

Original Contributions

Anthropogenic Landscape Change and Vectors in New Zealand: Effects of Shade and Nutrient Levels on Mosquito Productivity

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Abstract: Anthropogenic environmental changes, such as deforestation, agriculture, and introduced exotic species, have often coincided with an increase in mortality and morbidity from mosquito-borne diseases worldwide. Deforestation and agricultural development are likely to regulate immature mosquito populations through the addition of nutrients from livestock waste, decreased shade resulting in increased insolation (solar radiation), and the proliferation of artificial container habitats. We conducted a field experiment in Waikanae, New Zealand, to tease apart the relative effects of shade and nutrient levels on aquatic immature populations of two generalist mosquito species. Container habitats were subjected to five levels of detrital input (0–500-g sheep manure/liter of water) and three shade treatments (open, artificial shade, and forest canopy) in a factorial design. The native species *Culex pervigilans* constituted 98.9% of all late-instar larvae; the remainder being the exotic *Ochlerotatus notoscriptus*. We observed higher overall immature mosquito abundance and pupal productivity in open containers with medium detrital loads (5 g/L). Exotic mosquito abundance was low in all treatments and was excluded from containers in unshaded, or deforested, areas. No native or exotic mosquito abundance was observed in containers with extremely high detrital loads (500 g/L). As many exotic species thrive in similar high nutrient conditions, these containers and other larval habitats of similarly high nutrient levels represent potentially vacant niches for exotic mosquito invasion. These results indicate the importance of shade and nutrient level as central determinants of mosquito productivity in temperate climates, such as New Zealand, as well as show that anthropogenic environmental change can have flow-on effects on the ecology of disease-vector mosquitoes.

Key words: agriculture, deforestation, disease-vector, land use, temperate, containers

INTRODUCTION

Landscape change, especially deforestation and the subsequent addition of high livestock densities in agro-eco-systems, is considered to be the greatest driver of terrestrial

environmental change (Vitousek et al., 1996; Vitousek, 1997; Sala et al., 2000; Novacek and Cleland, 2001). Ecosystem modification from human activities has led to changes in mosquito biodiversity and ecology, and has often coincided with increases in mortality and morbidity from mosquito-borne diseases worldwide (Ziperman, 1973; Tesh, 1994; Gratz, 1999; Martens et al., 2000; Patz et al., 2000).

Three linked mechanisms by which deforestation and agriculture are likely to regulate immature mosquito populations are through the addition of nutrients from livestock waste, decreased shade resulting in increased solar radiation (or “insolation”), and the provision of artificial containers as breeding habitats. Livestock waste products can substantially increase the food available for larval mosquitoes in aquatic habitats. Mosquito larvae are primarily filter feeders and almost all of their food is dead organic matter (detritus) and associated microbes (Fish and Carpenter, 1982; Carpenter, 1983; Walker et al., 1991; Kitching, 2001). Deforestation allows substantially increased levels of solar radiation to reach breeding habitats at or near ground level. Increased insolation speeds up the rate of larval and pupal growth below an upper lethal threshold (Clements, 2000), as well as increasing photochemical, thermal, and microbial decomposition of detritus (Wetzel et al., 1995). Lastly, intensive agricultural practices (and their sequelae, urban settlements) have led to the proliferation of container habitats for native and exotic mosquito species to utilize, such as stock troughs, discarded tires, and plastic buckets (Laird, 1990, 1995). These container habitats may be particularly important in temperate areas that have few ground water bodies because of low rainfall over the warmest (summer) period of the year.

Another substantial driver of terrestrial environmental change is the human-aided introduction of organisms into new regions (Vitousek et al., 1996, Vitousek, 1997; Martens et al., 2000; Sala et al., 2000; Novacek and Cleland, 2001). The introduction of exotic mosquito species can have an interactive effect with landscape change on resident native species (Patz et al., 2000). The replacement of forest with pastureland has allowed disease vector mosquitoes to displace less opportunistic, nonvector species in nonnative areas, leading to the “emergence” and “reemergence” of some mosquito-borne diseases (Patz et al., 2000).

Predicting the impact of anthropogenic environmental change on the productivity of mosquitoes requires an intimate knowledge of the ecological processes involved (Patz et al., 2000). Changes in the shade and nutrient levels of aquatic habitats, and the introduction of exotic species,

singly and in combination, can substantially alter the local mosquito-borne disease risk. We know relatively little about the influence of changes in shade and nutrient levels on the growth and survival of endemic and exotic species in temperate climates. The majority of studies that have examined the effect of shade or nutrient level on mosquitoes have been either laboratory based or on wild populations in mostly tropical or subtropical climates (e.g., Carpenter, 1983; Chadee, 1993; Beehler and Mulla, 1995; Becker, 1995; Tun-Lin et al., 2000; Kaufman et al., 2002).

