

Increased Larval Mosquito Densities from Modified Landuses in the Kapiti Region, New Zealand: Vegetation, Water Quality, and Predators as Associated Environmental Factors

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Abstract: Landuse changes, including deforestation, agriculture, and urbanization, have coincided with an increase in vector-borne diseases worldwide. Landuse changes may alter mosquito populations by modifying the characteristics of aquatic larval habitats, but we still poorly understand the physical, chemical, and biological factors involved. We examined a total of 81 mosquito larval habitats for immature mosquitoes and 17 environmental variables in native forest, pastureland, and urbanland, at three locations in the Kapiti region, New Zealand. Significantly higher immature mosquito densities, predominantly of the endemic species *Cx. pervigilans*, were collected from urbanland and pastureland compared to native forest. Urbanland and pastureland habitats were mostly artificial containers compared to ground pools in native forest. Generalized linear modeling (GLM) revealed nine environmental variables that were significantly different between landuses. Of these variables, mosquito density was significantly (positively) correlated with bacteria and dissolved organic carbon. When location and date were controlled for in GLM, mosquito density was (negatively) related to the presence of vegetation and combined predators. The findings of this study support those from prior surveys in warmer climates suggesting greater mosquito-borne disease risk in anthropogenically-modified environments because of ecosystem disruption. Unlike most previous field-based work, this study suggests that in addition to habitat type, the presence of vegetation, water quality, and predators are also associated with mosquito density and may be involved in causal mechanisms. Urban containers and stock drinking troughs had high mosquito densities, suggesting that an initial step in directing control operations should be to focus on these habitats.

Key words: anthropogenic, disease-vector, landscape, nutrients, predator, temperate

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INTRODUCTION

Landuse changes, including deforestation, agriculture, and urbanization, 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 worldwide (Norris, 2004; Patz et al., 2004). Human activities can be responsible for fundamental changes to the physical, chemical, and biological characteristics of mosquito larval habitats that may cause increased female oviposition and larval survival (Patz et al., 2000; Norris, 2004; Patz et al., 2004). For example, deforestation can promote increased mosquito productivity by allowing substantially higher levels of solar radiation reach larval habitats, thus speeding up the rate of larval growth (Lindblade et al., 2000; Leisnham et al., 2004). Deforestation and agriculture can also alter mosquito populations by increasing detrital and microbial biomass on which mosquitoes feed as a result of livestock waste, fertilizer run-off, and increased detrital decomposition with warmer temperatures (Service, 1991; Wetzel et al., 1995).

Invertebrate predators can also substantially impact mosquito populations both directly and indirectly. For example, backswimmers (Hemiptera: Notonectidae) can consume high numbers of mosquito larvae as well as reduce oviposition by adult females (Murdoch et al., 1984; Blaustein et al., 1995). Backswimmers are common predators of immature mosquitoes in New Zealand, along with diving beetles *Rhantus pulverosus* and damselfly larvae (Zygoptera) (Graham, 1939). However, the relationship of these predators with landuse and mosquito populations has not been examined.

In general, studies of the relationship between landuse and mosquitoes have suggested that the proliferation of new larval habitats, such as dam creation from water development projects and artificial containers from urbanization, is the primary mechanism by which landuse change has increased mosquito productivity (Patz et al., 2000; Norris, 2004). Fewer studies have examined the influence of landuse on the environmental characteristics of larval habitats and the ecological factors involved.

New Zealand is an island nation in the South Pacific region with a temperate climate and a small mosquito fauna consisting of only 12 endemic and 4 exotic species of mosquitoes. Human settlement of New Zealand over the last two centuries has resulted in the clearance of over 70% of native forest, rapid pastoral transformation, and substantial disruption of waterways (Atkinson and Cameron, 1993). New Zealand has not yet experienced an epidemic of mosquito-borne human disease, but the conversion of much of New Zealand into an agro-ecosystem has led to

the spread of both endemic and, more recently, exotic disease-vector species (Laird, 1995).

