Relationships between mosquito densities in artificial container habitats, land use and temperature in the Kapiti-Horowhenua region, New Zealand

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Abstract   Land-use change, including deforestation for agriculture and urbanisation, has coincided with increases in vector-borne diseases worldwide. Land-use change is likely to regulate immature (larvae and pupae) mosquito populations through changes in local temperatures owing to manifold changes to the physical environment. However, we still poorly understand the relationship between land use, water temperature, and immature mosquito density. We conducted a field study in the Kapiti-Horowhenua region, New Zealand, to examine the relationship between land use, water temperature, and immature mosquito population dynamics in aquatic larval habitats. Artificial container habitats were sampled for immature mosquitoes in native forest, pastureland and urbanland, at three replicate locations, from October 2002 to April 2003. The endemic species *Culex pervigilans* constituted 94.5% of all late-instar larvae collected, the remainder being the exotic *Ochlerotatus notoscriptus*. On average, significantly higher pupal mosquito densities were recorded from urbanland containers compared with pastureland and native forest containers. A similar trend was observed for total mosquito densities, but did not reach statistical significance. Water temperatures in native forest typically did not show as much variation as those in urbanland and pastureland. Pastureland containers had significantly higher maximum and average daily water temperatures and lower minimum daily water temperatures than native forest containers. Using multiple regression analysis, total mosquito densities were best explained by the quadratic effects of maximum daily temperature and average daily temperature. The results of this study show that pastoral and urban development can increase water temperatures in container habitats, and that land-use change may be responsible for higher immature mosquito densities when habitat water temperatures do not consistently exceed a high threshold.

INTRODUCTION

Land-use changes, including deforestation for agriculture and urbanisation, are considered to be the greatest drivers of terrestrial environmental change (Vitousek et al. 1997; Sala et al. 2000) and have often coincided with increases in the range of mosquito-borne diseases around the world (Gratz 1999; Norris 2004; Patz et al. 2004). Land-use

changes are considered primary drivers of mosquito-borne disease because they modify the basic physical properties of the ecosystem, such as the predominant vegetation, hydrology, soil structure, and topography (Patz et al. 2004). These changes in turn alter the complex biotic and abiotic processes that typified the original ecosystem and the context within which vector species breed, develop, and transmit disease (Patz et al. 2000). Ultimately, as ecological disruption proceeds, the abundance and species composition of mosquito vectors can be affected by any number of flow-on effects, including the number of hosts, prevalence of larval habitats, or the temperature of larval habitats.

One of the most fundamental mechanisms by which land-use change is thought to alter the prevalence of disease-vector mosquitoes is by changing the water temperature of larval habitats (Lindblade et al. 2000; Patz et al. 2000). Deforestation usually leads to increased levels of solar radiation (or "insolation") reaching larval habitats, coinciding in changes in the composition of mosquito species, and leading to an overall increase in adult productivity (Walsh et al. 1993; Leisnham et al. 2004; Norris 2004). Elevated water temperatures can influence immature (larvae and pupae) mosquito populations directly by driving larval survival and development, and indirectly by increasing food availability as a result of driving detrital decomposition and microbial growth (Wetzel et al. 1995; Clements 2000; Lindblade et al. 2000). However, the association between land use and the water temperature of larval habitats is likely to be complex and dependent on the specific type of land use involved. For instance, urbanisation can lead to the shading of larval habitats from the replanting of vegetation and the presence of anthropogenic structures. However, urbanisation may also increase localised air temperatures by the presence of certain structures that radiate heat (Frankie & Ehler 1978; McIntyre 2000).

Few studies have quantified differences in the water temperature of larval mosquito habitats across different landscapes and related them to immature densities (e.g., Williams et al. 1994). Moreover, the vast majority of mosquito surveys that relate the density of immature stages to temperature do so within the same landscape, and collect water temperature data as either point measures at the time of mosquito sampling (e.g., Herrel et al. 2001; Sunish & Reuben 2001; Strickman & Kittayapong 2003) or infer it from ambient air temperatures (e.g., Lindblade et al. 2000; Fischer et al. 2002). Neither of these methods for collecting water temperature data accurately show daily temperature changes in larval habitats and may be subject to temporal and spatial inaccuracies. Furthermore, the influence of shade and water temperature on mosquito populations is likely to differ greatly according to mosquito species, habitat, and region (Nylin & Gotthard 1998; Clements 2000), thus making predictions across systems difficult.

The main objective of this study was to examine the influence of land use on the dynamics of immature mosquito populations in standardised container habitats. The Kapiti-Horowhenua region, New Zealand, was chosen for this study because it has three major types of land use: pastureland, urbanland, and native swamp forest. It also contains New Zealand's two most common mosquito species: the endemic *Culex pervigilans* Bergroth and the exotic *Ochlerotatus* (formerly *Aedes*) *notoscriptus* (Skuse), both of which are container-users and have public health importance (Weinstein et al. 1997). *Ochlerotatus notoscriptus* has been implicated as a potential vector of Ross River virus in Australia and the South Pacific (Watson & Kay 1998), and is increasing its distribution throughout New Zealand's North Island by mostly using pastureland areas (Laird & Easton 1994; Laird 1995). *Culex pervigilans* is a known vector of Whataroa virus, which primarily infects native bird populations (Maguire et al. 1967). There is limited serological evidence that Whataroa virus also infects humans (Miles 1973), and *C. pervigilans* has been assessed to be a species requiring testing for its potential as a vector of other human diseases (Weinstein et al. 1997). We hypothesise increased mosquito densities in the anthropogenically modified land uses of pastureland and urbanland compared to native swamp forest. A second objective of this study was to examine the relationship between land use, water temperature, and mosquito density.