New Zealand is an island nation with a temperate climate and a depauperate fauna of only 12 endemic and 4 exotic species of mosquitoes. The endemic *Culex pervigilans* Bergroth and the exotic Australian *Ochlerotatus* (formerly *Aedes*) *notoscriptus* (Skuse) are New Zealand’s two most common and widely distributed species, inhabiting a wide variety of habitat types (Belkin, 1968; Laird, 1990, 1995). New Zealand has not yet experienced an epidemic of mosquito-vector human disease (due mainly to its isolation), however, both *Oc. notoscriptus* and *Cx. pervigilans* have important public health significance (Weinstein et al., 1997). *Ochlerotatus notoscriptus* has been implicated as a potential vector of Ross River virus and dengue fever in Australia and the South Pacific (Maguire, 1994; Watson, 1998), while *Cx. pervigilans* is a known vector of the avarian Whataroa virus (Maguire et al., 1967; Miles, 1973) and has been assessed to be a species requiring testing for its potential as a vector of exotic human diseases (Weinstein et al., 1997).

Culex pervigilans and *Oc. notoscriptus* are ideal species to study the effects of shade and nutrient level on disease-vector mosquitoes in a temperate climate because they present an important potential public health threat, and they are commonly found together in container habitats (Laird, 1990, 1995) which can be easily experimentally manipulated and sampled. The aim of this article was to determine if changes in shade and nutrient levels, systematic of deforestation and agricultural landscape change, influence the immature abundance and pupal productivity of *Cx. pervigilans* and *Oc. notoscriptus*, by experimentally manipulating container habitats.

METHODS

Study Site

Waikanae, historically a catchment of temperate lowland native swamp forest, is approximately 70 km north of

Wellington (40°52'S, 175°03'E). This study was undertaken in the austral summer and autumn periods (January–April) of 2002, when the average maximum and minimum temperatures of the region were 19.6°C and 11.6°C, respectively. Since the first European settlement in the 1840s, like most of New Zealand's lowland swamp forest, Waikanae has been almost entirely drained and cleared for pastureland (Maclean, 1988). A 13-hectare bird sanctuary, Nga Manu Nature Reserve, is the only significant patch of forest remaining in Waikanae.

The study site consisted of a 400-m² area within this native forest, and two neighboring areas each about 200 m² in size that had been cleared of forest in the last 2 years and subsequently maintained as open grassed areas. The sites were chosen because they were secluded and secure from public interference. All three areas were within 50 m of each other, had similar topographies and were approximately equidistant from any water bodies that had immature mosquitoes, as determined by prior surveys [Leisnham and Snell, unpublished data].

Study Design and Materials

A model system was created for this experiment utilizing 6-liter circular black plastic bucket containers (22-cm diameter × 20-cm height) filled with 4 liters of water from a local ground water source filtered through a 0.5-mm mesh. The inside surface of each container was roughened with coarse sandpaper to provide a textured surface for *Ochlerotatus* eggs to attach. These containers are likely to provide an attractive breeding habitat for both species because both preferentially breed in a wide range of artificial containers, including plastic buckets (Belkin, 1968; Russell, 1993; Laird, 1995), and adult females of other species have shown preferential oviposition behavior for black containers compared to those of other colors (Yanoviak, 2001).

The containers were subject to five levels of initial nutrient (detritus) input and three types of shade in a factorial design (five nutrient levels × three shade types × four replicates of each combination, for a total of 60 containers). Each container was staked to the ground using a bamboo pole and covered with 0.5-mm galvanized wire mesh (intermesh gap = 20 mm) to prevent vertebrate animals from drinking the water.

Nutrient levels consisted of 0, 0.5, 5, 50, and 500 g of dried pelletized sheep manure (Kiwi™, Mount Maunganui, New Zealand; approximately 3% nitrogen, 2% phosphorus, and 4% potassium) per liter of water. The

water level for 4 liters was marked on the side of the container and the water in each container was topped off weekly throughout the experimental period to account for evaporation. The shade treatments consisted of open, artificial shade, and forest canopy. The artificial shade canopy consisted of 1600-cm² double-layered shade-cloth (Greenfield™, Auckland, New Zealand) that was clipped to a frame of four bamboo stakes and held 10 cm above the top of each container. Containers assigned to the artificial shade and open treatments were divided evenly between the two cleared areas. To examine temperature differences between shade treatments, a maximum and minimum thermometer was placed in one container of each shade treatment that had 0-g/L detrital input in March 2002.

