
|       | +                        | –  |                 |
| TSI   | 12                       | 0  | 1               |
| WI    | 10                       | 0  | 3               |
| CI    |                          | 12 | 1               |
| MAT   | 12                       | 0  | 1               |

Regression slopes in Suppl. Table S2.

<sup>1</sup>Significant,  $P < 0.05$ ; ns,  $P > 0.05$ .

**Table 2. Thermal conditions at eight sites where *Ae. albopictus* was first recorded after 1993.**

| no.                                   | Site       | Year      | TSI <sup>1</sup> | MAT(°C) <sup>2</sup> |
|---------------------------------------|------------|-----------|------------------|----------------------|
| First 30-year periods                 |            |           |                  |                      |
| 11                                    | Akita      | 1927-1956 | 1.16 (1.13-1.20) | 10.6 ± 0.1           |
| 13                                    | Miyako     | 1939-1968 | 1.13 (1.09-1.18) | 10.4 ± 0.1           |
| 35                                    | Ishinomaki | 1888-1917 | 1.28 (1.22-1.35) | 10.9 ± 0.1           |
| 38                                    | Yamagata   | 1890-1919 | 1.18 (1.14-1.22) | 10.7 ± 0.1           |
| Maximum available periods before 1980 |            |           |                  |                      |
| 26                                    | Oofunato   | 1964-1980 | 1.34 (1.31-1.37) | 11.0 ± 0.1           |
| 30                                    | Sakata     | 1971-1980 | 1.73 (1.69-1.77) | 11.9 ± 0.2           |
| 10-year periods before 1980           |            |           |                  |                      |
| 8                                     | Hachinohe  | 1971-1980 | 0.95 (0.91-1.00) | 9.8 ± 0.2            |
| 12                                    | Morioka    | 1971-1980 | 0.93 (0.89-0.98) | 9.7 ± 0.2            |

<sup>1</sup> Geometric mean and SE range in parentheses.

<sup>2</sup> Mean ± SE.

**Table 3. Years in which regression lines reached TSI = 1.1 or MAT = 10.5°C in northern Honshu, Japan.**

| no. | Site       | TSI <sup>1</sup> | MAT <sup>1</sup> |
|-----|------------|------------------|------------------|
| 2   | Aomori     | 1994 (1991-1999) | 2001 (1996-2010) |
| 4   | Fukaura    | 1930 (1776-1950) | 1954 (1837-1964) |
| 7   | Hachinohe  | 2001 (1994-2014) | 2011 (2002-2030) |
| 11  | Akita      | 1934 (1927-1940) | 1938 (1930-1943) |
| 12  | Morioka    | 2004 (1996-2016) | 2011 (2002-2027) |
| 13  | Miyako     | 1945 (1687-1959) | 1978 (1976-2040) |
| 26  | Oofunato   | 1943 (1881-1959) | 1952 (1899-1965) |
| 30  | Sakata     | 1945 (1918-1957) | 1940 (1913-1953) |
| 35  | Ishinomaki | 1860 (1822-1880) | 1867 (1820-1889) |
| 37  | Sendai     | 1916 (1904-1924) | 1910 (1894-1920) |
| 38  | Yamagata   | 1898 (1885-1907) | 1903 (1890-1912) |

Estimates with equations in Suppl. Table S2.

<sup>1</sup>Ranges in parentheses indicate early and late limits of estimates based on 95% CL of regression slopes.

## Figure legends

**Fig. 1.** Sites included in the analyses with *Ae. albopictus* records as of 2011. 1, Mutsu; 2, Aomori; 3, Ajigasawa; 4, Fukaura; 5, Hirosaki; 6, Iwasaki; 7, Hachinohe; 8, Hachimori; 9, Noshiro; 10, Kuji; 11, Akita; 12, Morioka; 13, Miyako; 14, Kakunodate; 15, Yamada; 16, Hanamaki; 17, Oomagari; 18, Ootsuchi; 19, Honjou; 20, Yokote; 21, Kitakami; 22, Kamaishi; 23, Yuzawa; 24, Mizusawa; 25, Sumita; 26, Oofunato; 27, Rikuzebtakata; 28, Higashiyama; 29, Ichinoseki; 30, Sakata; 31, Kesen-numa; 32, Shinjou; 33, Tsuruoka; 34, Furukawa; 35, Ishinomaki; 36, Shiogama; 37, Sendai; 38, Yamagata.