New Zealand's two most common and widespread species, the endemic *Culex pervigilans* Bergroth and the exotic *Ochlerotatus notoscriptus* (Skuse), 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 and Kay, 1998), and is increasing its distribution throughout New Zealand's North Island (Laird, 1995). *Culex pervigilans* is a known vector of Whataroa virus, which primarily infects native bird populations (Miles, 1973). There is limited serological evidence that Whataroa virus also infects humans (Maguire et al., 1967; Miles, 1973), and *Cx. pervigilans* has been assessed to be a species requiring testing for its potential as a vector of other human diseases (Weinstein et al., 1997). Both species have been found in a wide range of habitat types in New Zealand but usually from artificial containers (Laird, 1995). No studies have yet examined what habitat characteristics are associated with their distribution.

The first aim of this study was to examine the relationship between landuse and immature mosquito density in resident larval habitats in the Kapiti region, New Zealand. We hypothesize that there will be increased mosquito densities in habitats in anthropogenically-modified landuses compared to habitats in native forest. The second aim of this study was to determine if differences in mosquito densities between landuses are correlated with changes in the physical, chemical, and biological characteristics of the habitats, to shed light on environmental factors that are associated with the disease-vector mosquitoes.

METHODS

Study Sites

The study was undertaken in the Kapiti 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 with neighboring sites consisting of three landuse types (i.e.,

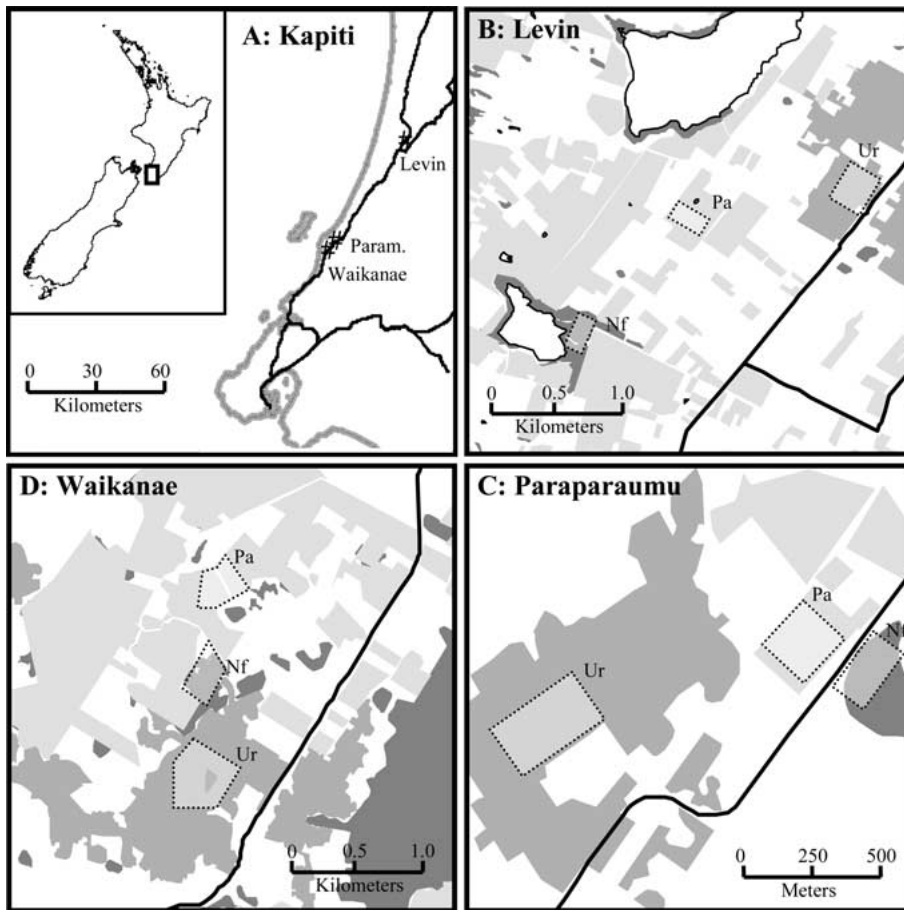


Figure 1. A: Map of the study locations: Levin, Paraparaumu (Param.), and Waikanae, in the Kapiti region, New Zealand. Positions of the specific landuse study sites within Levin (B), Paraparaumu (C), and Waikanae (D) are shown enclosed in dotted lines. Nf, native forest sites; Pa, pastureland sites; Ur, urbanland sites. Native forest land-cover is darkly shaded; urbanland is medium shaded; and pastureland is lightly shaded. Dark lines indicate state highways.

