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A growing degree-day model for determination of *Fasciola hepatica* infection risk in New Zealand with future predictions using climate change models

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Highlights

- A growing degree-day model is able to predict risk of fasciolosis in New Zealand
- No change in risk detected over the period 1972-2012 although varied year to year
- An increase in risk predicted by 2040 and 2090 but varied geographically
- The risk of fasciolosis in New Zealand is currently underestimated
- This risk will get more severe with Climate Change

Abstract

Infections of ruminants with *Fasciola hepatica* are considered to be of regional importance within New Zealand but there is very little recent information on its prevalence or severity other than anecdotal reports. Generally they are considered to be of secondary importance compared to gastrointestinal nematode infections. Utilizing data from Virtual Climate Stations (n = 11491) distributed on a 5 km grid around New Zealand a growing degree-day model was used to describe the risk of infection with liver fluke from 1972-2012 and then to apply the predictions to estimate the risk of fluke infections within New Zealand for the years 2040 and 2090. The growing degree-day model was validated against the most recent survey of infection within New Zealand in 1984. A strong positive linear relationship for 1984 between *F. hepatica* prevalence in lambs and infection risk ($p<0.001$; $R^2 = 0.71$) was found indicating the model was effective for New Zealand. A linear regression for risk values from 14 regions in New Zealand for 1972-2012 did not show any discernible change in risk of infection over this time period ($p>0.05$). Post-hoc comparisons indicate the risk in Westland was found to be substantially higher ($p<0.05$) than all other regions with Northland ranked second highest. Notable predicted changes in *F. hepatica* infection risk in 2040 and 2090 were detected although they did vary between different climate change scenarios. The highest average percentage changes in infection risk were found in regions with low initial risk values such as Canterbury and Otago; in these regions 2090 infection risk is expected to rise by an average of 186% and 184%, respectively. Despite the already high levels of infection risk in Westland, values are expected to rise by a further 76% by 2090. The model does show some areas with little change with Taranaki predicted to experience only very minor increases in infection risk with average 2040 and 2090 predicted changes of 0% and 29%, respectively. Overall, these results suggest the significance of *F. hepatica* in New Zealand farming systems is probably underestimated and that this risk will generally increase with global warming following climate change.

KeyWords: *Fasciola hepatica*, climate change, growing degree-day model, New Zealand.

Introduction

In New Zealand clinical disease is only occasionally observed in *Fasciola hepatica* infections in ruminants. Reductions in feed efficiency, growth and fertility resulting from *F. hepatica* parasitism indirectly affect the economic performance of ruminant production systems. In addition, direct losses arise from increased rates of liver condemnation at slaughter (Kaplan, 2001). Fasciolosis is a worldwide problem with an estimated total cost of bovine fasciolosis in excess of US$3billion (Spithill et al 1999). A number of recent studies have demonstrated the economic cost to cattle and sheep in Europe (Schweizer et al 2005; Charlier et al., 2007) and Australia (Piedrafita et al., 2010).

Several environmental factors impact the development of *F. hepatica*. The presence of water, the availability of lymnaeid snails as intermediate hosts and temperatures exceeding 10 °C are all required for the free-living stages of the *F. hepatica* life cycle to be completed (Soulsby, 1982). There are two suitable intermediate hosts present in New Zealand, *Lymnaea (Austropeplea) tomentosa* and *Pseudosuccinea* (*Lymnaea*) *columella*. The former is an indigenous species (Dell, 1956) with a somewhat restricted geographical distribution whilst the latter was unknowingly introduced into New Zealand at least as early as the 1940s (Pullan 1969; Pullan et al., 1972). *P. columella* has subsequently established itself as the most clinically relevant species being better adapted to New Zealand temperatures and more reproductively active (Harris and Charleston, 1977; 1980). *P. columella* is now readily found over the summer months throughout the whole of the North Island in permanently wet gullies and in several parts of the South Island although there have been no recent distribution studies in New Zealand.

A number of modelling strategies have been developed to predict the occurrence of *F. hepatica* (Ollerenshaw and Rowlands, 1959; Ross, 1970; Malone et al., 1987; Fuentes and Malone, 1999; McCann et al., 2010). The basis of some approaches is to use a form of a Growing Degree-Day (GDD) model to predict the development and availability of infective metacercariae. To date, all non-parasitic stages have been broadly included into the one model and none have considered snail availability separately. In the present study the model developed by Malone et al (1998) was investigated for its usefulness in forecasting *F. hepatica* infection risk within New Zealand. This model calculates GDDs above a minimum temperature of 10 °C and uses rainfall and evapotranspiration data as well as the number of days in each month where >1 mm rain has fallen (wet-days/month). The output of this model is a numerical value which indicates fluke risk and is broadly characterised into 4 bands ranging from “no risk” to “high risk” (Yilma and Malone, 1998). The occurrence of optimal climatic conditions to allow for rapid development from egg to encysted metacercaria logically confers a high risk of infection.