MATERIALS AND METHODS

The study was undertaken in the Kapiti-Horowhenua region in the southwestern part of the North Island, New Zealand (40°52′S, 175°03′E). The region, formerly an extensive area of lowland native swamp forest, was almost entirely drained and cleared for pastureland and subsequent urban development since the 1840s. Only relatively small (<20 ha) remnant patches of native forest have since been preserved as reserves (Maclean 1988). Three spatially distinct locations (Levin, Paraparaumu, and Waikanae) each
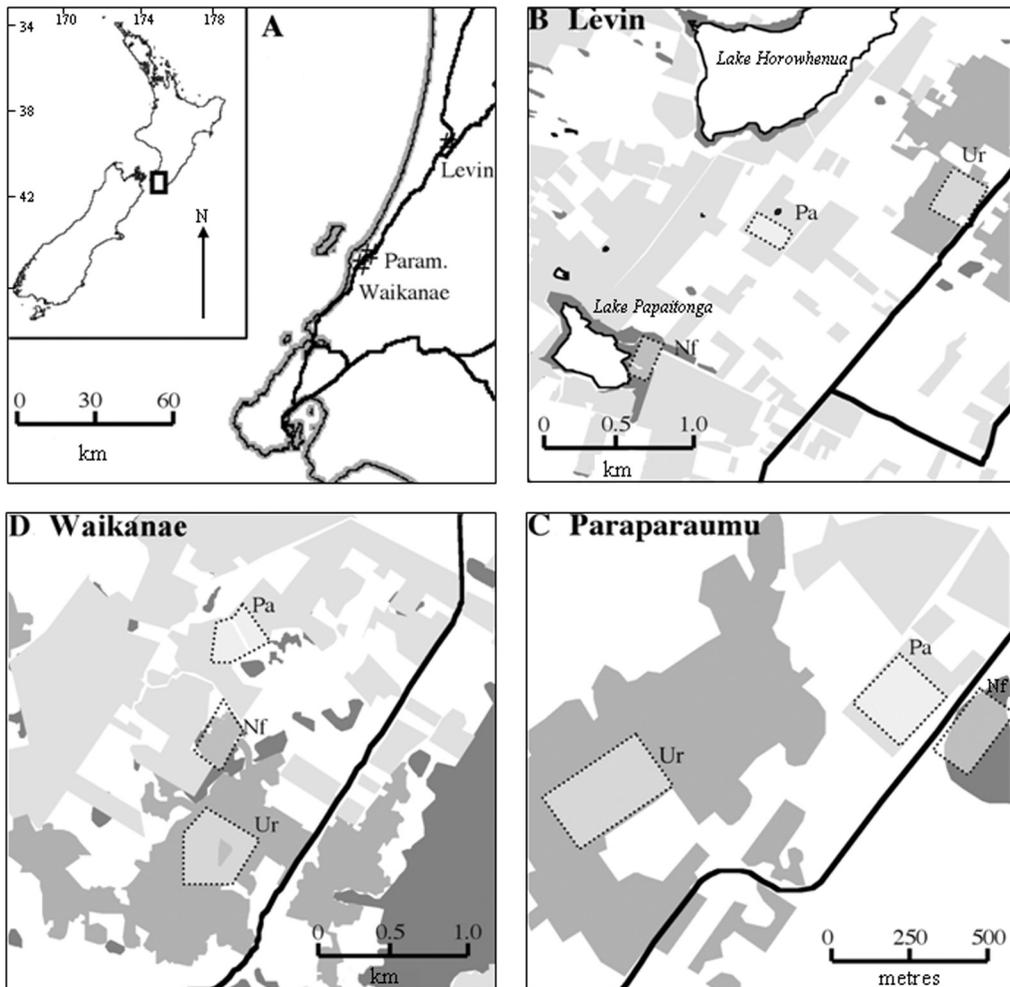
Fig. 1   **A**, Map of the study locations: Levin, Paraparaumu (Param.) and Waikanae, in the Kapiti-Horowhenua region, New Zealand. Positions of the specific land-use study sites within: **B**, Levin; **C**, Paraparaumu; and **D**, Waikanae are shown with dotted lines. (Pa, pastureland sites; Ur, urbanland sites; Nf, native forest sites). Native forest land-cover has dark shading; urbanland has medium shading; and pastureland has light shading. Black lines indicate state highways.

with neighbouring sites consisting of the three land-use types (i.e., three land uses × three locations = nine total sites) within 2–4 km² were selected for our study (Fig. 1). The land uses were: (1) native swamp forest, consisting of a variety of podocarp and hardwood species that provided full forest canopy; (2) pastureland, consisting of open grasslands of exotic plant species, which are intensively stocked with sheep and cattle and subjected to oversowing and fertilisation; and (3) urbanland, consisting of mainly suburban ecotypes conferring a variety of flora and fauna, as well as physical structures including roads, buildings, and drains. Sites are

indicative of the land-use types throughout the region and their selection attempted to control for geomorphology and climate so that the selected sites were as similar as possible in all respects except for their land use (e.g., all were c. 13–20 ha; <200 m a.s.l.; and of similar topographies).

Random coordinates were selected for five sampling points in each land-use site at each location using a topographical map broken into 1 m² grid squares. Coordinates that fell inside inaccessible areas (e.g., in the middle of ponds), inside unsecured areas (e.g., on public roads), within 30 m of another coordinate, or within 20 m of the edge of the site

(which acted as a buffer area) were reselected. Coordinates in native forest were under an entirely enclosed canopy cover; those in pastureland were in open sunlight and not surrounded by any sources of shade; and those in urbanland were surrounded by various structures (natural and anthropogenic) that appeared to provide medium levels of shade cover and radiant heat.

