



Freshwater invasions: using historical data to analyse spread

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ABSTRACT

Aquatic invasive species cause deleterious environmental and economic impacts, and are rapidly spreading through ecosystems worldwide. Despite this, very few data sets exist that describe both the presence and the absence of invaders over long time periods. We have used Geographical Information Systems (GIS) to analyse time-series data describing the spread of the freshwater invasive New Zealand mudsnail, *Potamopyrgus antipodarum*, in Victoria, Australia, over 110 years. We have mapped the snail's spread, estimated the percentage of stream length invaded through time, calculated the functional form of the spread rate, and investigated the role that the two proposed vectors — fish stocking and angling — have had in this invasion. Since it was first found in 1895, *P. antipodarum* has expanded its range in Victoria and now occurs throughout much of the southern and central areas of the state. The north of the state is relatively less invaded than the south, with the division corresponding approximately to the presence of the Great Dividing Range. We show that the snail's range has been increasing at an approximately exponential rate and estimate that 20% of total Victorian stream length is currently invaded. We also show that using long-term data can change the outcome of analyses of the relationship between vectors of spread and invasion status of separate catchments. When our time-series data were aggregated through time, the total numbers of fish stocking events and angling activity were both correlated with invasion. However, when the time-series data were used and the number of fish stocking events calculated up until the date of invasion, no relationships with stocking were found. These results underline the role that time-series data, based on both presences and absences, have to play when investigating the spread of invasive species.

Keywords

Biological invasions, dispersal, GIS, New Zealand mudsnail, *Potamopyrgus antipodarum*, time-series, vectors.

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INTRODUCTION

Invasive species have profoundly affected the abundance and diversity of native biota (Williamson, 1996; Mack *et al.*, 2000) and many have inflicted large economic costs (Leung *et al.*, 2002; Pimentel *et al.*, 2005). Compared to terrestrial ecosystems, lakes and rivers have been proven particularly vulnerable to invasive alien species (Sala *et al.*, 2000). Intensive human uses of these systems mean that human vectors of dispersal, such as recreational boating and intercontinental shipping, have been important mechanisms for the introduction and subsequent spread of aquatic invaders. Natural linkages among streams and lakes, and the effects of water flow, have also been important routes for the dispersal of aquatic invaders (Lodge *et al.*, 1998). Hence, protecting aquatic ecosystems from the impacts of future invasions requires an understanding of the patterns and mechanisms of spread for previous invaders.

Geographical Information Systems (GIS) have been used to identify suitable habitat for species through the analysis of multiple landscape variables (Guisan & Zimmermann, 2000). GIS can also be used to provide estimates of the potential spread of invasive species (Boag *et al.*, 1998; Haltuch *et al.*, 2000). Data describing a species' distribution are usually only available as point occurrences and this format does not provide a straightforward estimate of total area affected by the invasion. Thus, an important area of GIS modelling that needs development is identification of the area invaded by a species through time. Such analyses would allow estimation of the functional form of the spread of the invader, which could then be related to rates of ecological processes and vector activity over time. This would lead to a better understanding of how and why a species has spread, and how that species, and others that share its vectors, could best be controlled in the future. Unfortunately, few long-term data sets are available that can be used to describe the spread of an invader. Data sets for

invasive species usually only contain information from snapshot surveys of distribution, and often only have information on where the species is present. Absence data are often not available, and snapshot surveys cannot be used to describe how the species has spread over time. Models built on presence-only data can give an indication of large-scale spread, but only for species that are reliably recorded, and only if lack of presence data can be taken as evidence of absence. In cases where this is unlikely to be true, absence data will assist in determining exactly how widespread the species is, whereas presence only data are likely to bias estimates of total area occupied to be too high because one occurrence in a system may force the assumption that all sites in that system are invaded.