Adult Trapping

A CO₂ gas/light trap (Clarke Engineering Technologies, Inc., Roselle, IL) was placed at each of the areas with breeding containers as well as at two additional small open sites (along cleared tracks through the forest), and at three additional sites within the forest, to total four open and four forest traps. Each trap was at least 40 m away from its nearest neighbor. Adult trapping occurred over 3 consecutive nights from January 28–30, 2002. The trapping was conducted 1–3 days prior to the start of immature sampling to determine adult habitat preferences while avoiding effects on oviposition and hence pupal productivity (see below). Each trap was activated before dusk (~16:30 hours) and run until after dawn (~8:30 hours). This time includes the most common biting period for New Zealand's mosquitoes (Belkin, 1968; Lee et al., 1982–1989), and was during the period of no access to the reserve. No data were recorded from one forested and one open trap on January 28 and 30, respectively, due to trap malfunctions. The relatively high trap density (eight traps within ~4000 m²) aimed to determine the relative habitat preferences of resting adult mosquitoes and relate our container samples to adult mosquito species' abundance.

Sampling Immatures

Sampling immatures started 2 weeks after the containers had been placed in the field and was conducted weekly over summer and early autumn (January 31–April 4, 2002). Sampling was carried out using standard dipping techniques (Russell, 1993). One liter of water (approx-

mately 25% of each container) was sampled from each container by dipping a 500-ml dipper twice. Each liter of water was poured back into its respective container through a 0.2-mm mesh. The immatures that were strained in the mesh were then placed in a container of approximately 30% ethanol and brought back to the laboratory where they were preserved in 70% ethanol for subsequent identification and counting. The dipper and mesh strainer were thoroughly rinsed with clean water before sampling the next container. Throughout the experimental period, much of the water in the containers of the 500-g/L treatment had been soaked-up by the high manure content, resulting in a mainly thick muddy base with puddles of surface water. When sampling these containers, as much water as possible (200–400 ml) was sampled from the surface using four to five dips.

All immature mosquitoes from each container were sorted and identified. 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. Pupae could not be keyed. Total mosquito productivity was estimated as the number of immatures that had reached the pupal stage and is called “pupal productivity” henceforth for clarity. Sampling is likely to have relatively minor impacts on mosquito population dynamics given that the study is conducted during the time of the season with high adult (oviposition) activity.

Statistical Analyses

Means of total immature, pupal, and adult abundance were compared using repeated measures analysis of variance (ANOVA) with corrections being made for multiple comparisons using the Holmes factorial method (Zar, 1999). Analysis of immature data had fixed factors of detrital load and shade treatment; analysis of adult data had the fixed factor of habitat type. Means and standard errors are reported throughout; all tests were two-tailed, and significance was assigned at the 5% level. Immature and adult data were log transformed ($Y' = \log Y + 1$) and larval data were collapsed into three equal time periods (early, middle, and late), which were the sum of three sample occasions, to help normalize the data prior to analysis. The residuals were examined for normality and homogeneity using histograms and probability plots. Additional frequency data were analysed using 2×2 contingency tables with Yates correction for continuity (Zar, 1999).

Validating the Immature Sampling Method

The immature sampling method was validated to check for bias towards collecting either *Cx. pervigilans* or *Oc. notoscriptus*. A plastic container was filled with water in the laboratory and 25 field-collected larvae of each species were added. Twelve samples were then taken from the containers using the above dipping method. Each sample was returned to the container before taking the next sample to not deplete immature numbers. Ten-minute breaks were taken between samples to allow immatures to resume regular behavior. The mean number of each species collected over all 12 samples was then compared using a paired *t*-test.

RESULTS

The two most common container-breeding mosquito species in New Zealand, the native *Culex pervigilans* and the introduced *Ochlerotatus notoscriptus*, were recorded from the experimental containers. *Culex pervigilans* was the most common species, constituting 98.9% ($n = 2163$) of total third and fourth instar larvae collected (*Oc. notoscriptus*, $n = 24$). Of the first and second instar larvae, 99.7% ($n = 14,990$) were *Culex* spp. and 0.3% ($n = 44$) were *Ochlerotatus* spp. Since *Cx. pervigilans* and *Oc. 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 *Cx. pervigilans* or *Oc. notoscriptus*.

Laboratory tests showed that the dipping method did not equally sample the two species, with significantly higher numbers of *Cx. pervigilans* (6.5 ± 0.7) collected compared to *Oc. notoscriptus* (2.6 ± 0.6) ($t_{0.05,11} = -3.99$, $P < 0.01$). Although *Cx. pervigilans* is nearly three times as likely to be sampled, this sample bias is not sufficient to account for the overwhelming dominance of *Cx. pervigilans* in all treatments in the field.