In October 2002, one model larval habitat using a 6-litre circular black plastic container (22 cm diam. × 20 cm height) was secured to the ground as close to each sampling point as possible using a wooden stake. Each container was filled with 4 litres of water from a local groundwater source filtered through 0.2 mm mesh, and 20 g of dried pelletised sheep manure (Kiwi™, Mount Maunganui, New Zealand; c. 3% nitrogen, 2% phosphorus, and 4% potassium) was added. Each container was then covered with 0.5 mm galvanised wire mesh (intermesh gap = 20 mm) to prevent vertebrate animals from drinking the water. The inside surface of each container was roughened with coarse sandpaper to provide a textured surface for *Ochlerotatus* eggs to attach. This type of container and initial nutrient concentration (5 g/litre) has been shown to be suitable mosquito habitat and promote high *C. pervigilans* and *O. notoscriptus* productivity (Leisnham et al. 2004). The initial water line was marked on each container and used to check for evaporation. Containers were topped up if needed at 2-weekly intervals from the time they were positioned until sampling. In total, each land-use site at each location had five study containers that provided larval habitat, giving a total of 45 containers (3 sites × 3 locations × 5 replicates of each combination = 45).

Mosquito sampling was started 2 weeks after the containers had been placed in the field and was conducted approximately monthly (every 28–41 days) from 22 October 2002 to 28 April 2003. This period was during the austral summer and around the time when there is greatest mosquito activity (Leisnham et al. 2004). On each sampling date, all containers in each land-use site at each location were sampled for mosquitoes using a conventional dipping method (Service 1995). One litre of water (c. 25% of each container) was sampled from each container by twice dipping a 500 ml dipper. Each litre of water was then poured back into its respective container through 0.2 mm mesh. Mosquitoes collected from each container were kept separate and brought to the laboratory where they were preserved in 70% ethanol for subsequent identification and counting under a microscope at 10–40× magnification. The dipper and mesh strainer were thoroughly rinsed with clean water before sampling the next container.

Third and fourth instar larvae were identified to species level using the key of Winterbourn et al. (2000). First and second instar larvae were keyed to genus level only. No key for New Zealand pupae is available. Because the pupal stage is the penultimate moult before adult emergence (Snell 2005), pupal density was examined separately because it is the best indicator among the immature stages of adult productivity (Leisnham 2004).

Although immature mosquito density does not necessarily correlate to the productivity of the larval habitat for adult mosquitoes, it is commonly used as real-time surrogate for adult productivity in surveillance and control surveys (WHO 1982; Service 1995). The removal of mosquitoes by sampling was considered unlikely to have major impacts on densities in subsequent sampling dates given that the study was conducted during the time of season with high adult activity.

Water temperature data were collected from three randomly selected containers in each land use at Waikanae. One water-resistant temperate probe (Optic Stowaway Temperature Logger, Onset Computer Corporation, Bourne, MA, United States) was placed in each container after mosquitoes were collected during the first sampling date in October and retrieved on the last sampling date in April. The probes collected maximum, minimum, and average daily water temperatures every hour. The National Institute for Water and Atmospheric Research (NIWA) provided regional climate data (maximum, minimum, and average daily air temperatures and daily rainfall) for stations in Paraparaumu and Levin over the sampling duration. Paraparaumu is c. 10 km south of Waikanae and its NIWA climatic data were representative of both of these locations.

Statistical analyses

Means of mosquito densities and water temperatures were analysed using a mixed model two-way repeated measures analysis of variance (ANOVA) with corrections for *post-hoc* pair-wise comparisons using the Bonferroni method (Zar 1999). For the purpose of ANOVAs, all mosquito data were combined into three sampling periods: early season (October to December); mid-season (January and February); and late season (March and April), which were the average of the relevant sample dates. Analyses of mosquito data had the fixed factors of land use and sampling period and the random factor of location.
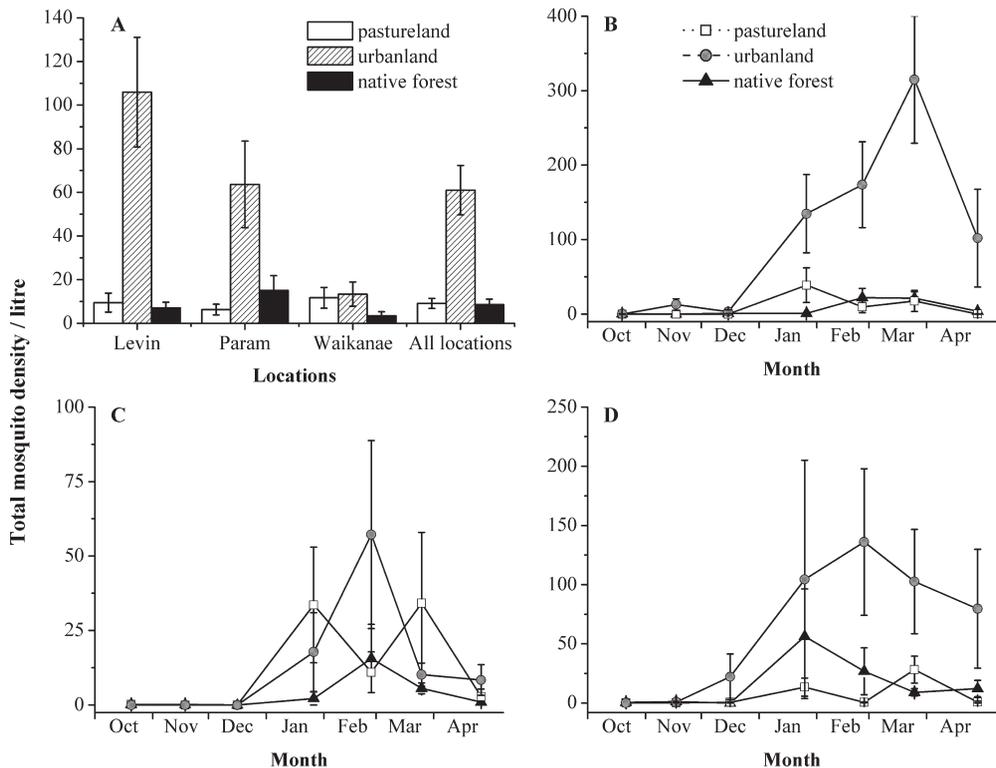
Fig. 2 Mean total mosquito density (± SE) in containers in pastureland, urbanland, and native forest, at three locations in the Kapiti-Horowhenua region, New Zealand from October 2002 to April 2003. **A**, All locations: *n* = 15; **B**, Levin: *n* = 5; **C**, Paraparaumu (Param): *n* = 5; **D**, Waikanae: *n* = 5.