Studies pertaining to the epidemiology of *F. hepatica* in New Zealand are limited. A 1984 abattoir survey of sheep and cattle (Charleston et al. 1990) investigated the prevalence of fluke infection or fluke-associated liver lesions within the 14 regions of New Zealand. The most useful data was that obtained for lambs and indicated the overall prevalence in New Zealand was 4.4%, being higher in the North Island (7.5%) compared with the South Island (1.1%). The regional prevalence of *F. hepatica* infection was generally low although marked variation between regions clearly showed that there was a correlation with differing climatic conditions. Additionally, information on the seasonal distribution of *F. hepatica* infections was also provided which showed that affected lamb livers first appeared in February (late summer) with a gradual increase in prevalence through to July (mid-winter). These results were in agreement with the December-January onset of the transmission period observed in other epidemiological studies performed in the Hawkes Bay (Pullan and Mansfield, 1972) and Manawatu regions (Harris and Charleston, 1976).

New Zealand's National Institute of Water and Atmospheric Research (NIWA) have recently developed a series of Virtual Climate Stations (VCS). These are distributed on a 5 km^2 grid across the country. Each VCS provides estimates of weather data which has been interpolated from actual weather stations (Mackintosh 2001; Tait et al., 2006; Tait et al., 2012) and this has been retrospectively estimated for each VCS back to 1972.

The impact of climate change has been the subject of considerable debate in New Zealand and internationally for many years. To quantify the effects of climate change a suite of global climate models (GCMs) have been adapted for New Zealand by NIWA (Mullan et al., 2008). To represent the data from GCMs into a regional context, NIWA have developed downscaling methods to produce rainfall and potential evapotranspiration (PET) data relevant to New Zealand topography (Clark et al. 2011). This allows translation of the global scale portrayed in GCMs into a more local context. The GCMs operate within narrative storylines called emission scenarios. These scenarios describe the demographic, economic and technological forces that impact the future of greenhouse gas emission. The present study uses predictions within the A1B, A2 and B1 scenarios as these have been the focus to date for predictions of climate change for New Zealand (Clark et al., 2011). According to the Special Report on Emission Scenarios (Nakicenovic and Swart, 2000), A1B describes a future world where there is rapid economic growth, a mid-century peak followed by a subsequent decline of global population all accompanied by rapid development of new technologies. It indicates that the technological emphasis is balanced between fossil and non-fossil sources. The A2 storyline describes a world reliant on preservation of local governance, the result being regional rather than global economic development characterised by slow, fragmented growth and technological change; in this storyline there is a continuously increasing population. The B1 storyline has an underlying theme of unity, sustainability and environmental consciousness; the global population follows the same pattern observed in A1B.

The aim of this study was to assess the past and current geographical risk of *F. hepatica* infection in New Zealand ruminants. The infection risk was also extrapolated to 2040 and 2090 based on climate change model scenarios to assess any future risk changes.

Materials and Methods

VCS Data

Data were provided by NIWA in a daily format for the period 1972-2012 for each separate VCS (n = 11491). The only required parameter that was not explicitly reported was mean temperature and this was approximated by averaging the maximum and minimum temperature for each day. Data were aggregated to the level of calendar month and the number of wet-days (>1 mm of rain) per month calculated for each VCS.

Model

The calculation of *F. hepatica* infection risk was carried out with a model developed by Malone et al. (1998) for determination of fluke risk in East Africa. This model takes into consideration the primary climatic parameters that impact the *F. hepatica* life cycle.

$$[GDD \times \text{days in month, if } (R-(PET \times 0.8)) > 0] + [(GDD \times WD)\ X\ ((R - PET)/25), \text{ if } R - PET > 0]$$

Where:

GDD = (average monthly mean temperature) – 10
R = total monthly rainfall (expressed as mm/month)
PET = potential evapotranspiration (mm/month)
WD = the number of wet-days per month with > 1 mm rain

Further work described by Yilma and Malone (1998) provided indices to allow for classification of calculated risk scores.

No risk	≤ 600
Low risk	601 – 1500
Moderate risk	1501 – 3000
High risk	> 3000

The model of Malone et al. (1998) was modified to make it more suitable for New Zealand conditions. To compensate for the fundamental differences from an east African climate, average monthly mean temperature was utilised in preference to annual temperature so as to better reflect a seasonal climate. The high resolution of climate data provided on a 5 km^2 grid network spanning the entirety of the country also allowed for refinement of the model. A GDD multiplier value of 6 used in the original model represents the average number of rainy days per month in east Africa where greater than 1 mm of rain fell. As rainfall data was available on a nationwide 5 km^2 scale, the adapted model used site-specific GDD multipliers rather than a countrywide generalisation. For past data the actual number of wet days was calculated using daily rainfall values. However, the forecast climate change data was only available on a monthly basis. Therefore, for an estimation of the number of future wet days/month to be made, a mean of the previous 41 years (1972-2012) was used to approximate the mean number of wet days for each VCS. To allow for consistency and for ease of automating the calculation of risk scores, a 340 day year was used throughout this study (28 day months) which consequently may result in a slight underestimation of the yearly risk value.