Here we describe the spread of the freshwater invasive snail, *P. antipodarum*, in Victoria, Australia, over a 110-year period. We have assembled a comprehensive data set for the spread of *P. antipodarum* that incorporates both presence and absence data, as well as the associated date of sampling. Analysing the long-term data set with GIS, we have mapped the distribution of *P. antipodarum* for each of six time periods and estimated the corresponding invaded stream lengths. Despite the strengths of using a spatially explicit approach, such as GIS, to gain a visual representation of which areas are invaded, the estimates of the stream lengths invaded are heavily affected by the locations of the samples. Hence, we compared the results of the GIS method to an effort-weighted approach that takes both spatial and temporal variation in the data into account. This second approach used presence and absence data to determine the catch per unit effort (CPUE) for different time periods. CPUE in any region can be multiplied by the area of that region to give an estimate of the percentage of area invaded. In this manner, the CPUE approach was used to provide a complementary (to the GIS analysis) estimate of the percentage of Victorian streams invaded for each time period and to determine the pattern and functional form of the spread for this species.

Identification of the principal vectors of spread for any invasive species is crucial so that management action can effectively target the sources of incoming propagules (Everett, 2000; Floerl & Inglis, 2005). Although predictions of the spatial dynamics of invaders have often been hindered by a lack of knowledge about the transport of propagules, such knowledge is the key to any attempts at understanding and predicting the relative importance of different vectors of dispersal (Johnson & Padilla, 1996). Combining descriptive spread information with data on vector pressure over time allows inferences about the mechanisms of spread. Therefore, we have gathered data to assess the degree to which two vectors, fish stocking and angling, have influenced spread in Victoria. There is anecdotal evidence that these two mechanisms are major causes of the spread of *P. antipodarum* in the USA, where this species is also invasive (Bowler, 1991; Hosea & Finlayson, 2005). We obtained time-series data of fish stocking events in Victorian streams that allowed us to conduct two different analyses. The first is the 'naïve' case in which we do not make use of the time-series information from the *P. antipodarum* data set. If there were only data available from a snapshot survey of where the invader was found at one point in time, then this is an

appropriate method for modelling the invader's dispersal patterns (e.g. Capelli & Magnuson, 1983). For the second analysis of stocking, we use our time-series data to determine whether total stocking events until date of invasion is related to invasion status. In the case of angling, data were only available for a single time period, and we thus analyse these data only in the 'naïve' fashion. The fish stocking analysis was conducted over two spatial scales (i.e. entire state and single catchment). The latter scale was used to determine whether habitat heterogeneity at the whole state scale affected the model results.

Thus, our main objectives are to first synthesize presence and absence data and map the progress of *P. antipodarum*'s invasion across Victoria over the last 110 years. Second, we use the assembled data to delineate the likely percentage of Victorian stream length invaded at the end of six time periods. Third, we describe the functional form of the rate of spread and, finally, we analyse the influence of stocking and angling on the spread of *P. antipodarum*.

METHODS

Study species

The exotic hydrobiid snail *P. antipodarum* has been established in south-eastern Australia for over a century. *Potamopyrgus antipodarum* is native to New Zealand but is now established in Australia, Europe, Japan, and most recently North America (Ponder, 1988; Bowler, 1991). It is parthenogenic, highly fecund, and ovoviviparous, all of which increase the likelihood of populations establishing when individuals are released into new areas (Wallace, 1992). Population densities can reach 800,000 m⁻² (Dorgelo, 1987) in the northern hemisphere, but the highest reported density in Australia is 49,260 m⁻² (Schreiber *et al.*, 1998).

Only one study has been undertaken to investigate the impacts of *P. antipodarum* in Australia, and this was conducted in a single stream. Schreiber *et al.* (2002) found that the colonization of native macroinvertebrates was positively correlated to *P. antipodarum* densities. A similar study in the USA found the reverse pattern, with high densities of *P. antipodarum* associated with low colonization rates of native macroinvertebrates (Kerans *et al.*, 2005). However, densities of *P. antipodarum* colonizing the experimental plots differed markedly between the two studies (4500 vs. ~20,000 individuals/m², respectively). A possible shift from facilitation to competition as snail densities increase shows that the relationship between *P. antipodarum* and other macroinvertebrates is complex (Kerans *et al.*, 2005). In a highly productive stream in the USA, *P. antipodarum* was reported to dominate carbon and nitrogen fluxes, make up 97% of the invertebrate biomass, and consume 75% of the gross primary production, resulting in likely community level impacts (Hall *et al.*, 2003). It has also been shown that *P. antipodarum* has very poor nutritional value and is able to pass undigested through the guts of fish. Because the snail can become the dominant macroinvertebrate species, it is likely to lead to reductions in the available resources for higher consumers (Haynes *et al.*, 1985; McCarter, 1986).