Analyses of water temperature data had the fixed factors of land use and month.

Linear and quadratic effects of temperature on mosquito densities were tested using regression analyses (Zar 1999). Daily water temperatures and mosquito densities were averaged over the entire sampling duration. The regression analyses used these replicate averaged values. Relationships were examined using scatterplots.

Residuals of all data were examined for normality and homogeneity using histograms and probability plots. All mosquito and temperature data were log transformed (Y' = log Y + 1) before analysis, and tested for normality and homogeneity using Kolomogorov-Smirnov test and Levene's test, respectively (Zar 1999). Means and standard errors are reported throughout unless otherwise stated; all tests were two-tailed, and significance was assigned at the 5% level (Zar 1999). All analyses were undertaken using the software program SPSS (2003).

RESULTS

A total of 538 pupae and 7734 larvae were recorded in the study, consisting of the two most common mosquito species in New Zealand, the endemic *C. pervigilans* and the exotic *O. notoscriptus*. *Culex pervigilans* was the most common species, constituting 94.5% (*n* = 1264) of total third and fourth instar larvae collected (*O. notoscriptus*, *n* = 73). Of the first and second instar larvae, 97.5% (*n* = 6238) were *Culex* sp. (*Ochlerotatus* sp., *n* = 159). Since *C. pervigilans* and *O. notoscriptus* were the only species of third and fourth instar larvae collected, it is likely that these first and second instar larvae were also either *C. pervigilans* or *O. notoscriptus*, making *C. pervigilans* constitute an estimated total of 7502 out of 7734 (97.0%) total larvae collected.

Mosquito population dynamics

Total mosquito and pupal densities were highest in urbanland during most sampling dates, peaking in
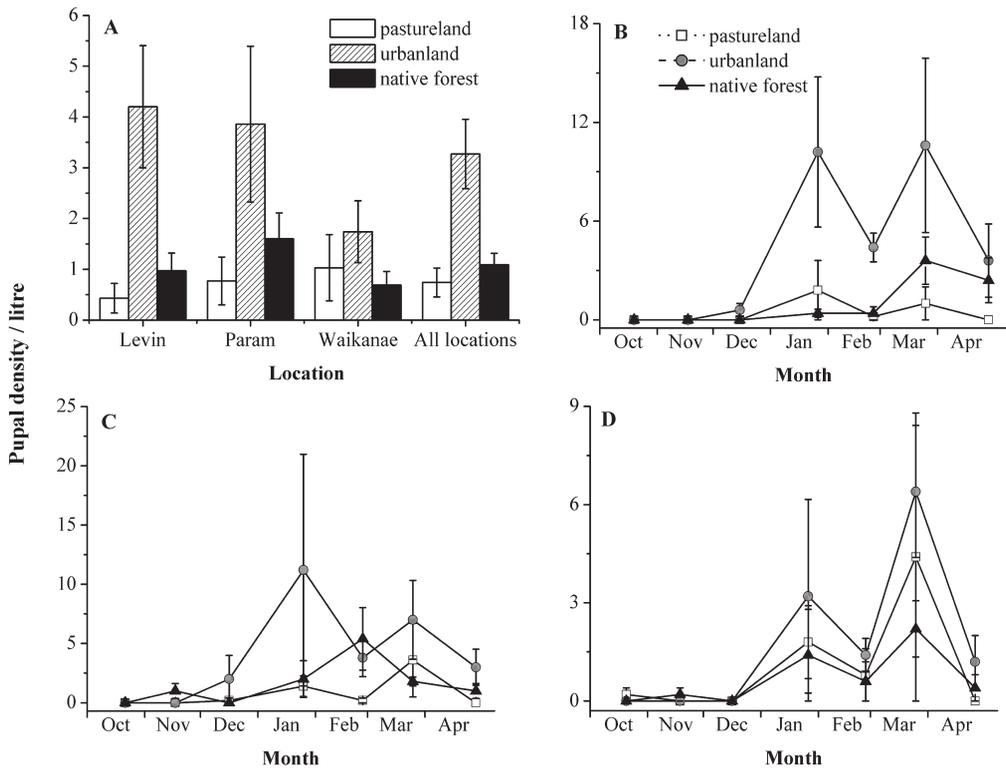
Fig. 3 Mean pupal density (± SE) in containers in pastureland, urbanland, and native forest, at three locations in the Kapiti-Horowhenua region, New Zealand from October 2002 to April 2003. **A**, All locations: $n = 15$; **B**, Levin: $n = 5$; **C**, Paraparaumu (Param): $n = 5$; **D**, Waikanae: $n = 5$.

Table 1 Effect of land use and sampling period on total mosquito and pupal densities in study containers: results from repeated measures analysis of variance. (MS, mean squared value.) Bold type denotes significance at the 5% level.