**Fig. 2.** Records of *Ae. albopictus* and changes in TSI and MAT in Hachinohe (no. 7) and Morioka (no. 12). Solid line, TSI = 1.0 or MAT = 10°C; dotted line, TSI = 1.1 or MAT = 10.5°C; dashed line, linear regression of TSI or MAT with time (years) (equations in Suppl. Table S2); downward arrows, years in which 5-yr geometric mean starting from each year was significantly larger than TSI = 1.1 (details in the text).

**Fig. 3.** Changes in TSI in Mutsu (no. 1), Aomori (no. 2), Fukaura (no. 4), and Miyako (no. 13). Solid, dotted, and dashed lines, are the same as in Fig. 2; vertical bar, 5-yr geometric mean (5GM) starting from each year (top diamond) and lower 95% CL for one-tailed test (bottom); downward arrows or horizontal bars at the top of each panel, years or periods when 5GM is significantly >1.1; upward arrow, year when regression lines reached 1.1 (solid) and its late limit (open).

**Fig. 4.** Changes in ranges thermally suitable for *Ae. albopictus* establishment in northern Japan. (A) A view by Kobayashi et al. (2002, 2008a), no new records north of the 1968 boundary until 1993; (B), (C) Ranges estimated in this study, boundaries are arbitrary except for sites on

maps and applied to lowlands (<200 m).