Potamopyrgus antipodarum is known to spread both passively and actively. It has been estimated that populations can move

upstream at a rate of 1 km/year (Lassen, 1975). Observations of the snail passing live through the gut of several fish species, only to reproduce within an hour, indicates that the snail's spread can be aided by fish movement (Haynes et al., 1985). It has been suggested that the commercial movement of aquaculture products, such as live trout or eggs for fish stocking, may be an important vector of *P. antipodarum* spread (Bowler, 1991). Additionally, given that the snails are operculate and can resist desiccation for several days, they may easily be moved by birds, angling gear, or boats (Haynes et al., 1985). Floating downstream independently or on aquatic vegetation has also been observed (Vareille-Morel, 1983; Ribi & Arter, 1986).

Distribution maps

Data on *P. antipodarum* occurrence in Victoria were obtained from two sources: the assembled records of the Australian Museum and Schreiber *et al.* (2003). The combined data set spans the period from the first record of *P. antipodarum* in Victoria in 1895 until 2004. In total there were 170 presence and 462 absence sites recorded. Sampling methods for many of the earliest samples are not available, so we removed data from any sampling efforts that did not identify any gastropods. Our assumption is that if any gastropods were recorded, then the presence or absence of *P. antipodarum* was likely to have been accurately ascertained. Sites where other gastropods were found, but *P. antipodarum* were not found, were treated as absences. We note that for the presence sites the dates given are the sampling dates and not the date of invasion. It is not possible to calculate date of invasion for each site given the patchy temporal and spatial nature of our dataset.

All presence and absence records were imported into the GIS program ArcGIS (ESRI, 1999) and converted to a Universal Transverse Mercator projection (zone 55, GDA94). To aid interpretation, the 110-year data set (1895–2004) was partitioned into six time periods. We plotted the location of all presence and absence records made during each time period, producing a series of six maps that show *P. antipodarum* spread across Victoria. Each map illustrates the presence locations from the time period shown and those accumulated from past time periods. For presentation clarity we only show the absence data sampled during the specified time period.

Percentage of Victorian stream length invaded through time

Data on the occurrence of *P. antipodarum* give a visual representation of where invasions have occurred, but because it is based on point data, it does not allow examination of the total region affected by this species. We used GIS to estimate the total likely distribution at each time period and to calculate the percentage of Victorian stream length affected by the invasion. A map of Victorian streams was derived from a 9-s digital elevation model (DEM) (approximately 250 m resolution) obtained from Geoscience Australia (<http://www.ga.gov.au>). The hydrological map was converted into a Universal Transverse Mercator projection

(zone 55, GDA, 1994) and resampled for 1×1 km pixels to coincide with the approximate spatial accuracy of the *P. antipodarum* occurrence points.

We have assumed that once *P. antipodarum* is found at a site, it will remain there indefinitely. Hence, for each time period, presences were assumed to accumulate forwards through time. In locations of reported absences, the snail was assumed to have never been there, and absences were thus treated cumulatively in a backward nature for each time period. For each stream pixel, we determined whether it was closest to a presence or an absence point to assign it an invasion status. We penalized overland travel heavily to force analysis along stream lines. We note that although upstream movement is possible (Lassen, 1975), it is likely to be slower than the downstream movement because there are more mechanisms facilitating downstream spread. However, our data were not sufficient to infer rates of upstream or downstream spread because not all sites were sampled in each time period. Hence, our model uses the neutral assumption of no difference in upstream and downstream spread rates.

Separate cost distance functions were run to determine the distance of the centroid of each pixel from its closest presence or absence point. A minimum cost distance function was then used to determine the invasion status of each pixel. Thus, we were able to determine the distribution of stream lengths deemed to be invaded and map the results for each time period. Because the area of streams invaded is based on 1×1 km pixels, it is likely to overestimate the area actually affected. To gain a more accurate measure, we calculated the percentage of total Victorian stream length invaded. To determine the functional form of the rate of spread of *P. antipodarum* in Victoria, linear and exponential regression models were applied to the GIS estimates of percentage of stream length invaded over time.