Factor	d.f. effect	MS effect	d.f. error	MS error	F	P
Total mosquito density						
Land use	2	5.790	4	0.469	5.56	0.070
Sampling period	2	13.060	4	0.079	165.60	**<0.001**
Land use × sampling period	4	0.469	8	0.265	1.11	0.228
Pupal density						
Land use	2	1.301	4	0.261	13.74	**0.016**
Sampling period	2	1.944	4	0.261	70.09	**<0.001**
Land use × sampling period	4	0.261	8	0.068	0.990	0.450

Levin during March at a mean of 315 individuals ± 85/litre and 10.6 individuals ± 5.3/litre respectively (Fig. 2 and 3). When data were averaged over the sampling duration for all locations combined, total mosquito density was over six times higher in urbanland compared to pastureland and native forest (Fig. 2A). Pupal density was only three times higher

(Fig. 3A). However, differences between land uses were more consistent between the replicate locations for pupal density compared to total mosquito density, with total mosquito numbers being particularly similar between land uses at Waikanae (Fig. 2A). As a result, the main effect of land use was significant for pupal density (Table 1) (with significantly higher

density in urbanland compared to pastureland and native forest; $P < 0.05$), but did not reach the 5% significance level for total mosquito density (Table 1). Analyses of *C. pervigilans* density gave the same conclusions as analyses of total mosquitoes and pupae, likely reflecting the overwhelming dominance of the native species in samples. When considering *O. notoscriptus* separately, we found that the species was almost entirely collected in urbanland and native forest (122 and 106 larvae, respectively), with only four larvae collected from one pastureland container in Levin.

Mosquitoes colonised containers in low numbers at all locations until January 2003. Mean densities then generally increased with higher regional temperatures before declining late in the season as regional temperatures declined (Fig. 2B–D, 4). Both total mosquito density and pupal density showed a significant effect of sampling period, with significantly higher total mosquito and pupal densities in the middle and late sampling periods compared with the early sampling period (pair-wise comparisons: $P < 0.01$). There was no significant difference between land uses in total mosquito and pupal densities between the middle and late sampling periods (pair-wise comparisons: $P > 0.10$). In all locations, densities were consistently low in native forest over the entire sampling duration. However, neither total mosquito density nor pupal density showed a significant interaction effect between land use and sampling period.

Container temperature

Containers in pastureland and urbanland had more extreme water temperatures than those in native forest (Table 2). The two highest recorded temperatures were from a container in pastureland (40.5°C) and one in urbanland (39.0°C). Both of these temperatures were nearly twice as high as the maximum temperature recorded from a container in native forest (21.8°C). Pastureland containers recorded the lowest minimum temperatures of all containers, with the lowest recorded value at 2.9°C, over two times lower than the minimum recorded temperature from a native forest container (5.7°C). On average, daily temperatures showed a declining gradient from pastureland through urbanland to native forest (Table 2).

Water temperatures in native forest typically did not show as much variation throughout the day as those in urbanland and pastureland. For example, mean temperatures in pastureland fell by 17.4°C (77.3%) between 1400 h on 21 February 2003 to
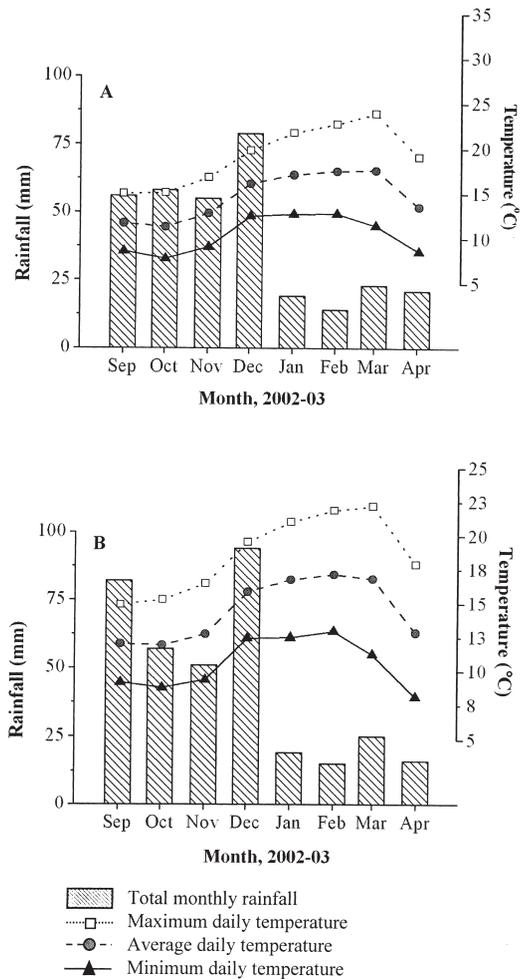
Fig. 4 Regional climatic data for **A**, Levin and **B**, Paraparaumu/Waikanae, New Zealand from September 2002 to April 2003. Rainfall estimates are the total amount for the entire month. Daily temperatures are the mean values for each month.

0800 h the following morning, compared with only 11.6°C (64.1%) in urbanland and only 6.05°C (43.7%) in native forest over the same period (Fig. 5). The night previously, mean temperatures in native forest fell by 1.3°C.

Water temperature data were combined into months for clarity and are shown in Fig. 6. Mean maximum, minimum and average daily water temperatures rose to their highest levels from December to March before declining in April. Seasonal variation in

temperatures resulted in a significant main effect of month on all temperature measures (Table 3). ANOVAs also indicated a significant main effect of land use on all temperature measures. Containers in pastureland had significantly higher maximum and average daily temperatures and significantly lower minimum daily temperatures compared with containers in native forest ($P = 0.01–0.05$). All other pair-wise comparisons between land uses were not significant ($P > 0.10$). These overall trends between land uses were consistent within most individual months. Pair-wise comparisons revealed that the significant interaction between land use and month for all temperature measures occurred because of a reversal of trends after October (Fig. 6).