Total Immature Mosquito Abundance

Mean total immature abundances in different treatments are given in Figure 1. It shows that mosquitoes colonized open containers with 0.5- and 5-g/L detrital loads more rapidly and at higher numbers than other treatments. No immatures were sampled from the containers with 500 g/L detrital load at any time over the experiment. To allow statistical analysis of the data, we therefore eliminated this detrital treatment from the ANOVA model because it had no within-data variance. While the mean immature abun-

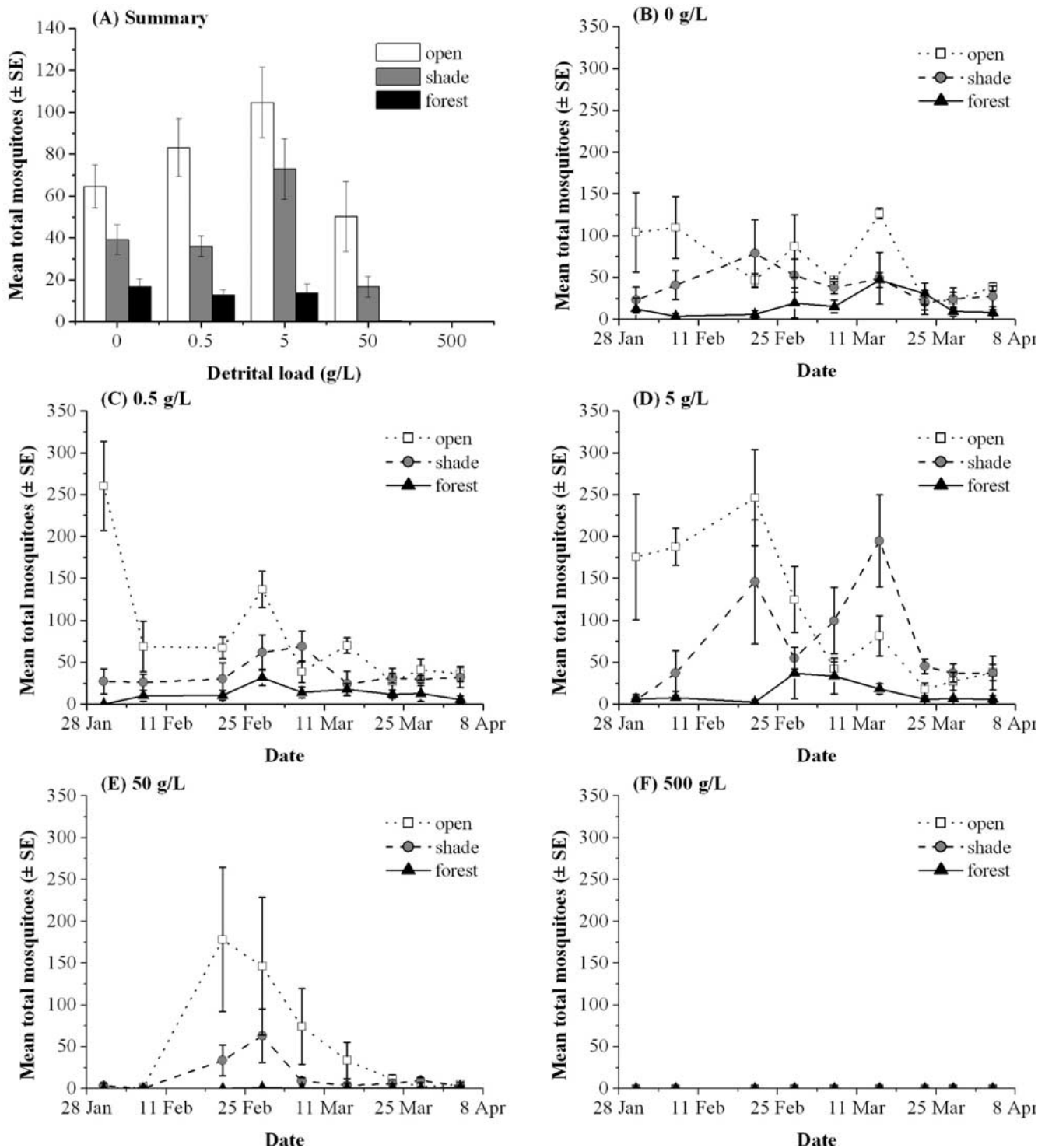


Figure 1. Mean total immature mosquito abundance in containers under different shade treatments and with different levels of detrital input in Nga Manu Nature Reserve from January–April 2002; $n = 4$ for each treatment, error bars are 1 SE. **A:** Summary; **B:** 0 g/L; **C:** 0.5 g/L; **D:** 5 g/L; **E:** 50 g/L; **F:** 500 g/L.

dance was, on average, low at the 50-g/L detrital level across the three shade treatments, mean immature abundance steadily increased with detrital load in open and artificially shaded containers in the deforested patches over the 0–5-g/

L range compared to remaining relatively low and constant in containers under the forest canopy. Despite this pattern, the interaction between detrital load and shade treatment was not significant (Table 1). There was, however, a sig-

Table 1. Effects of Shade Treatment and Detrital Load on Total Immature Mosquito Abundance and Pupal Productivity: Results from Two-way Repeated Measures Analysis of Variance