Model validation

The 1984 survey data (Charleston et al., 1990) provided data on *Fasciola* prevalence within lambs on a regional basis (n=14) around New Zealand. For validation of the adapted Malone et al. (1998) model to be performed similar cordoning of the VCS risk values was required. The survey data most appropriate for validation of the model was that recorded for lambs. The prevalence of liver fluke or associated liver lesions within regions was considered the response variable while the 1984 risk values acted as the explanatory variable. From this, a linear regression between the regional prevalence and regional *F. hepatica* infection risk was developed. Additional data exploration using polynomials, a generalised additive model and logistic transformation was also conducted. For these analyses only 13 regions were used as the original survey did not provide a recorded prevalence for the mostly urban Auckland locality.

Creation of national risk maps

The climate data and correlated risk values were calculated and geographically contextualised using the software package R (R Development Core Team, 2008). The R packages used in the present study were RODBC (Ripley and Lapsley, 2014), raster (Hijmans et al., 2014), maptools (Bivand et al., 2014a), plotKML (Hengl et al., 2014), sp (Pebesma and Bivand, 2005) and rgdal (Bivand et al., 2014b). The calculated *F. hepatica* risk value for each 5 km^2 VCS was an attribute for each VCS location. With the data arranged in this format a graphical representation of *F. hepatica* infection risk was created by assigning a colour gradient to the calculated infection risk values.

Analysis of past data

The availability of 41 years of past climate data allowed statistical analysis to be undertaken to identify any regional and chronological trends. As a means of determining any notable changes in *F. hepatica* infection risk for the period 1972-2012 a linear regression approach was used. Risk was aggregated within a region and the median value together with the 25th and 75th percentile was subsequently calculated (Table 1). The regional boundaries used were those current in 1984 to enable comparison with survey data from that time. Fluke risk for each year from 1972-2012 was considered the outcome with any change in infection risk levels being explained by the progression of time by year. To identify regional differences in mean infection risk over the 41 year period a Tukey honest significant difference (TukeyHSD) test with a confidence interval of 95% was carried out. The goal of the TukeyHSD test was to isolate which regions had significantly different ($p<0.05$) levels of infection risk relative to other regions. Statistical analyses used the software package R.

Climate change data

Future climate conditions were predicted using values obtained from NIWA (Mullan et al. 2008). The datasets contained predictions from 45 different GCMs across the three emission scenarios (A1B, A2 and B1) considered in a New Zealand context. Estimates were provided for 2040 and 2090 extrapolated from 1990 as the base year. PET data and temperature data were provided as the raw values that the 1990 value was expected to change by, whereas rainfall data was recorded as a percentage change from the 1990 base value. As the occurrence of one emission scenario discounts the possibility of the others occurring, values were produced and analysed for each. NIWA provided data for all 16 GCMs in the A1B scenario, 14 for A2 and 15 for B1. Within each of these 3 scenarios a frequency distribution of GCMs was created allowing the median and the 25th and 75th percentiles to be estimated.

Distribution of livestock within New Zealand

Data was obtained from Statistics New Zealand for the year 2014 by province. These areas are different from those used to calculate risk maps but still show the national distribution of stock density.

Results

Model validation

A strong positive linear relationship for 1984 between *F. hepatica* prevalence in lambs and infection risk ($p<0.001$; $R^2 = 0.71$) was found (Fig. 1). Three outliers were present: Northland, Bay of Plenty and Hawkes Bay. The deviance from the expected trend in the case of Northland and Bay of Plenty arose from high calculated risk levels without a corresponding rise in prevalence whereas the opposite was true for Hawkes Bay. Other models were investigated but provided no better fit to the data.

Modelled risk values

Past and future risk values were calculated for each VCS across the country (Fig. 2, Table 1). The national risk map for 1990 has been selected as it is the baseline year upon which the 50-year (2040) and 100-year (2090) climate change predictions have been made. Additional risk profiles for 1972-2012 are provided in the supplementary data.

Notable changes in *F. hepatica* infection risk in the 100-year climate change period were detected. The highest average (i.e. across all three emission scenarios) percentage changes in infection risk were found in regions with low initial risk values such as Canterbury and Otago; in these regions 2090 infection risk is expected to rise by an average of 186% and 184%, respectively. Despite the already high levels of infection risk in Westland, values are expected to rise by a further 76% by 2090. Curiously, Taranaki is predicted to experience very minor increases in infection risk with average 2040 and 2090 predicted changes of 0% and 29%, respectively.

A high risk of *F. hepatica* infection was consistently observed in particular regions of the country (Table 1) that had presumed ideal climate conditions.