Monthly changes in container temperatures closely followed those of regional air temperatures (Fig. 6). Regression analyses using daily data showed that regional average ($r^2 = 0.912–0.937$), maximum ($r^2 = 0.780–0.871$) and minimum temperatures ($r^2 = 0.801–0.897$) all had a strong and significant effect on counterpart container values ($P < 0.001$).

Relationships between container temperatures and mosquito densities

Variation in total mosquito density was best (and significantly) explained by the quadratic effects of maximum and average daily temperatures (Table 4, Fig. 7A,B). A model of a quadratic effect of minimum daily temperature had the highest r^2 coefficient of all the models explaining variation in pupal density. However, a model illustrating a linear effect of minimum temperature also had a relatively high r^2 coefficient and a P value that was closest to the 5% level of significance, compared to other models explaining variation in pupal density (Table 4, Fig. 7C).
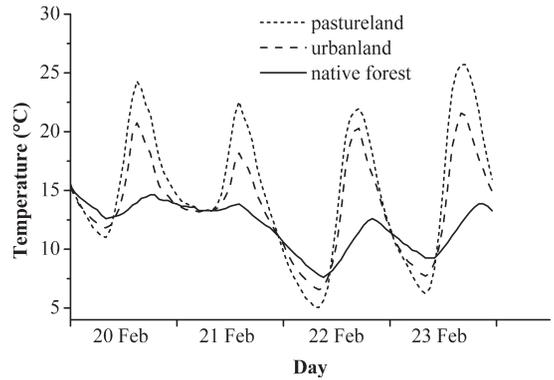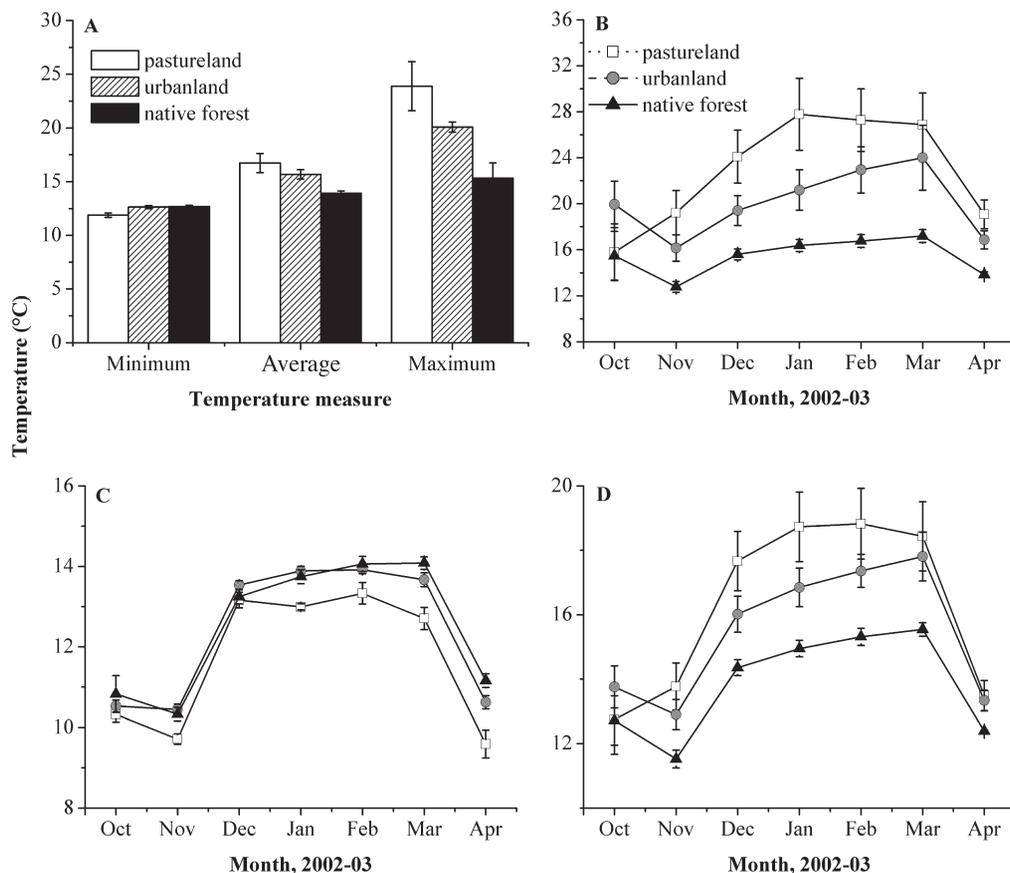

Fig. 5 Mean hourly water temperature from containers in pastureland, urbanland, and native forest at Waikanae, New Zealand from 20 to 23 February 2003. No standard error bars are shown for clarity.

DISCUSSION

The results of this study, dipping from experimentally positioned artificial container habitats, support previous findings that land use can influence the density of immature mosquitoes in larval habitats. Overall, significantly higher pupal density of the native mosquito species *C. pervigilans* was collected from urbanland containers compared with pastureland and native forest containers. A similar trend was observed for total mosquito density, but it did not reach the 5% level of significance ($P = 0.070$). Prior experiments have shown the sampling method that was used in this study to be effective at estimating *C. pervigilans* density and give reliable conclusions on the relationship between *C. pervigilans* density

Table 2 Maximum and minimum recorded water temperature, and mean daily average temperature, from containers in pastureland (Pa), urbanland (Ur), and native forest (Nf) at Waikanae, New Zealand from 23 October 2002 to 27 April 2003 (187 days). Mean values ± 1 SE.