Factor	Effect		Error		F-value	P-value
	df	MS	df	MS		
Total immature mosquito abundance						
Shade	2	14.570	36	0.463	31.498	<0.001*
Detritus	3	5.012	36	0.463	10.836	<0.001*
Date	2	1.538	72	0.206	7.457	0.001*
Shade × detritus	6	0.592	36	0.463	1.280	0.291
Shade × date	4	1.876	72	0.206	9.093	<0.001*
Detritus × date	6	0.086	72	0.206	0.417	0.865
Shade × detritus × date	12	0.175	72	0.206	0.847	0.603
Pupal productivity						
Shade	2	1.825	36	0.153	11.929	<0.001*
Detritus	3	3.096	36	0.153	20.244	<0.001*
Date	2	0.835	72	0.122	6.864	0.002*
Shade × detritus	6	0.816	36	0.153	5.338	0.001*
Shade × date	4	0.160	72	0.122	1.319	0.271
Detritus × date	6	0.146	72	0.122	1.198	0.317
Shade × detritus × date	12	0.139	72	0.122	1.145	0.339

df, degrees of freedom; MS, mean squared values.

*Significant.

nificant main effect of detrital load and shade treatment (Table 1). Abundance at the 50-g/L detrital level was significantly lower than all the other levels tested ($P < 0.05$), while mean densities in the 0-, 0.5-, and 5-g/L treatments were not significantly different from each other ($P = 1.00$). Multiple comparisons of means indicated that open and artificially shaded containers had significantly higher numbers of immatures than forested containers ($P < 0.01$), while the open and shaded containers were not significantly different from each other. A higher maximum water temperature was experienced by the open water container with the temperature probe over the month of March (37°C), compared to the artificially shaded container (28°C) which, in turn, had a higher temperature than the forested container (20°C), suggesting that all the open containers in this study were likely to experience greater insolation.

Immature abundance did vary considerably over the course of the experiment, resulting in a significant interaction between shade treatment and time (Table 1). Open containers had significantly more immature mosquitoes in the early part of the experiment compared to the last part ($P < 0.01$), while forested containers had significantly lower numbers of immature mosquitoes early in the experiment

compared to the middle and last parts ($P < 0.01$). Immature mosquito abundance did not vary across time in shaded containers ($P > 0.10$).

Since *Oc. notoscriptus* constituted 1.1 and 0.3% of total late and early instar larvae, respectively, removing them from the analysis did not affect the conclusions of the ANOVA analysis (data not shown). When considering *Oc. notoscriptus* larvae separately, we found that the species had a strong preference for forested and artificially shaded containers with 84% ($n = 57$) and 15% ($n = 10$) of individuals collected from these treatments, respectively. Only one individual was found in an open container.

Pupal Productivity

Estimated mean pupal productivity was highest in open containers with 5- and 50-g/L detrital loads (Fig. 2). There was a significant interaction between detrital load and shade treatment (Table 1). Pupal productivity showed a similar trend to total immature abundance in containers situated under forest canopy, remaining relatively low and constant over the 0–5-g/L detrital range with zero productivity at the 50-g/L level ($P > 0.50$ for differences