Past data analysis

Since the annual *F. hepatica* infection risk for any one year was considered to be independent from the previous or following year, a linear regression for risk values from all 14 regions for 1972-2012 provided the most effective method for determining any trends in the past data. There was no discernible change in risk of infection over time ($p>0.05$) for the 41-years of past data.

There was a significant difference in risk between the 14 regions of New Zealand over this same period ($p<0.001$). Post-hoc comparisons indicate the risk in Westland was found to be substantially higher ($p<0.05$) than all other regions with Northland ranked second highest. Groupings of regional differences are summarised in Table 1.

Discussion

This study has shown that the existing GDD model utilised in East Africa and elsewhere is able to demonstrate the risk of fasciolosis within New Zealand when used with the VCS data that is now available. Having validated its ability to predict risk it was then possible to combine this GDD model with climate change predictions to assess that fasciolosis will become more important within New Zealand over the coming century. GDD models have been proven to be useful tools to describe many biological systems worldwide. Of particular relevance to animal and human health is the application of GDD models for parasitic or vector-borne diseases including cardiopulmonary dirofilariosis (Genchi et al., 2011), visceral leishmaniosis (Nieto et al., 2006), schistosomiosis (Yang et al., 2006) and the distribution of the tick *Ixodes scapularis* (Ogden et al., 2006) among others. The Malone et al., (1998) study provided the original GDD model used in this present study which has acted as the foundation upon which further refinement was undertaken. In itself this GDD model evolved from the earlier Ollerenshaw *Mt* index (Ollerenshaw and Rowlands, 1959) which is largely based around rainfall and availability of moisture. The high resolution of the VCS network in New Zealand allowed the Malone et al. (1998) model to be applied across this 5km grid network and resulted in a more sensitive and well-suited fit for New Zealand. Any deviances in the New Zealand climate from the East African climate that the model was originally developed for were compensated for via the model adaptations described in the methods.

Past survey data of the prevalence of fluke in lambs from Charleston (1990) acted as a means of verifying the accuracy with which calculated risk scores from the adapted Malone et al. (1998) model could explain *F. hepatica* prevalence in New Zealand. There is a strong indication that the model is effective in predicting the distribution of *F. hepatica* around New Zealand with the R^2 value in a linear model of 0.71. While validation was most adequately described by a linear model the three outliers of Hawkes Bay, Northland and Bay of Plenty represented anomalies in the prediction of *F. hepatica* distribution; these discrepancies can likely be biologically explained. The high prevalence and relatively low predicted risk encountered in Hawke's Bay may be a product of the distinctively drier climate experienced in this region, especially over the warmer summer months, when compared to the remainder of the North Island (Mackintosh 2001). Subsequently, the climate may appear unsuitable for *F. hepatica* development but low rainfall resulting in poor grass growth may force animals to graze closer to wetland areas where lymnaeid snails may reside, thus actually increasing fluke transmission (Ollerenshaw, 1966; Kenyon et al., 2009). A converse explanation may also apply to the low prevalence, high predicted risk regions of Northland and Bay of Plenty. The warm humid summers and mild winters experienced in the more northern regions of the North Island (Mackintosh 2001), although ideal for *F. hepatica* development, may indicate that grass growth is more even throughout the year and this higher availability of feed elsewhere could imply that lambs are less likely to graze areas that are wet enough to harbour lymnaeid snail species. Snails and fluke metacercariae, even though attached to vegetation or rocks, can also be washed away in periods of high rainfall which is experienced in this region from time to time (Rapsch et al., 2008).

Consideration of past *F. hepatica* infection risk provides an insight for regions of the country that may already require more substantial measures to control this parasite. However, definitive judgment of true infection risk cannot be made on the basis of this model alone as the relevance of the scale of the risk index described by Yilma and Malone (1998) may not apply directly to New Zealand. Differences in snail species and geography may warrant development of a novel New Zealand *F. hepatica* GDD model and further evaluation of the significance of risk values. Despite this, the adapted Malone et al. (1998) model used in the present study affords the opportunity to ascertain the current risk of infection for a location relative to the rest of New Zealand as well as the predicted change that may now develop from the current situation. To interpret this on a regional basis, it is clear that provinces such as Westland and Northland have historically had significantly elevated levels of *F. hepatica* infection risk in comparison to the rest of the country. After considering prevalence results from Charleston et al. (1990) that indicated lamb infection rates of up to 30% in some parts of New Zealand and the reliability of the adapted Malone et al. (1998) model in predicting these as high risk areas, it is justifiable to claim that the significance of *F. hepatica* in New Zealand farming systems is probably underestimated. Currently *F. hepatica* is considered a parasite of potential rather than established importance in New Zealand being known to occasionally cause clinical disease in cattle, sheep and deer (Charleston and McKenna, 2002). Studies summarising the subclinical effects on production have been extensive (Charleston, 1997) and given the intensity of risk in particular areas of the country there is evidence to suggest that the agricultural sector may be dealing with a wider scale problem than is currently believed. Fig. 3 illustrates the distribution of different livestock in New Zealand in 2014 and it is apparent that areas with a high predicted risk of liver fluke are also those where there is a higher density of cattle, both dairy and beef.