Fig.1

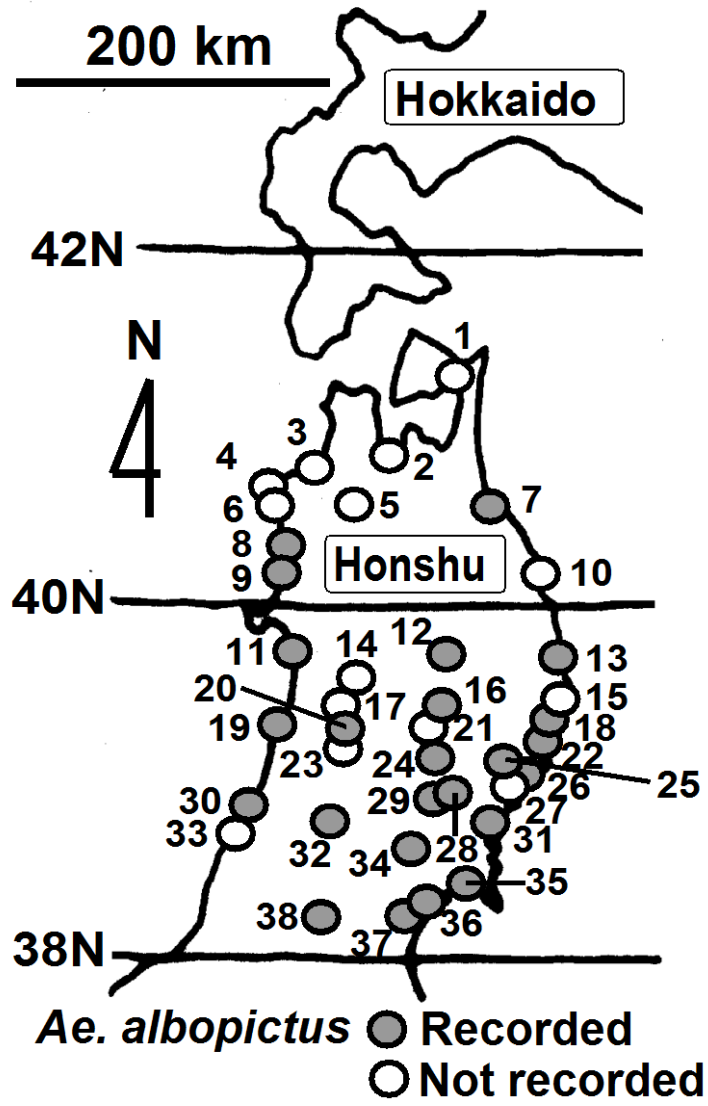


Fig. 2

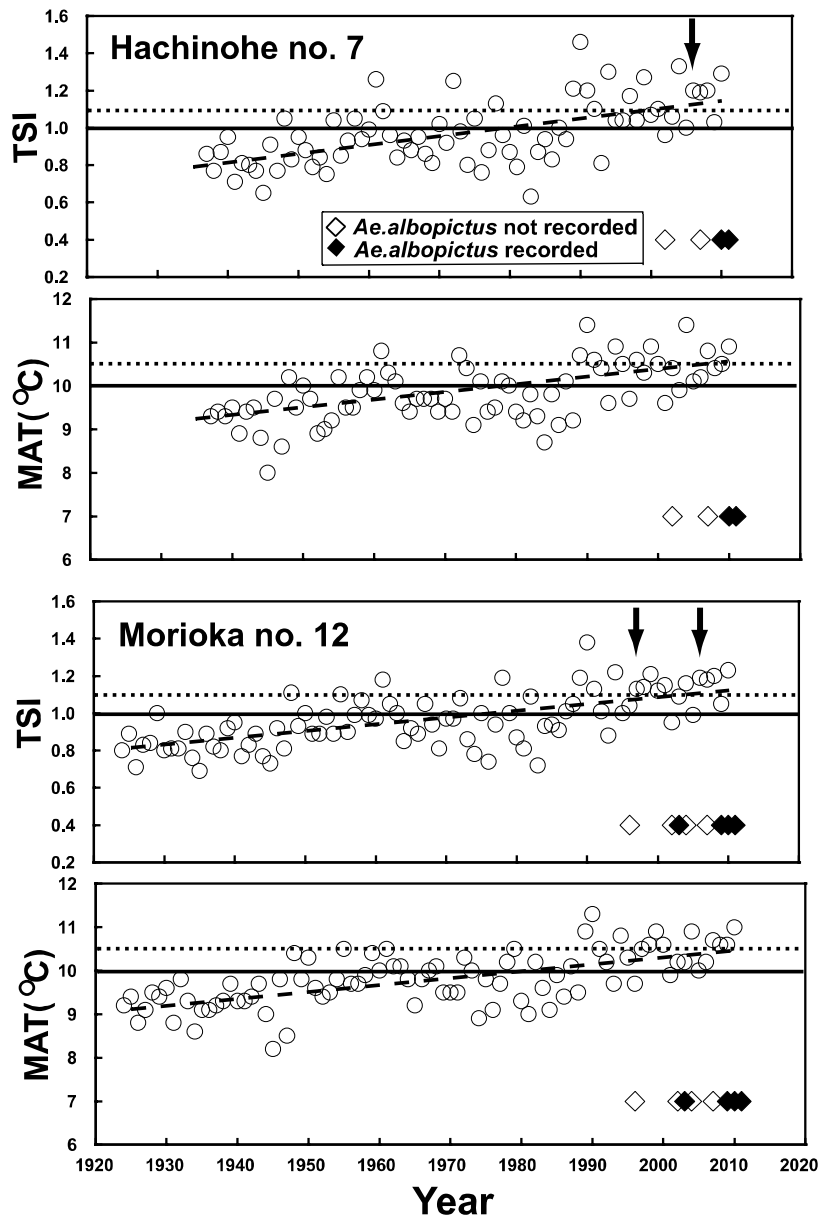