To take account of spatial and temporal variation in sampling effort among catchments and through time, a second method was employed to calculate the functional form of the spread. The percentage of stream length invaded was calculated as the CPUE of sampling. The CPUE approach expresses the number of presence sites as a function of the total number of sampling occasions within separate Victorian catchments over each time period. Hence, spatial and temporal variation in sampling effort is incorporated into the estimate of the percentage of stream length invaded.

The Australian Water Resources Council (1975) has delineated 29 catchments in Victoria. Each catchment can be considered a separate spatial unit because the catchments are divided by barriers that can only be crossed overland, by passing through marine systems, or by moving long distances through the River Murray. Although jump dispersal is possible via a transport vector (e.g. human movement), it is extremely unlikely that the freshwater snail is capable of independent overland spread. There was no sampling of *P. antipodarum* in two of the catchments (Millicent Coast and Avoca River), so these catchments were removed, leaving 27 catchments in the analysis.

CPUE was calculated for each catchment:

$$X_c = \frac{P}{(p + a)}$$

$$AI_t = \sum (X_c \times area_c)$$

where c = catchment number; X_c = individual catchment CPUE; p = number of presences recorded per catchment; a = number of absences recorded per catchment; $area_c$ = area of streams within catchment; AI = area of streams invaded; and t = time period.

As for the GIS method, the total area invaded at the end of each time period was converted to the percentage of Victorian stream length invaded. Linear and exponential models were fitted to the percentage of stream length invaded through time calculated by CPUE. Thus, two estimates of the functional form of the spread were derived — one from the GIS results and the other from the CPUE analysis.

Impact of stocking on spread

To determine whether fish stocking has been a significant vector of *P. antipodarum* spread, we compared the number of stocking events to invasion status for each of the 27 Victorian catchments. Records of fish stocking in Victoria for the period 1871–1990 were obtained from Barnham (1991). Later records (1990–2004) were obtained from reports of the Victorian Department of Primary Industries (DPI, 2004). The numbers of stocking events were aggregated for each catchment over each time period. Values ranged from no stocking events to a maximum of 1410 events in a single catchment between 1871 and 2004.

We took two approaches to testing whether fish stocking has been a major vector of *P. antipodarum* spread in Victoria. First, we took the intentionally naïve approach of comparing the total number of stocking events (1871–2004) in a catchment to the invasion status (i.e. presence/absence of *P. antipodarum*) of that catchment in 2004 using logistic regression. This simulates a simple method by which vector data can be analysed when only data from a single time period are available (e.g. Capelli & Magnuson, 1983). We assess the strength of the null model of the logistic relationship using the likelihood ratio P -value from a chi-squared statistic and the c -value derived from the receiver operator curve. A c -value of 1.0 indicates a perfect relationship and a c -value of < 0.5 indicates no relationship (Hanley & McNeil, 1982; Centor, 1991).

Second, we used the time-series of invasion to compare catchment invasion status to the total number of stocking events until *P. antipodarum* was found in that catchment. Additional stocking events after invasion are not relevant for invasion success, and the use of time-series data allowed us to exclude these events from this analysis. For catchments in which *P. antipodarum* has not been found, we used the total number of stocking events until 2004 because invasion had not yet occurred. Logistic regression was again used. In contrast to our first analysis, this method reduces the probability of finding a spurious relationship because the number of stocking events in invaded catchments does not increase after the invasion was detected. This type of analysis is only possible when adequate time-series data of species spread and vector intensity are available.