Analysis of the effects of future climate change has the same limitations encountered when considering current and past data. It is not yet possible to relate the relevance of Malone's risk index to New Zealand and hence a definitive verdict on the severity of *F. hepatica* infections over the next several decades cannot be easily predicted. However, regardless of the context of the calculated risk values, there is a near certain pattern of nationwide increases in *F. hepatica* infection risk (Fig. 2), especially for emission scenario A2 in 2090. Every region in New Zealand is shown to have elevated levels of average infection risk when the climatic parameters for 2040 and 2090 are run in the adapted Malone et al. (1998) model (Table 1); the one exception being Taranaki which returned an average increase of 0% by 2040. This provides a strong indication that regardless of the current role of *F. hepatica* in production losses in New Zealand farming systems, stricter diagnostic protocols and more intensive control measures will soon need to be developed and may already be required in some parts of the country such as Westland. A permutation of both changing climate and the likelihood that the importance of this parasite is probably already underestimated should be the foundation for further consideration of this parasite as a significant factor in future production losses.

Similar studies looking at the effects of climate change on *F. hepatica* infections have been undertaken elsewhere around the world. By comparison with New Zealand, a similar modelling exercise in the United Kingdom (UK) and the whole- of-Europe has demonstrated that the risk of infection in those locations has increased steadily over the past four decades (Fox et al.,2011; Caminade et al., 2015). Both studies used the Ollerenshaw *Mt* index which has a similar tiered categorization of the risk of disease to the Yilma and Malone (1998) index but has the advantage it was developed in the UK and can be directly interpreted for that country. Thus, not surprisingly, the predicted increase in the UK follows the general pattern shown for passive surveillance records. Similarly, the whole-of-Europe study found a steady increase over the last 40 years, particularly the last decade. The UK study also found the mean risk is predicted to get higher over the next 60 years but will show spatio-temporal variation in that western areas will generally have a higher risk and some eastern areas will have reduced risk. The whole-of-Europe study predicted that conditions would be favorable for the spread of fasciolosis into more northern areas of Europe. Within this general increase, the risk would decrease during the warmer dryer summer months but increase over the adjacent spring and autumn periods. However, the predictions varied depending on the climate change scenario with little change predicted if the lower emission scenario was considered. Mas-Coma et al. (2009) likewise found climatic variables to be the driving force behind increases in the impact of trematode-associated diseases and concluded that climate change will have pronounced population effects on these parasites. Thus all studies to date indicate a general trend of increasing risk of fasciolosis associated with climate change. Indeed, the strong epidemiological link between *F. hepatica* infections and climate anomalies warranted its addition to the list of diseases linked to variations in the El Niño Southern Oscillation (Magrin et al., 2007). All considerations of the effects of climate change cannot be considered solely on the basis of their direct impacts on *F. hepatica* development. Accompanying changes in farming systems (Rivington et al., 2007), animal production (Nardone et al., 2006) and anthelmintic resistance (Fairweather and Boray, 1999) will all similarly impact the role that *F. hepatica* will play in future New Zealand farming systems.

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Fig. 1. Linear model of the prevalence of fluke in lamb livers from the 1984 survey (Charleston et al. 1990) compared to the calculated risk values for different regions in New Zealand.

Fig. 2. The risk of infection with *Fasciola hepatica* for the base year 1990 and the median risk for 3 global climate models (A1B, A2 and B1) in 2040 and 2090.

Fig. 3. Map of New Zealand showing the location of different regions as used during the 1980s (see Table 1 for key to acronyms) and the density of different animal species by province in 2014.