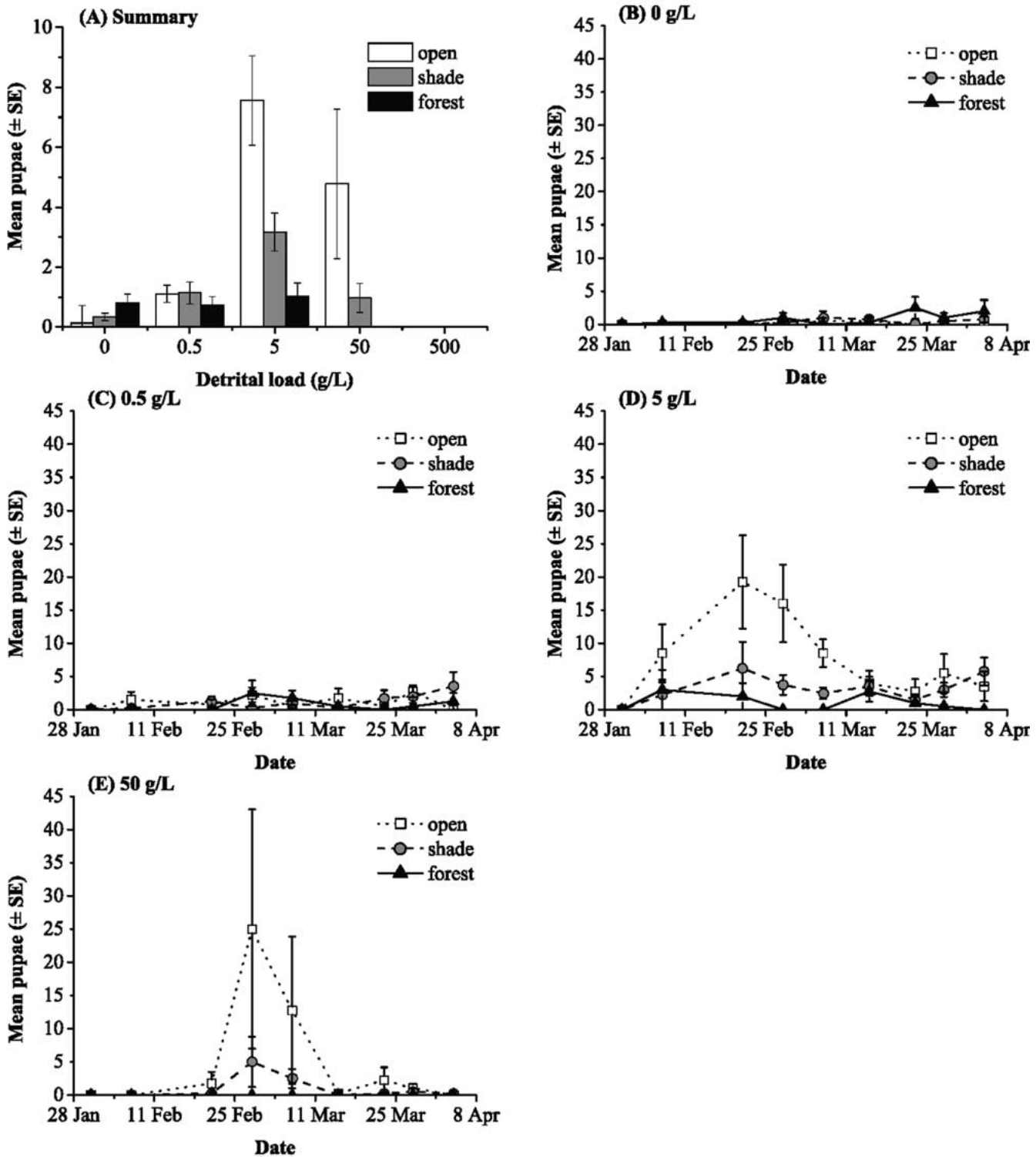


Figure 2. Mean pupal productivity in containers under different shade treatments and with different levels of detrital input in Nga Manu Nature Reserve from January–April 2002. No pupae were observed in the 500-g/L treatment; $n = 4$ for each treatment, error bars are 1 SE. **A:** Summary; **B:** 0 g/L; **C:** 0.5 g/L; **D:** 5 g/L; **E:** 50 g/L.

between detrital load across the forest treatment). However, pupal productivity was significantly higher in open containers with 5 g/L compared to all other treatments ($P <$

0.05). Pupal productivity was also higher in artificially shaded containers with 5 g/L compared to artificially shaded containers with 0 and 50 g/L, and in containers under

forest canopy with 0, 0.5, and 50 g/L ($P < 0.05$). Open containers with 50 g/L sometimes had very high numbers of pupae, and one 50 g/L replicate yielded the two most productive samples with 78 and 46 individuals. The number of pupae in open containers with 5- and 50-g/L detrital loads peaked in the third and fourth sample periods, respectively (36 and 43 days after the start of the experiment), but there was no significant interaction between time and detrital load and/or shade treatment (Table 1). There was a significant time effect (Table 1), with pupal productivity being significantly higher in the middle part of the experiment compared to the early part ($P < 0.01$).

Adult Mosquito Abundance

A total of 804 adult female mosquitoes were collected from the adult traps over the 3 trapping nights, of which 731 were in sufficiently good condition for identification, and numbers of each species are illustrated in Figure 3. *Culex pervigilans* and *Oc. notoscriptus*, as well as the ground-pool breeders *Coquillettidia iracunda* (Walker) and *Ochlerotatus antipodeus* Edwards (Belkin, 1968), were collected. *Culex pervigilans* made up nearly three-quarters of all females and totalled nearly nine times more than *Oc. notoscriptus* (Fig. 3).

Overall, nearly three times as many adult mosquitoes were caught in the forested areas ($n = 600$) as in the open areas ($n = 204$). Of the three areas with breeding containers, the forested area had four to five times as many mosquitoes as the two open areas (116.5 ± 5.5 vs. 26.0 ± 1.5 and 21.3 ± 5.7). Adult *Oc. notoscriptus* appeared to favor forested sites more than did *Cx. pervigilans* with nearly six times as many *Oc. notoscriptus* females being caught in forested areas compared to open areas, as opposed to only three times as many for *Cx. pervigilans* (Fig. 3). However, contingency table analysis revealed that there was no significant difference in species' preference to site type ($\chi^2_{0.05,1} = 3.13$, $P > 0.05$). There was also no significant difference in the total number of mosquitoes ($F_{1,4} = 1.473$, $P = 0.292$), number of *Cx. pervigilans* ($F_{1,4} = 3.516$, $P = 0.134$), and the number of *Oc. notoscriptus* ($F_{1,4} = 1.229$, $P = 0.330$) between forested and open sites. The lack of statistical significance in this analysis was likely to be due to high variation in the catches over a limited number of nights sampled.