In these logistic regression analyses, the independence of the spatial unit is important because the spatial proximity of an

uninvaded catchment to an invaded catchment may influence its probability of becoming invaded in the next time period (Legendre, 1993; Koenig, 1999; Lichstein *et al.*, 2002). To assess whether spatial autocorrelation has affected the spread of *P. antipodarum* in Victoria, we included an independent, categorical variable to each logistic regression analysis to explain the connection of each catchment to known invaded catchments (Cliff & Ord, 1973). For each invaded catchment, the autocorrelation variable was a bivariate indicator of whether any adjacent catchments were invaded before *P. antipodarum* was first sampled. For catchments that remained uninvaded in 2004, the autocorrelation variable was a measure of whether any of the adjacent catchments are invaded. We ran the logistic regression models with and without the autocorrelation variable and compared the relative parsimony of the model results with Akaike's Information Criterion (AIC). Models with smaller AIC values represent more parsimonious descriptions of the data. Model AIC value differences of less than two points indicate that the two models are indistinguishable, differences of four to seven indicate that the poorer model has considerably less support, and differences of greater than 10 indicate that the poorer model has essentially no support (Burnham & Anderson, 2002).

Victorian environments range from temperate rainforest to desert, and this heterogeneity could obscure any relationships between fish stocking and *P. antipodarum* presence/absence. To test whether there is a signal of stocking in a more homogenous environment than the entire state, we looked for a similar relationship at the spatial scale of a single catchment. We chose the Otways catchment in south-west Victoria which is unique in Victoria because it contains a large number of streams that flow directly into the ocean and can thus be considered independent with respect to *P. antipodarum* invasion. The Otways catchment has been relatively well sampled for *P. antipodarum*, and the streams have experienced different numbers of stocking events (i.e. from none to 153 events).

Using the derived stream layer from the 9-s DEM, and the hydrology toolkit in ArcMap, we delineated 64 separate basins in the Otways catchment. Of the 64 Otways basins, 27 basins had been sampled for *P. antipodarum* and 14 of these basins had been stocked. We used a contingency table and a chi-squared approach to test whether stocked catchments are more likely to contain *P. antipodarum* than catchments that have never been stocked for the 27 sampled basins. It was not appropriate to repeat the logistic regression analysis used for the whole of Victoria because many streams have never been stocked, and because 11 of the 14 streams that have been stocked are invaded. Hence, any results would be based on data too limited to make inferences about the influence of the number of stocking events.

Effect of angling on spread

Records of angling activity in Victorian freshwaters were obtained from a survey of angling clubs conducted in 1983 (Barnham, 1983). Results from this survey identified 101 angling destinations (generally rivers or lakes) and the percentage of total Victorian angling effort at each site. Values ranged from no activity

in a catchment (Mallee and Millicent coast) to 15.8% of all angling effort in a single catchment (Goulburn catchment). These data were partitioned into the 27 Victorian catchments for which we had records for *P. antipodarum*. Using logistic regression, these data were then analysed to determine whether catchments that experienced greater angling activity are more likely to be invaded. Models both with and without the inclusion of the spatial autocorrelation variable (described above) were tested. Because the angling data come from a single survey the methods employed for this analysis are the same as those used in the first analysis of the number of fish stocking events, and they thus suffer from the same limitations. In the case of angling, time-series data are not available to isolate the degree of angling over time that is sufficient for invasion.

To determine whether our stocking and angling analyses are independent, we used linear regression to explore for relationships between the total number of stocking events and angling effort in the 27 Victorian catchments. For this analysis, we compared the total number of stocking events from 1871 to 2004 to the angling data (aggregated as just described).

RESULTS

Distribution maps

Since it was first found in 1895, *P. antipodarum* has expanded its range in Victoria (Fig. 1a–f), and now occurs throughout much of the southern and central areas of the state. The north of the state is relatively less invaded than the south, with the division corresponding approximately to the presence of the Great Dividing Range (GDR) (Fig. 1a).

Once *P. antipodarum* was found in a catchment, our data did not reveal a clear tendency for either downstream or upstream invasion. Presence sites were often found upstream of absence sites, and there were also instances where the presence data were not continuous, as absence sites were interspersed among presence sites. These general observations from the data reveal that *P. antipodarum* is patchily distributed and indicate that jump dispersal from within or outside of catchments is possible. Further analysis of our data also suggests the existence of local expansion both upstream and downstream from initial invasion sites, although the point sampling nature of these data makes it impossible to infer whether this is caused by multiple independent invasions or the spread of an established population.