3 landuses \times 3 locations = 9 total sites) within 2–4 km² were selected for our study (Fig. 1). The landuses were: (i) native swamp forest (Nf), consisting of a variety of podocarp and hardwood species that provided full forest canopy interspersed by scrub in wetter areas; (ii) pastureland (Pa), consisting of open grasslands of exotic plant species, which are intensively stocked with sheep and cattle of introduced origin; and (iii) urbanland (Ur), consisting of various ecotypes that provide a variety of flora and fauna, as well as physical structures including roads, buildings, and drains. Sites are indicative of the landuse types throughout the region and were selected while attempting to control for geomorphology and climate (e.g., all were approximately of equal size: 13–20-ha; < 200-m above sea level; and of similar topography) so that the selected sites were as similar as possible in all respects except for their landuse.

Study Design

Mosquito sampling was undertaken from January to March 2003. This is during the warmest months in the austral summer period, with an average daily temperature of

16.9°C (range = 10.6°–22.4°C) in the region [National Institute of Water and Atmosphere, unpublished data], and when mosquito densities are generally at their highest (Leisnham et al., 2004). At each location, mosquitoes were sampled on three occasions that were 21 days apart. On each sampling occasion, three map coordinates were selected randomly for each of the three landuses within the location, using a topographical map broken into 1-m² grid squares, and the larval habitat closest to each point was sampled. Thus, a total of 27 habitats were sampled across all three landuses within a location, giving a total of 81 habitats. Any water body was considered a potential larval habitat, as per Laird (1988).

While larval and pupal densities do not necessarily correlate with adult emergence success, they are commonly used as a surrogate for adult productivity in surveillance and control surveys, and ecological studies (WHO, 1982; Service, 1995). Because the pupal stage is the penultimate molt before adult emergence, pupal density was examined separately because it is the best indicator among the immature stages of adult productivity.

Mosquito Sampling Procedure

During each sampling occasion, larval habitats were first visually examined for immature mosquitoes (larvae and pupae) and their aquatic predators. Mosquitoes and predators, such as backswimmers, diving beetles and damselflies, were easily observed and identified to Family by in situ visual inspection, as they come to the water surface to breathe. Predators were not quantified because dipping was found to rarely collect them due to their quick movement and relatively low densities. To estimate larval mosquito densities, each habitat was sampled using a conventional dipping method (Service, 1995). A total of 1-L of water was sampled from each habitat by dipping 200-ml five times at equal intervals around the habitat's entire circumference. Each liter of water was poured back into its respective habitat through a 0.20-mm mesh. The number of dips and volume of water sampled per habitat were feasible and comparable, given time constraints locating and sampling larval habitats that were often difficult to access. For habitats with less than 1-L of water, the entire volume of water was sampled. Immatures that were strained in the mesh from dipping were then placed in a separate container for each habitat, and all containers were brought back to the laboratory where mosquitoes were preserved in 70% ethanol for subsequent identification and counting. The dipper and mesh strainer were thoroughly rinsed with distilled water before sampling the next habitat. All third and fourth instar larvae were counted and identified to species level, and first and second instar larvae to genus level using the key of Winterbourn et al. (2000). No key to New Zealand mosquito pupae is available.

Physicochemical Measurements

The water depth and area of each habitat were measured, and the presence of potential shade cover and surrounding vegetation (within a 0.5-m radius) subjectively assessed. Three 100-ml water samples were taken from the first two habitats sampled in each landuse site on all sample occasions. For each sample, four 25-ml sub-samples were collected at the edge of the habitat around its entire circumference, using a 50-ml syringe (sampling depth: ~ 2 cm). To minimize water disturbance, water was collected before sampling for mosquitoes. One sample was used to measure bacteria using total plate count methodology at 22°C (American Public Health Association, 1992). Another sample was used to measure and dissolved organic carbon (DOC) using stan-