Fig. 1

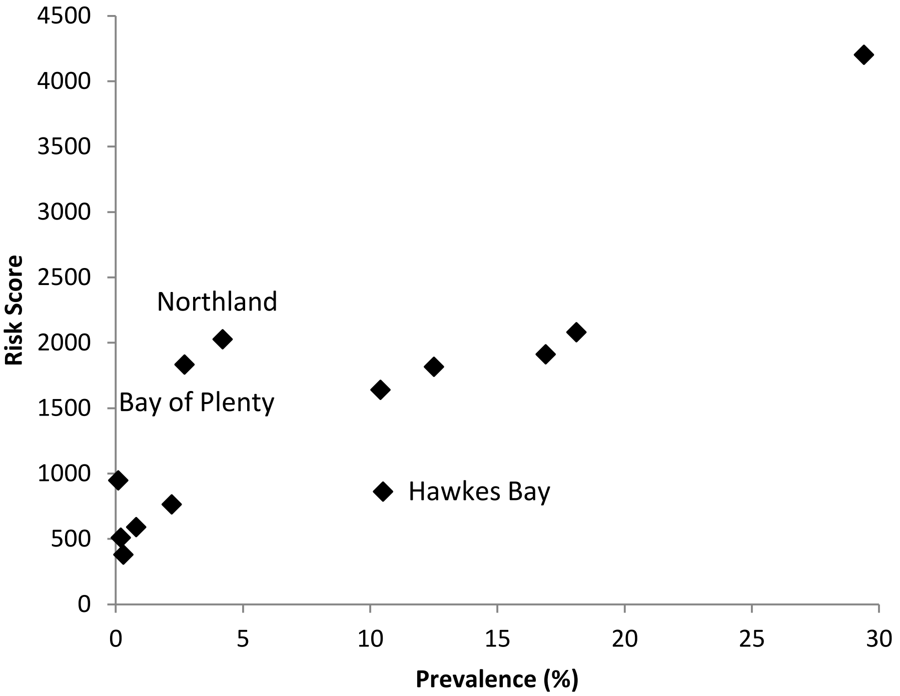
4500
4000
3500
3000
2500
2000
1500
1000
500
0
Risk Score
Northland
Bay of Plenty
Hawkes Bay
0
5
10
15
20
25
30
Prevalence (%)

Fig. 2.

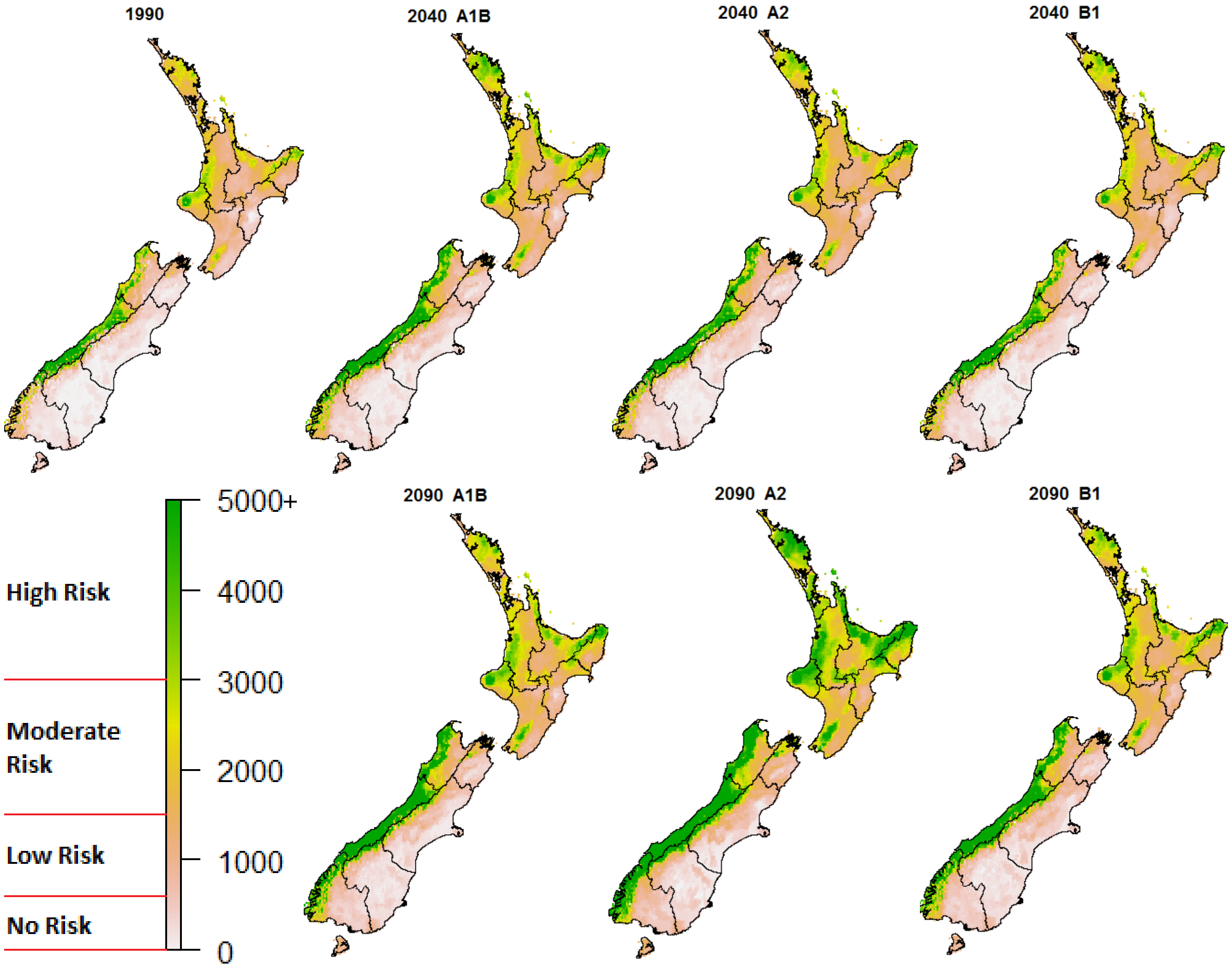
1990
2040 A1B
2040 A2
2040 B1
2090 A1B
2090 A2
2090 B1
High Risk
Moderate Risk
Low Risk
No Risk
5000+
4000
3000
2000
1000
0