Percentage of Victorian stream length invaded through time

Since the GIS predictions of the distribution of stream lengths invaded are built from the occurrence data, they show the same trends of a heavy invasion in southern and central Victoria (Fig. 1a–f). The percentage of stream length invaded, estimated by both GIS methods and CPUE analysis (Fig. 2), has increased approximately exponentially through time. For both analyses the proportion of variation explained by the exponential regression was greater than that explained by the linear regression (GIS:

exponential $R^2 = 0.950$, linear $R^2 = 0.780$; CPUE exponential $R^2 = 0.901$, linear $R^2 = 0.775$). Until the most recent time period the estimates of percentage stream length invaded are very similar for the two analyses. Extrapolation of the GIS exponential regression estimates that 29% of Victorian stream length is currently invaded (i.e. 2006), and that 73% of Victorian stream length will be invaded by 2020. Extrapolation of the CPUE results gave a more conservative estimate of 20% by 2006, and 34% by 2020.

Impact of stocking on spread

For the naïve model, stocking effort was strongly linked to catchment invasion status for both the model with the autocorrelation variable ($\chi^2 = 6.61$, likelihood ratio $P = 0.037$, $c = 0.816$, AIC = 32.21) and without ($\chi^2 = 7.09$, likelihood ratio $P = 0.008$, $c = 0.816$, AIC = 27.73). Despite this, our second logistic regression, which utilized our long-term data set and included only the number of stocking events until invasion, was not significant for either the model with the autocorrelation variable ($\chi^2 = 0.073$, likelihood ratio $P = 0.964$, $c = 0.576$, AIC = 38.74) or without ($\chi^2 = 0.137$, likelihood ratio $P = 0.711$, $c = 0.567$, AIC = 36.68). These results indicate that although total stocking events are a good predictor of invasion status, fish stocking itself probably is not the dominant mode of spread of *P. antipodarum*. The Victorian models that included the autocorrelation variable were not as parsimonious as those without the variable, given that their AIC values were at least two points higher. Therefore, at a state-wide level, spatial autocorrelation did not severely impact the model results. In the Otways catchment (Fig. 3), there was no evidence that the invasion status of a basin is related to whether stocking had occurred ($\chi^2 = 0.31$, $P > 0.50$). Hence, these results support the findings of the statewide time-series model.

Effect of angling on spread

There was a strong relationship between the presence of *P. antipodarum* in a catchment and angling activity for models with the spatial autocorrelation variable ($\chi^2 = 11.64$, likelihood ratio $P = 0.003$, $c = 0.882$, AIC = 27.18) and without ($\chi^2 = 10.65$, likelihood ratio $P = 0.001$, $c = 0.878$, AIC = 26.16). Models that included the autocorrelation term were indistinguishable from those without as indicated by similar AIC scores. Linear regression showed that the number of stocking events and angling activity for each catchment were significantly related (F -ratio = 0.828, $P = 0.008$) but the R^2 value of 0.235 suggests that, at the catchment scale, anglers decide where to fish on grounds other than just stocking rate.

DISCUSSION

Long-term spatial data sets describing species' range expansions are rarely available. Here, we have shown that in the case of the invasive *Potamopyrgus antipodarum* in Victoria, Australia, such a data set can be used to resolve the patterns and processes of spread. The use of time-series data in analyses on the effects of mechanisms of spread can give different results to those that are