dard methodology (American Public Health Association, 1992). The third sample was filtered through glass microfiber filters (100 mm diameter Whatman[®] GF/C, Whatman International Ltd, Maidstone, UK) and frozen, before thawing for later analyses for nitrate, nitrite, ammonia, ortho-phosphate, and sulfate, with a multi-test water analyzer (Aqua Analyzer 2, Orbeco-Hellige, Farmingdale, NY) using standard methods (American Public Health Association, 1992). Zero values may represent the lower resolution of the methods (0.14–5.21 $\mu\text{mol/L}$) rather than actual zero values. For each habitat, pH and conductivity were also measured using hand-held meters (YSI Model 60 pH meter and YSI Model 80 conductivity meter, YSI Inc, Yellow Springs, OH). No pH and conductivity measures were taken from two habitats in native forest and one habitat in pastureland from which other chemical measurements were made due to meter malfunctions. A total of six habitats from each landuse at each location had their water sampled giving a total of 54 samples for each chemical measurement (6 samples \times 3 landuses \times 3 locations), except for pH and conductivity, which had 51 samples.

Statistical Analyses

Chi-squared tests were used to examine if the proportion of habitats with mosquitoes differed between landuses. The relationships of landuse with mosquito density, physicochemical characteristics, and predator presence/absence were examined using Generalized Linear Modeling (GLM). Residuals of response variables were checked for their distribution and variance using histograms and scatter plots and the most appropriate link function (Gaussian, Poisson, or binomial) was used. All analyses included landuse as a fixed variable, and location and date (which was nested within location) as random variables. Corrections were made for post-hoc pairwise comparisons in GLM analyses using the Holmes factorial method (Zar, 1999).

Spearman rank correlation analyses were used to indicate the direction and strength of linear associations between continuous habitat variables and mosquito density, and GLM analyses were undertaken to ensure that associations were significant when location and date were added to models as random factors. Linear and polynomial relationships were checked using scatterplots: no polynomial relationships were evident. Multicollinearity was detected by means of Variance Inflation Characteristics (VIF), with a VIF above 2.5 for a variable indicating a problem (Allison, 1999); however, none were evident.

Table 1. Number and Type of Mosquito Larval Habitats Sampled in Pastureland, Native Forest, and Urbanland in the Kapiti Region^a

Habitat category	Pastureland	Native forest	Urbanland
Ponded streams	2 (2, 0, 1)	1 (0, 0, 0)	
Lake edges		1 (0, 0, 0)	
Swamps and marshes		1 (0, 0, 0)	
Shallow permanent ponds		1 (0, 0, 0)	4 (2, 0, 0)
Shallow temporary pools		9 (3, 0, 0)	
Intermittent ephemeral puddles	1 (1, 0, 1)	10 (1, 0, 0)	
Natural containers		4 (0, 0, 0)	
Artificial containers	24 (9, 0, 1)		23 (13, 4, 7)
Total	27 (11, 0, 3)	27 (4, 0, 0)	27 (15, 4, 7)

^aData shown are pooled from three locations for brevity and clarity. Numbers of habitats with *Culex pervigilans* larvae, and *Ochlerotatus notoscriptus* larvae and pupae, are given in parentheses in that order. Habitat classification was according to Laird (1988).

Means and standard errors are reported throughout; all tests were two-tailed, and significance was assigned at the 5% level.

RESULTS

Mosquito Density in Different Landuse Types

Mosquitoes were recorded from 31 out of the 81 habitats sampled (38.3%) (Table 1). The proportion of mosquito-positive habitats was significantly higher in urbanland (0.56, $n = 15$) and pastureland (0.44, $n = 12$) compared to native forest (0.15, $n = 4$) (χ^2_1 -values = 5.68 and 9.83, P -values = 0.017 and 0.002), but not between urbanland and pastureland ($\chi^2_1 = 0.667$, $P = 0.414$). Mean mosquito densities in the three landuse types are shown in Figure 2. No mosquitoes were found in water bodies of native forest at Levin. There was a highly significant relationship between landuse and mosquito density ($F_{2,4} = 10.87$, $P < 0.001$), with pastureland and urbanland having 45 and 42 times higher