Fig. 3

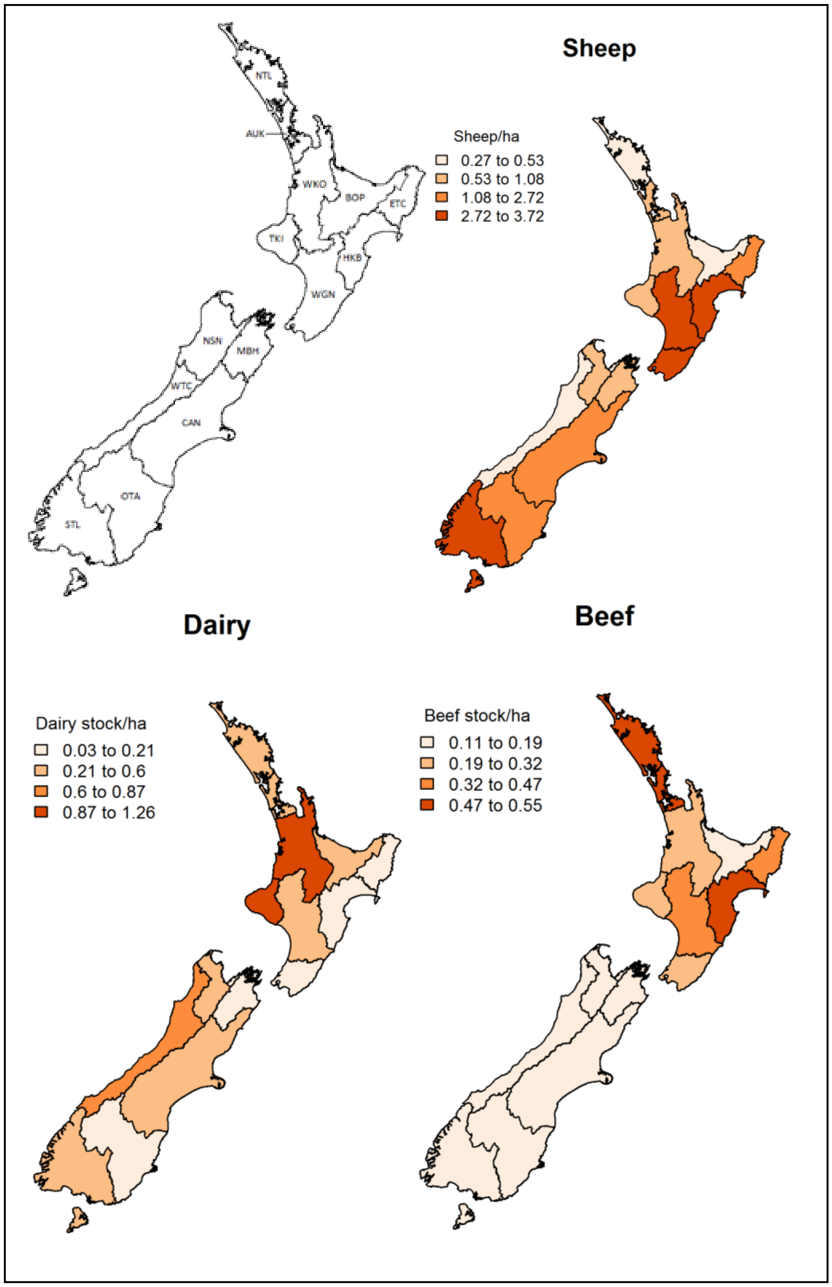
NTL
AUK
WKO
BOP
ETC
TKI
HKB
WGN
NSN
MBH
WTC
CAN
OTA
STL
Sheep
Sheep/ha
0.27 to 0.53
0.53 to 1.08
1.08 to 2.72
2.72 to 3.72
Dairy
Dairy stock/ha
0.03 to 0.21
0.21 to 0.6
0.6 to 0.87
0.87 to 1.26
Beef
Beef stock/ha
0.11 to 0.19
0.19 to 0.32
0.32 to 0.47
0.47 to 0.55

Table 1. Past and Future (greenhouse gas emission scenarios A1B, A2 and B1) *F. hepatica* infection risk with comparison to Charleston et al. (1990) survey data.