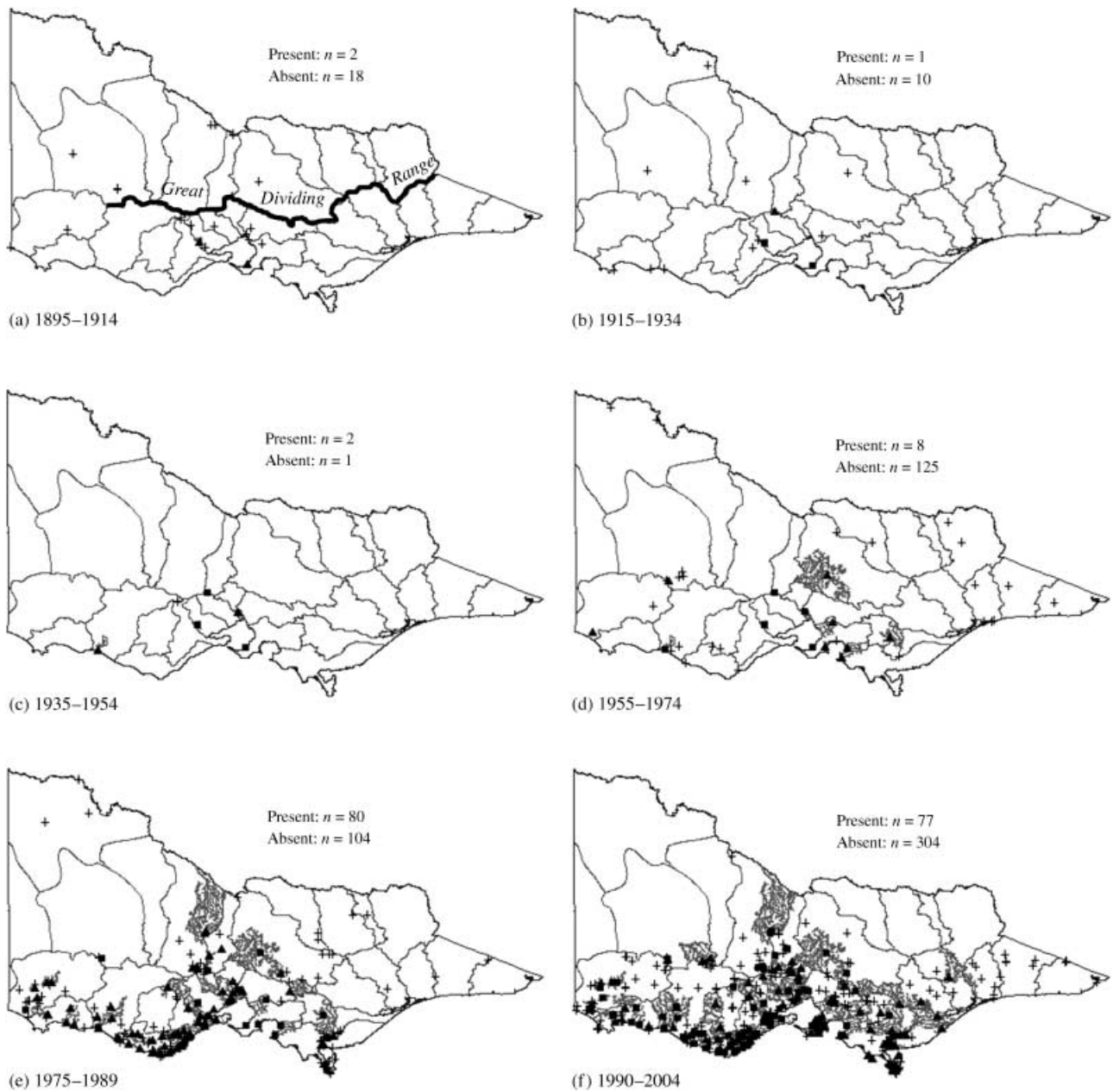


Figure 1 The known and estimated Victorian distribution of *Potamopyrgus antipodarum* for six time periods from 1895 to 2004. + = absent, \blacktriangle = present, \blacksquare = present in past time period, grey area = estimated stream area invaded (see text for details of calculations). Dark line in Figure 1 (a) indicates the location of the Great Dividing Range.

from a single time period. Additionally, the acquisition of historical absence data is crucial for detailed retrospective analyses of spread.

Using presence and absence data collected over the 110-year period since *P. antipodarum* was first observed in Victoria we have mapped the snail's spread over six time periods and shown that invasion has mainly occurred in the southern and central regions of Victoria. Currently it is unclear if *P. antipodarum* is unable to survive in other areas, or whether, given enough time, its range will increase into regions where it does not currently exist. However, it is possible that its range is being restricted by

environmental or biotic factors. In southern Victoria, Schreiber *et al.* (2003) found that the presence of *P. antipodarum* was positively correlated to disturbed environments with multiple land uses. The area of the GDR was not well sampled in their analysis but the highland region has been relatively less affected by land-use change. Thus, the GDR may act as a dispersal barrier slowing the invasion of *P. antipodarum* to northern Victoria.