Fig. 3

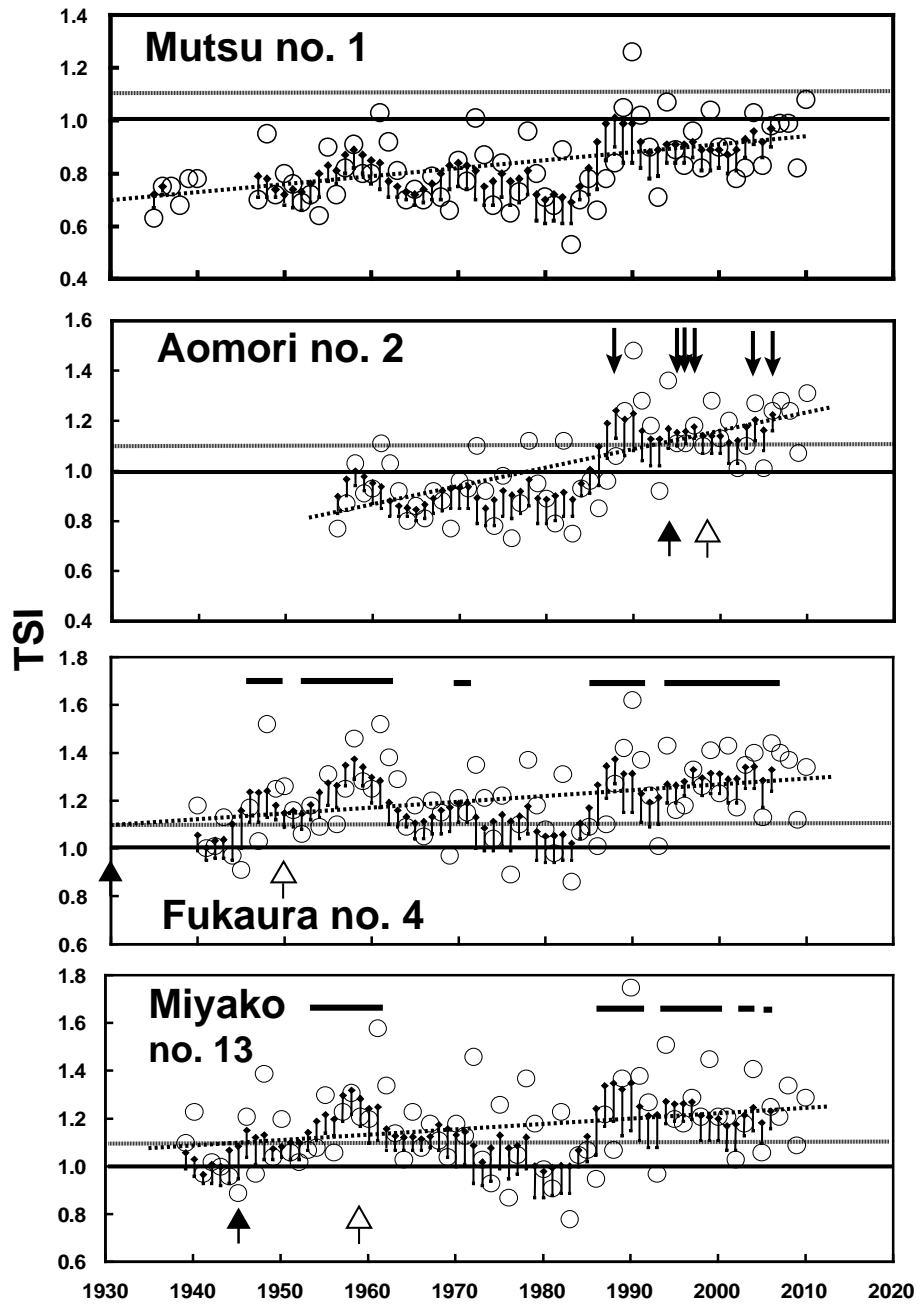


Fig. 4