Region	1984 Survey: % Lambs Infected (±SD)	1984	1990	1972-2012 Median (25%, 75% quartiles)	2040 Median (25%, 75% quartiles)			2090 Median (25%, 75% quartiles)		
					A1B (n=16)	A2 (n=14)	B1 (n=15)	A1B (n=16)	A2 (n=14)	B1 (n=15)
Northland (NTL)	4.2(± 0.92)	2028	1911	2232 (1946, 2935) [b]	2531 (2235, 2799)	2494 (2155, 2634)	2238 (2150, 2569)	2864 (2325, 3274)	3125 (2622, 3493)	2381 (2179, 2661)
Auckland (AUK)	N/A[1]	1837	1854	1606 (1406, 2030) [c]	2263 (2025, 2446)	2147 (2011, 2271)	2003 (1891, 2274)	2564 (2303, 2852)	2765 (2504, 3008)	2171 (1989, 2371)
Waikato (WKO)	12.5(± 1.03)	1818	1676	1467 (1142, 1836) [c]	1973 (1769, 2186)	1854 (1707, 1979)	1758 (1561, 1909)	2553 (2282, 2854)	2696 (2555, 3074)	2142 (1826, 2214)
Bay of Plenty (BOP)	2.7(± 1.07)	1835	1545	1327 (902, 1713) [c]	1923 (1698, 2078)	1787 (1686, 1900)	1587 (1470, 1812)	2576 (2314, 2939)	2894 (2625, 3278)	1955 (1758, 2305)
East Coast (ETC)	10.4(± 0.93)	1642	1587	1587 (1040, 1991)	2062 (1856, 2418)	2049 (1828, 2205)	1802 (1678, 2119)	2821 (2495, 3421)	3206 (2664, 3724)	2194 (1973, 2608)
Hawkes Bay (HKB)	10.5(± 1.04)	864	842	926 (644, 1260) [d]	1184 (1004, 1348)	1130 (1042, 1307)	1040 (926, 1247)	1812 (1558, 2057)	1961 (1607, 2350)	1316 (1138, 1602)
Taranaki (TKI)	16.9(± 2.04)	1913	2524	1571 (1199, 1901) [c]	2660 (2445, 2968)	2545 (2303, 2683)	2360 (2191, 2547)	3422 (2992, 3762)	3527 (3374, 4078)	2838 (2467, 2959)
Wellington (WGN)	2.2(± 0.34)	765	1029	764 (561, 1023) [de]	1373 (1217, 1570)	1293 (1205, 1401)	1199 (1089, 1311)	1816 (1576, 2030)	1893 (1750, 2126)	1493 (1304, 1588)
Marlborough (MBH)	0.8(± 0.77)	592	457	454 (341, 558)[ef]	620 (537, 697)	573 (511, 620)	491 (468, 572)	974 (826, 1149)	1083 (965, 1222)	687 (643, 793)
Nelson (NSN)	18.1(± 3.05)	2082	1666	1744 (1352, 2032) [c]	2365 (2086, 2469)	2198 (2046, 2275)	1921 (1771, 2128)	3345 (2930, 3699)	3576 (3344, 4145)	2545 (2298, 2699)
Westland (WTC)	29.4(± 7.81)	4204	4353	3668 (3048, 4345)[a]	5743 (5115, 6088)	5218 (5159, 5672)	4798 (4347, 5308)	8098 (7084, 8243)	8610 (7997, 9801)	6249 (5649, 6583)
Canterbury (CAN)	0.2(± 0.13)	511	305	366 (251, 443)[f]	561 (449, 663)	507 (448, 542)	454 (407, 524)	947 (767, 1061)	1016 (912, 1153)	660 (578, 717)
Otago (OTA)	0.3(± 0.17)	380	237	249 (183, 362)[f]	430 (351, 485)	373 (347, 417)	340 (293, 384)	732 (583, 772)	781 (704, 899)	508 (438, 557)
Southland (STL)	0.1(± 0.14)	949	752	816 (577, 924) [de]	1206 (1045, 1305)	1061 (1018, 1199)	998 (834, 1092)	1935 (1632, 2084)	2252 (1893, 2410)	1419 (1194, 1562)
North Island	7.5(± 0.35)	1485	1485	1411 (1051, 1645)	1847 (1649, 2005)	1754 (1624, 1883)	1601 (1504, 1804)	2397 (2163, 2623)	2608 (2336, 2903)	1887 (1707, 2102)
South Island	1.1(± 0.15)	1125	953	952 (779, 1112)	1386 (1219, 1510)	1261 (1199, 1352)	1142 (1035, 1262)	2104 (1777, 2203)	2288 (2054, 2568)	1556 (1396, 1685)
New Zealand	4.4(± 0.2)	1279	1181	1138 (902, 1352)	1592 (1394, 1717)	1511 (1375, 1539)	1341 (1254, 1494)	2213 (1940, 2387)	2414 (2177, 2606)	1700 (1563, 1834)

[a- f] Regions not sharing a superscript had significantly different ($P<0.05$) infection risk means for the 1972-2012 period.

[1] Data not collected for Auckland in original survey