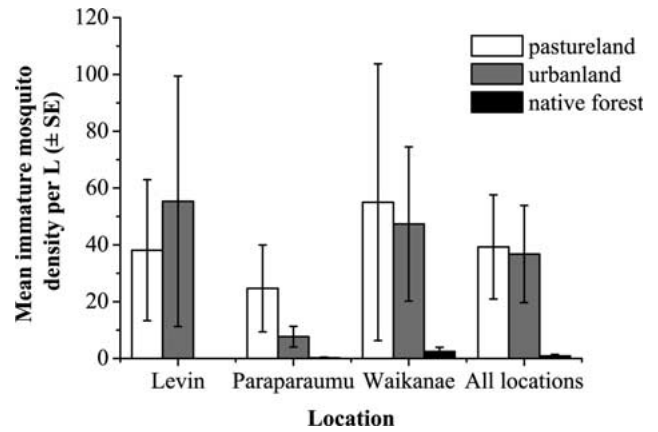


Figure 2. Mean mosquito density in larval habitats from pastureland, native forest, and urbanland. Data collected from January to March 2003; $n = 9$ for each treatment at separate locations and 27 across all locations; error bars are 1 SE.

average densities than native forest, respectively (pairwise comparisons: $P < 0.001$). Mosquito densities in urbanland and pastureland were not significantly different from one another ($P = 0.95$). Pupae were restricted entirely to modified landuses, being collected from 7 habitats in urbanland and 3 habitats in pastureland (10 habitats in total).

A total of 46 pupae and 1016 larvae were recorded during the study, consisting of the two most common mosquito species in New Zealand, the endemic *Cx. pervigilans* and the exotic *Oc. notoscriptus*. *Culex pervigilans* was the most common species, constituting 90.7% ($n = 245$) of the total number of third and fourth instar larvae collected (*Oc. notoscriptus*, $n = 25$). Of the first and second instar larvae that could only be identified to genus level, 98.4% ($n = 734$) were *Culex* sp. and 1.6% ($n = 12$) were *Ochlerotatus* sp. Since *Cx. pervigilans* and *Oc. notoscriptus* were the only species of third and fourth instar larvae collected at all three locations, it is likely that these first and second instar larvae were also either *Cx. pervigilans* or *Oc. notoscriptus*. Because *Oc. notoscriptus* constituted only a low proportion of total late and early instar larvae, we did not analyze them separately, though removing them from the dataset did not affect the conclusions of the GLM analysis (results not shown). All *Oc. notoscriptus* larvae were collected from only four urban habitats, all being artificial containers. Although mosquitoes were less likely to have been collected from large habitats, such as those in native forest, densities were likely to have been sufficiently low to avoid detection using our methods and thus not greatly affect the conclusions above.

Table 2. Physicochemical Characteristics of Habitats in Pastureland, Native Forest, and Urbanland^a

Habitat characteristic	Pastureland	Native forest	Urbanland	F-Statistic	P-value
Proportion shaded	0.0 ^b	0.70 ^c	0.67 ^c	33.37	<0.001
Proportion with vegetation	0.15 ^b	0.89 ^c	0.30 ^b	30.26	<0.001
Depth (m)	0.30 (0.02) ^b [0.02–0.47]	0.16 (0.06) ^c [0.01–1.50]	0.17 (0.03) ^c [0.01–0.50]	6.19	0.004
Area (m ²)	4.35 (2.55) ^b [0.02–70.00]	111.53 (87.21) ^c [0.01–2351.00]	0.87 (0.55) ^d [0.01–15.00]	33.18	<0.001
Bacteria (cfu/μl)	14.92 (6.1) ^b [0.44–110.00]	61.36 (52.32) ^{b,c} [1.20–950.00]	121.50 (57.17) ^c [0.59–950.00]	8.49	0.001
pH	8.09 (0.32) ^b [4.84–9.47]	6.87 (0.16) ^c [5.97–8.45]	7.34 (0.21) ^c [5.75–9.66]	9.91	0.001
Conductivity (mS/cm)	208.33 (36.42) [81.70–682.00]	262.01 (18.87) [87.70–357.20]	263.77 (38.10) [98.40–636.00]	1.58	0.226
DOC (g/m ³)	7.00 (1.11) ^b [1.60–19.00]	17.24 (8.78) ^c [1.10–152.00]	23.45 (5.10) ^c [1.30–76.00]	6.93	0.004
Nitrate (μmol/L)	3.08 (0.82) ^b [0.35–15.61]	66.62 (45.52) ^c [0.00–794.77]	4.29 (2.32) ^b [0.0–42.58]	22.04	<0.001
Nitrite (μmol/L)	0.09 (0.05) [0.00–0.64]	0.12 (0.08) [0.0–1.36]	0.10 (0.05) [0.0–0.72]	0.27	0.272
Ammonia (μmol/L)	50.11 (27.83) [0.00–393.42]	31.74 (16.73) [2.35–281.86]	45.25 (17.10) [1.17–311.22]	0.67	0.522
Phosphate (μmol/L)	7.38 (2.89) [0.00–39.28]	3.07 (1.75) [0.00–32.12]	5.05 (2.35) [0.00–40.54]	2.06	0.146
Sulfate (μmol/L)	155.87 (113.97) [5.21–2082.08]	120.12 (36.99) [0.00–614.21]	111.04 (51.08) [0.0–812.01]	0.42	0.659