DISCUSSION

The results of this study, using experimentally manipulated container habitats, found that changes to the type of shade

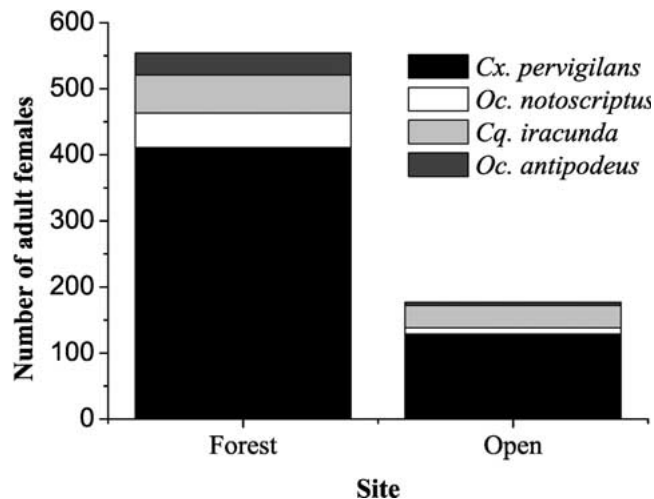


Figure 3. Numbers of adult female mosquitoes (from identifiable specimens) of four species collected from four sites in forest and open habitat in Nga Manu Nature Reserve over 3 trapping nights from January 28–30, 2002.

and detrital input of aquatic habitats resulted in changes to the resident population dynamics of the native mosquito species *Cx. pervigilans*. These results, on a generalist species in a temperate climate, support previous findings of laboratory studies (e.g., Fish and Carpenter, 1982; Carpenter, 1983; Chadee, 1993) and tropical/subtropical field studies on other species (Becker, 1995; Beehler and Mulla, 1995; Tun-Lin et al., 2000) that shade and nutrient level have central roles in determining aquatic immature mosquito dynamics.

Detritus from livestock waste products provides nutrients to immature mosquitoes mainly via increased microbial biomass (Carpenter, 1983), while insolation from decreased shade increases endothermic growth and promotes further microbial growth through greater detrital decomposition (Wetzel et al., 1995; Clements, 2000). Our results showed that *Cx. pervigilans* colonized open and artificially shaded containers with low-to-medium detrital loads more quickly and in higher numbers than containers with higher loads under forest canopy. Higher immature mosquito abundance in these containers was probably due either to the influence of shade and nutrient level on female ovipositional preferences or mortality factors influencing the survival of eggs and larvae. Oviposition preference is a life-history trait under strong selective pressure, and a number of studies on other species have shown that water chemistry and temperature appear to be important cues (Clements, 2000). Adult females oviposited in the deforested patches despite being higher in abundance in forested

areas around the breeding containers, suggesting adult females were choosing open and artificially shaded containers based on their higher insolation. It is less clear whether higher abundances in low-to-medium nutrient containers were due to this nutrient ranges' influence on female choice or immature survival.

The results from this experiment showed that open containers with medium-to-high detrital loads had higher pupal productivity, which peaked midway through the experimental period as larvae from eggs from colonizing adults earlier in the experiment presumably matured. These data suggest that a relatively higher proportion of larvae in these containers survived through to pupae because of extensive resident microbial communities to feed from, and higher endothermic growth due to the interlinked mechanisms of nutrient addition and increased insolation. These results agree with findings from field and laboratory studies on other mosquito species (e.g., Carpenter, 1983; Walker et al., 1991; Beehler and Mulla, 1995; Tun-Lin et al., 2000; Kaufman et al., 2002). Although containers with ultra-high detrital loads probably had greater microbial activity, the lack of immatures from them may have been because their extreme organic enrichment was toxic to eggs and immatures, and/or repelled adult females. Another explanation may be because of much lower quantities of water sampled from these containers (200–400 ml) and the much thicker consistency of the water, making filter feeding more difficult.