Container	Land use	Max. temp. (°C)	Min. temp. (°C)	Mean daily average temp. (°C)
Pa1	Pastureland	34.07	2.92	16.97 ± 0.22
Pa2	Pastureland	40.50	4.68	18.14 ± 0.25
Pa3	Pastureland	29.77	3.50	15.09 ± 0.21
Ur1	Urbanland	36.33	5.79	16.20 ± 0.20
Ur2	Urbanland	34.10	5.58	14.79 ± 0.19
Ur3	Urbanland	39.01	5.71	16.02 ± 0.20
Nf1	Native forest	18.34	7.01	13.49 ± 0.15
Nf2	Native forest	20.65	6.06	14.08 ± 0.17
Nf3	Native forest	21.84	5.72	14.20 ± 0.17

Fig. 6 Mean daily water temperature data (± SE) from containers in pastureland, urbanland, and native forest at Waikanae, New Zealand. Data collected over the sampling duration, from October 2002 to April 2003. For clarity, daily measures for each replicate container are averaged over each month (*n* = 15–31). Each point or bar on the graphs represents the overall mean of the three replicate containers in each treatment. **A**, All temperature levels; **B**, maximum; **C**, minimum; **D**, average.

Table 3 Effect of land use and month on daily water temperatures of containers at Waikanae, New Zealand: results from repeated measures analysis of variance. (MS, mean squared value.) Bold type denotes significance at the 5% level.

Factor	d.f. effect	MS effect	d.f. error	MS error	*F*	*P*
Mean minium daily temp. (°C)						
Land use	2	0.005	6	0.001	8.734	**0.017**
Month	6	29.0	36	0.049	590.6	**<0.001**
Land use × month	12	0.30	36	0.049	6.141	**<0.001**
Mean average daily temp. (°C)						
Land use	2	40.6	6	6.96	5.830	**<0.001**
Month	6	39.0	36	0.218	179.1	**<0.001**
Land use × month	12	0.873	36	0.218	4.007	**0.001**
Mean maximum daily temp. (°C)						
Land use	2	0.163	6	0.018	8.862	**0.016**
Month	6	3.300	36	0.050	66.07	**<0.001**
Land use × month	12	0.100	36	0.036	2.78	**0.008**
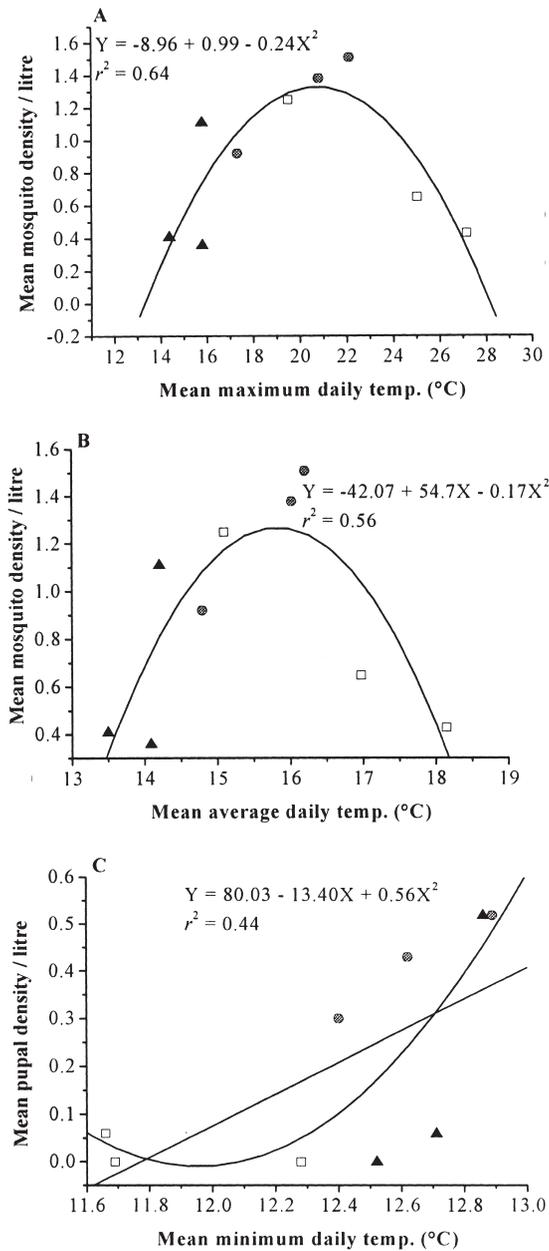
Fig. 7 Quadratic and linear relationships of: **A**, mean daily maximum temperature and total mosquito density; **B**, mean daily average temperature and total mosquito density; and **C**, average daily minimum temperature and pupal density, from models yielding the highest r^2 coefficients from regression analyses (see Table 4). Each point on the graphs represents the mean of daily values over the entire sampling duration. Note that the y-axis is log_{10} transformed.

and land use, but be 2.5 times less likely to sample *O. notoscriptus* (Leisnham et al. 2004, 2005). This sample bias, however, does not appear sufficient to account for the overwhelming dominance of *C. pervigilans* in all land uses in this study.

This study found a significant association of container water temperature with mosquito density and land use at Waikanae. Pastureland containers, which were placed in open sunlight, had significantly higher maximum and average daily temperatures and lower minimum daily temperatures than those in native forest, which were under an entirely enclosed canopy cover. Total mosquito density was best and significantly explained by the quadratic effects of maximum daily temperature and average daily temperature, with urbanland containers (which had medium levels of shade cover) showing the highest total mosquito and pupal densities. These results suggest that the presence of vegetative cover can play a strong regulatory role on water temperatures and on mosquito populations in larval habitats, and agree with findings from other studies that have found low mosquito densities in habitats with little shading vegetation (Becker 1995; Sunish & Reuben 2001; Fischer et al. 2002).