DOC, dissolved organic carbon.

^aData shown are pooled from three locations for brevity and clarity. All values are means ($n = 16–27$) except for proportion shaded and proportion with vegetation, which represent the proportion of total habitats in each landuse. Means are shown ± 1 SE in parentheses, and the range in square brackets. Significant P -values are shown in bold type and significant differences between landuses denoted by different superscripts (^{b,c}, or ^d) (generalized linear models).

Physicochemical Characteristics of Habitats

The types of larval habitats sampled were considerably different between landuses (Table 1). Artificial containers predominated in pastureland and urbanland constituting 88.9% ($n = 24$) and 85.2% ($n = 23$) of all habitats in these landuses respectively, where as ground water bodies were the most common habitat in native forest (85.2%, $n = 23$) (Table 1). All natural water bodies (ground pools and natural containers) and artificial containers in urbanland (e.g., plastic buckets, birdbaths, and metal drums) were likely filled with rainwater. In contrast, all 24 artificial containers in pastureland were stock drinking troughs and were filled with filtered groundwater [Jonathan Smith, personal communication]. Overall, artificial containers were the most common category of habitat found, constituting 58.0% ($n = 47$) of all the habitats sampled.

The physicochemical characteristics of larval habitats and results of GLM analyses are presented in Table 2. Landuse was related to physicochemistry, with significant differences in shade and vegetation cover, habitat depth and area, pH level, and bacteria, DOC, and nitrate concentrations. A significantly higher proportion of habitats in native forest (0.70) and urbanland (0.67) were shaded compared to pastureland, which had no shaded habitats. A significantly higher proportion of habitats in native forest (0.89) were surrounded by vegetation (usually with closed canopy cover), compared to in urbanland (0.30) and pastureland (0.15). Shade cover in urbanland came from a variety of sources, such as trees, corrugated iron fences, garages, and houses, which rarely provided overhead cover. Habitats in pastureland (88.9% of which were stock drinking troughs, $n = 24$) had an average depth nearly twice that of habitats in native forest and urbanland (Table 2),

which were mainly relatively shallow ground water bodies and containers, respectively (Table 1). The average area of habitats showed a significant size gradient from urbanland (smallest) through pastureland to native forest (largest) (Table 2). A gradient of bacteria concentration existed from pastureland (lowest) through native forest to urbanland (highest). Pairwise comparisons revealed significant differences between pastureland and urbanland, although low sampling power meant that differences between native forest and pastureland and between native forest and urbanland were not significant. A gradient from pastureland (lowest) through native forest to urbanland (highest) also existed for DOC concentration. A significant difference in DOC concentration existed between pastureland and native forest, and pastureland and urbanland, but not between native forest and urbanland. Habitats in pastureland had significantly higher pH levels than those in native forest and urbanland, although average pH levels of all three landuses were close to neutrality (Table 2). Ammonia was the most common form of environmental nitrogen in pastureland and urbanland habitats, compared to nitrate in native forest. Nitrate concentration was significantly higher in native forest compared to pastureland and urbanland, while ammonia concentration was not significantly differently between landuses. Relatively little nitrogen was in the form of nitrite in all three landuses.