The native *Cx. pervigilans* was the overwhelmingly dominant mosquito species in the experimental containers across all treatments. The only other species recorded in the containers, the exotic *Oc. notoscriptus*, was in small numbers and restricted almost entirely to containers under the forest canopy where there were significantly lower numbers of *Cx. pervigilans*. The absence of *Oc. notoscriptus*, especially from open habitat, may be because the more ubiquitous native competitively excluded it. *Culex pervigilans* is usually cited as New Zealand's most common mosquito species, often utilizing every larval habitat type in very high numbers (Graham, 1939; Belkin, 1968; Laird, 1995). *Culex pervigilans* has also been historically identified as a mosquito of open swampland, and is known to invade clearings in large swamps (Ross et al., 1964). *Ochlerotatus notoscriptus* is New Zealand's second most common species, but it appears to prefer habitats that are protected from direct sunlight and was only rarely found in open containers in this study, as well as previous studies (Lee et al., 1984; Laird, 1990, 1995). *Ochlerotatus notoscriptus* is also more common in the more northern, warmer parts of NZ, and its

spread southward has been largely confined to farming areas and urban settlements (Belkin, 1968; Laird and Easton, 1994). The precise mechanisms, whether physiological, behavioral, or ecological, that limit the abundance of *Oc. notoscriptus* in open habitats where *Cx. pervigilans* is often abundant require further testing in controlled conditions.

In a broad context, the results of this study support the findings from previous studies that landscape change can increase the abundance of a potential disease-vector mosquito species (Ziperman, 1973; Tesh, 1994; Gratz, 1999; Martens et al., 2000; Patz et al., 2000). However, *Cx. pervigilans* (along with New Zealand's 11 other endemic species) is considered to presently pose a relatively low human disease risk compared to *Oc. notoscriptus* and other exotic species already established in the country, (e.g., *Cx. quinquefasciatus* Say and *Oc. camptorhynchus* [Thomson]), and those that threaten to invade from overseas (e.g., *Aedes albopictus* [Skuse] and *Aedes aegypti* [L.]).

Nevertheless, *Cx. pervigilans* is a vector of the avian Whataroa virus (Maguire et al., 1967; Miles, 1973), and is thought to be a vector for avian malaria, which has been shown to kill native birds and predispose them to predation in Hawaii (Holder et al., 1999). Furthermore, its competence as a vector of a number of human diseases, such as Ross River virus and dengue fever, remains unknown and its widespread distribution and year-round abundance in almost any habitat make it a species requiring further ecological investigation (Weinstein et al., 1997).

With respect to vector-borne disease, the greatest public health concern for New Zealand is the invasion and spread of exotic disease-vector mosquitoes (Weinstein et al., 1995, 1997). In this study, containers with ultra-high detrital loads (500 g/L) and those under forest canopy at high detrital loads (50 g/L) lacked any immature mosquitoes, including *Cx. pervigilans*, suggesting they are a potentially vacant niches for new exotic species. This result is of local public health concern since the container-breeding mosquito species *Cx. quinquefasciatus*, a laboratory vector of Murray Valley encephalitis virus and a suggested carrier of Ross River virus (McLean, 1953; Lindsay et al., 1996), has a strong preference for highly polluted water (Lee et al., 1989), and is already well established in New Zealand (Laird, 1988, 1995). This species is, so far, limited to mostly northern parts of New Zealand (which probably explains why it was not recorded in our experimental containers or adult traps) but appears to be spreading southward by utilizing artificial containers in agricultural environments, such as black used tire casings (Laird, 1990).

The majority of potential exotic invaders are from warmer climes than New Zealand, and are likely to be more limited by New Zealand temperatures or other environmental parameters than *Cx. pervigilans*. However, worldwide climate change (mainly global warming and intermittent temperature oscillations) may increase the risk of major exotic disease-vector species, particularly the cold-hardy *Ae. albopictus* and *Oc. japonicus* (Theobald). These species have threatened to invade New Zealand in used tires and establish in the northern part of the country (Laird and Easton, 1994; Weinstein et al., 1997).

The public health threat from exotic disease-vector species in New Zealand is likely to be aided by the fact that the local human population is nonimmune and susceptible, knowing little about mosquito disease and anti-mosquito measures to minimize the risk of infection, and there are limited diagnostic services for these mosquito-borne diseases which could result in a delay in recognizing an outbreak (Weinstein et al., 1995). Furthermore, increasing international travel and commerce to New Zealand are likely to increase the virus pool available to potential native and exotic disease-vector species.

The effects of deforestation, agriculture, and the introduction of exotic species on mosquito populations are likely to be interactive and complex. The processes involved, including the changes to nutrient levels and insolation of aquatic breeding habitats, are becoming better understood with experimental (primarily laboratory controlled) studies. In the meantime, deforestation and ensuing changes in landscape, such as agriculture, continue to coincide with increases in morbidity and mortality from mosquito-borne disease worldwide. Using a manipulative experimental approach in the field, this study has shown that a common generalist mosquito species can rapidly invade and utilize container habitats in a modified temperate environment. Results from this study and field surveys around the world (Gratz, 1999; Martens et al., 2000; Patz et al., 2000) suggest that there is greater risk from mosquito-borne diseases in modified environments and that ecosystem integrity may thus protect against arboviral introduction and spread (Parkes and Panelli, 2001).

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