Growth and development of mosquitoes, like most insects, is mostly positively related with temperature within a range defined by lower and upper temperature thresholds (Clements 2000). Since there is higher egg and larval survival in favourable temperatures, and associated strong selection pressure for females to oviposit in such conditions, higher larval densities are commonly correlated with higher temperatures between species-specific upper and lower thresholds (Clements 2000). The findings of this study are consistent with the notion that urbanland has temperature conditions that promote higher growth, development and population density for *C. pervigilans* compared to pastureland and native forest. We found that pupal density was nearly significantly explained by a linear effect of minimum daily temperature ($P = 0.054$). This insignificant relationship may suggest that the development of immatures to the pupal stage is more dependent upon the regular attainment of a minimum threshold temperature. However, its low r^2 value (0.353) and the higher explanatory power of a quadratic effect ($r^2 = 0.439$, $P = 0.075$) confuse the relationship between temperature and pupal density. It appears that there may be a variety of other factors more strongly influencing pupal density in addition to temperature. These may include type and amount of allochthonous material (e.g., leaf fall), algal

colonisation, competition and predation (Blaustein et al. 1995; Washburn 1995). Differences in any one of these factors may explain the difference in mosquito densities when comparing total numbers (6 times) with pupal numbers (3 times) between urbanland and both pastureland and native forest.

Most past studies on land-use change and mosquito-borne disease risk have focused on increasing insolation resulting from deforestation as the main mechanism by which land-use change can influence mosquito density (Walsh et al. 1993; Patz et al. 2000). Replacement of natural vegetation with agricultural crops has been shown to increase numbers of sunlit larval habitats, alter evapotranspiration rates and modify ambient air temperatures; all of which have been suggested to change the water temperatures of larval habitats and the abundance of immature mosquitoes (Walsh et al. 1993; Lindblade et al. 2000). Findings from other field studies have shown a direct association between water temperature and mosquito presence or abundance (e.g., Williams et al. 1994; Sunish & Reuben 2001; Shililu et al. 2003; Strickman & Kittayapong 2003). This is one of the first studies to quantify water temperature differences of mosquito larval habitats in urbanland, pastureland and native forest, and relate them to immature mosquito density.

Regional air temperatures appeared to drive monthly changes in container water temperatures during this study. Although regional temperatures were close to normal levels, the Kapiti-Horowhenua region experienced notably low rainfall from January to April in 2003. Only 74.2 and 77.4 mm of rain fell in Paraparaumu and Levin, respectively; 26.6% and 24.5% of normal levels for this time of year (NIWA unpubl. data). Rainfall is often a key factor in regulating regional mosquito populations by providing larval habitat (Chapman et al. 2000; Gubler et al. 2001; Fischer et al. 2002). Low numbers of O. notoscriptus and the absence of other mosquito species in this study may be a result of a lack of preferable larval habitats owing to the low rainfall. The most common larval habitats of O. notoscriptus are artificial and natural containers (Lee et al. 1989; Laird 1990, 1995). These habitats are often primarily filled with water by rainfall (Laird 1988). The prevalence of C. pervigilans in urbanland in this study may support previous findings that this species can breed in a range of marginal habitats in modified areas (Belkin 1968; Laird 1990, 1995).

Although the water temperatures recorded in the containers in this study allow meaningful comparisons between land uses, they are likely to be higher than could be found in most other habitats because of their heat absorbent properties (i.e., plastic, small, and black). Therefore, although we found low mosquito densities in pastureland containers in this study, other habitat types in pastureland, such as stock drinking troughs, may have lower average temperatures that can sustain larger immature mosquito populations (Leisnham et al. 2004). Containers in open sunlight may be particularly important mosquito habitat if they provide favourable temperatures for algae that provide food for mosquito larvae (Williams et al. 1994). The results of this study also conflict with findings from a concurrent study in Waikanae and Paraparaumu using similar experimental containers but which were removed from the field and sub-sampled after homogenising their water (Leisnham et al. 2004). The concurrent study showed that larval C. pervigilans densities were not significantly related to land use (Leisnham 2004). Further field surveys will have to be undertaken across an increased number of locations to further understand the relationship

Table 4 Adjusted r^2 coefficients and F values from regression analyses modelling linear and quadratic effects of daily water temperature on total mosquito and pupal densities. Temperatures were mean values collected from replicate container habitats from October 2002 to April 2003. Bold type denotes significance at the 5% level.

Factor	Total mosquito density			Pupal density		
	r^2	F value	P value	r^2	F	P
Linear models						
Maximum	–0.139	0.027	0.875	–0.107	0.229	0.647
Average	–0.137	0.037	0.853	–0.127	0.099	0.762
Minimum	–0.113	0.186	0.679	0.353	5.364	0.053
Quadratic models						
Maximum	0.641	8.143	**0.020**	0.064	1.274	0.353
Average	0.558	6.051	**0.036**	0.052	1.220	0.359
Minimum	0.113	1.508	0.295	0.439	4.128	0.075

between larval *C. pervigilans*, temperature, and land use.

Little is known of the basic ecology of New Zealand's mosquito species and data on exotic species from overseas populations may be of limited value since species commonly adapt to local environmental conditions (Mattingly 1957). Using standardised artificial container habitats, this study has shown that a common generalist mosquito species can invade and utilise anthropogenically-modified environments in a temperate region. Although longitudinal data on mosquito densities before, during and after cultivation of native swamp forest are not available in the Kapiti-Horowhenua region, the design of this study allowed a spatial comparison of remnant native forest sites with neighbouring land-use types that were historically native forest, giving an indication of the impacts of land-use change. Results from this study and field surveys around the world (Gratz 1999; Norris 2004; Patz et al. 2004) suggest that there is a greater risk from mosquito-borne diseases in anthropogenically modified land uses.

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