Observations of Predators

Macroinvertebrate predators were recorded from 29 out of the 81 total habitats sampled (35.8%), with three taxa being represented (Table 3). Although few predators were recorded during the survey, all taxa that were observed appeared to show strong landuse preferences. The backswimmer (Notonectidae) *Anisops* sp. was the only taxon observed in all three landuses, but was found mainly in pastureland. Diving beetle larvae (Dytiscidae) were never observed in urbanland, while adults were only found in pastureland stock troughs. Damselfly larvae (probably the common *Austrolestes colenonis* or *Xanthocnemis zealandica*) were only found in ground pools in native forest. Overall, there was a significant difference between landuses in the proportion of habitats with predators ($F_{2, 78} = 16.85$, $P < 0.001$), with pastureland (0.59) and native forest (0.44) having significantly higher proportions of predator-positive habitats compared to urbanland (0.04) (pairwise comparisons: P -values < 0.05). Different predatory taxa were only observed co-existing in a habitat on 3 of the 29 occasions,

Table 3. Number of Habitats in Pastureland, Native Forest, and Urbanland with Predators^a

Predator	Landuse		
	Pastureland	Native forest	Urbanland
Backswimmers (<i>Anisops</i> sp.)	13 (0.48)	4 (0.15)	1 (0.05)
Damselflies (Zygoptera)	0 (0.00)	5 (0.19)	0 (0.00)
Diving beetles (Dytiscidae)			
Adults	6 (0.22)	0 (0.0)	0 (0.0)
Larvae	3 (0.11)	3 (0.11)	0 (0.0)
Total	7 (0.26)	3 (0.11)	0 (0.0)
All predators	16 (0.59)	12 (0.44)	1 (0.05)

^aData shown are pooled from three locations for clarity. Numbers in parentheses represent the proportion of total habitats in each landuse ($n = 27$).

when backswimmers were observed with adult diving beetles in pastureland stock troughs.

Relationships between Habitat Characteristics and Mosquito Density

Mosquito density showed generally weak correlations with all habitat characteristics, but a significant positive association with bacteria ($r_s = 0.319$, $P = 0.02$, $n = 54$) and DOC ($r_s = 0.286$, $P = 0.04$, $n = 54$) concentrations, and was near the 5% level of significance with ammonia concentration ($r_s = 0.252$, $P = 0.066$, $n = 54$). No other continuous habitat variables were significantly correlated with mosquito density (r_s -values = 0.016–0.206, P -values = 0.14–0.82, $n = 51$ –54). Univariate GLM, which controlled for location and date effects, revealed that ammonia ($F_{1, 53} = 44.07$, $P < 0.001$) and phosphate ($F_{1, 53} = 8.83$, $P = 0.005$) concentrations showed a significant positive association, and the presence of vegetation ($F_{1, 79} = 5.23$, $P = 0.025$) and combined predators ($F_{1, 79} = 4.82$, $P = 0.03$), a significant negative association, with mosquito density (other characteristics: F -values_{1, 50–79} = 0.04–2.97, P -values = 0.09–0.83).

Correlations between continuous habitat characteristics were generally weak (except for between depth and area, $r_s = 0.653$), and VIF values were below 2.5, indicating nonproblematic multicollinearity and allowing the use of multiple GLM procedures. When all habitat characteristics were added to a multiple GLM either all at once or in a

stepwise manner, none emerged as being a significant predictor.

DISCUSSION

The results of this study support previous findings that landuse can influence the density of immature mosquitoes in larval habitats (Gratz, 1999; Patz et al., 2000). Significantly higher densities of mosquitoes, predominantly of the species *Cx. pervigilans*, were collected in urbanland and pastureland habitats. These habitats were mostly artificial containers compared to ground pools in native forest. This study also found a significant relationship between landuse and nine environmental variables. Of these variables, mosquito density was significantly (positively) correlated with bacteria and dissolved organic carbon, and when location and date were controlled for in GLM, mosquito density was (negatively) related to the presence of vegetation and combined predators.

Most past studies on landuse change and mosquitoes have focused on increasing insolation as a result of deforestation as the main mechanism by which landuse change can influence the conditions of larval habitats (Service, 1991; Walsh et al., 1993; Patz et al., 2000; Leisnham et al., 2004). The results of this work are in accordance with those of previous studies, by showing that urban and pastureland habitats, which had the highest mean mosquito densities, had a significantly lower probability of being surrounded by vegetation compared to native forest habitats. This study also classified habitats as being shaded or open, but found no significant association between the presence of shade and mosquito density. This result may be due to a number of factors, one being that some structures that were considered to shade habitats (such as corrugated iron fences and painted houses in urbanland) also provided radiant heat energy (McIntyre, 2000).

Another mechanism by which landuse could alter vector mosquito densities is by modifying the organic content of larval habitats (Becker, 1995; Gratz, 1999; Leisnham et al., 2004). Previous work has shown that larvae of most mosquito species feed primarily on bacteria whose growth is stimulated by DOC (Fish and Carpenter, 1982; Merritt et al., 1992; Kaufman et al., 2002). Landuse is also likely to alter the presence of invertebrate predators, which have long been shown to have a strong regulatory role on mosquito populations (Murdoch et al., 1984; Blaustein et al., 1995). Predators, bacteria, and DOC were likely to

have been regulating mosquito populations in this study. Urbanland habitats had high average organic enrichment and a low probability of having predators, which is in accordance with previous studies that have recorded elevated mosquito densities from urban landscapes with lower numbers of predators and poor sanitation (e.g., Becker, 1995; Gratz, 1999). Native forest ground pools, which had on average low mosquito densities, had low average concentrations of bacteria and DOC as well as a higher probability of having predators compared to artificial container habitats in urbanland.

Relationships between mosquito density and environmental factors in this study, however, appear to be dependant upon landuse type. Mosquito populations in pastureland habitats may not be substantially regulated by predators or organic enrichment. Pastureland habitats, which had high average mosquito densities, had a high probability of having predators and low organic enrichment. There may be a number of factors sustaining high mosquito densities in pastureland habitats in spite of potentially high predation pressure and limiting food. One possible reason may be that the most common pasture habitat was stock drinking troughs, which provided a practically permanent habitat with presumably high average water temperatures. Although we measured 17 characteristics of larval habitats that are thought to influence immature mosquito populations, other factors that are related to landuse that were not measured may also be important. These factors may include visual, olfactory, and directional cues at the ecotype or landscape level that stimulate oviposition by adult females (e.g., increased host abundance) (Clements, 2000).

Based on the results from this study, educating the public to limit the number of artificial containers that may fill with water and accumulate high organic content (e.g., disused plastic buckets, trash cans) may lower the regional abundance of vector species, as suggested in other studies (e.g., Knudsen, 1995; Moloney et al., 1998; Tauil, 2001). This action might be particularly pertinent in New Zealand given the low prevalence of natural mosquito predators in the country (Laird, 1990, 1995). Past mosquito control operations in agricultural landscapes have usually focused on preventing the establishment of ground water larval sites created by irrigation schemes and mechanization (Service, 1991; Klingenburg et al., 2002). This study suggests that artificial containers in pastureland, such as stock drinking troughs, which although receiving little nutrient enrichment, may be important larval habitats to control. Stock

troughs may be particularly important sources of adult mosquitoes in temperate climates that experience low summer rainfall and thus have relatively few habitats that persist for a long enough time to support even one generation of mosquitoes. A control method to limit their effectiveness as permanent larval habitat may be regular emptying and refilling. Comparing the total amount of larval habitat that stock troughs provide with that of other water bodies in different landuses would also be important when considering control operations. This question was beyond the scope of this study but will be important to address in future work, despite the obvious difficulties in measuring larval habitat area in native forest and urbanland where access may be problematic.

Longitudinal data on mosquito densities before, during, and after cultivation of native swamp forest are not available in the Kapiti region. However, the design of this study allowed a spatial comparison of habitats in remnant native forest sites with habitats in neighboring landuse types that were historically native forest, giving an indication of the impacts of landuse change. While this study has identified important factors correlated with mosquito densities, further knowledge of the mechanisms by which landuse can effect mosquito populations is likely to be achieved by manipulative experiments. This study provides an important first step in identifying appropriate environmental determinants of immature mosquito density for further study in such controlled experiments.

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