GIS methods have allowed us to use point occurrence data to estimate the percentage of streams invaded over time. We have thus been able to make the best possible inferences from our data, and this has indicated that the area invaded has increased

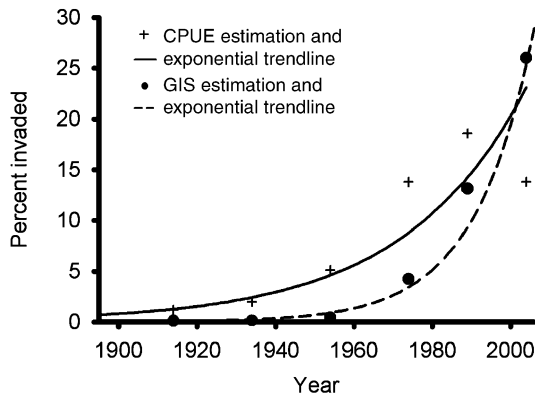


Figure 2 Changes in estimated percentage of total Victorian stream length invaded by *Potamopyrgus antipodarum* from 1895 to 2004 calculated with GIS methods (+), and by a catch per unit effort (CPUE) approach (●). Each point is the estimated percentage invaded at the end of the time periods shown in Figure 1. The exponential curves fitted to these data (GIS, $R^2 = 0.950$; CPUE, $R^2 = 0.901$) are shown.

exponentially over time. Despite having a spatially and temporally extensive data set, our analysis remains strongly dependent on the number and location of point occurrences. The assignment of invasion status of each pixel to the closest presence/absence point means that large spatial gaps in sampling data may have resulted in the over- or underestimation of the invasion within those gaps. Despite this, we have made a reasonable and unbiased estimate of spatial spread based on the data available. Although GIS has opened new possibilities in the manner in which data can be analysed, caution in interpretations of the results is recommended (Guisan & Zimmermann, 2000; Van Horne, 2002).

As an alternative to the GIS method, the CPUE approach does not give a spatially explicit view of the invasion, but this method does take into account spatial and temporal variation in

sampling effort. The CPUE analysis estimates that 20% of total Victorian stream length is currently (2006) invaded by *P. antipodarum* and that this figure will rise to 34% by 2020. Despite their differences, both the GIS and the CPUE approaches found that, over its 110 years invasion, the snail has increased its range at an approximately exponential rate. The snail's invasion began slowly and has accelerated in the past 30 years, possibly due to an increase in disturbed environments (Schreiber *et al.*, 2003) and/or greater numbers and intensity of anthropogenic vectors as a result of human population growth. A similar slow rate of invasion leading to rapid spread was found for the zebra mussel (*Dreissena polymorpha*) in the Belarussian Lakes. After 200 years of invasion, zebra mussels have invaded 93 (16.8%) of 553 studied lakes, with at least 20 becoming invaded in the past 30 years (Karatayev *et al.*, 2003). Anthropogenic vectors are known to be some of the major vectors of zebra mussel spread (Buchan & Padilla, 1999; Johnson *et al.*, 2001). Despite this, in the Belarussian Lakes, zebra mussels were not more common as a function of fishery intensity or the size of the average annual catch (Karatayev *et al.*, 2003).

Our results have clear ecological and management implications, but without long-term data it would not have been possible to estimate the functional form of the spread rate. We note here that the pattern of expansion will inevitably level-off when the snail reaches the bounds of its potential habitat. At this time, an asymptotic model may be a more appropriate fit to the area invaded over time, but at present there are insufficient data to know at what point the snail's spread will level-off. The predicted area invaded by 2020 from the GIS analysis (73%) is unlikely to occur given that an asymptotic model will likely be a better fit by the time the area occupied becomes this large.

To test whether the availability of long-term data might change the conclusions from the statistical analyses of the vectors of spread, we tested in two ways whether fish stocking has been a major contributor to *P. antipodarum* spread. The first test, which assumed no time-series data, showed that the number of stocking

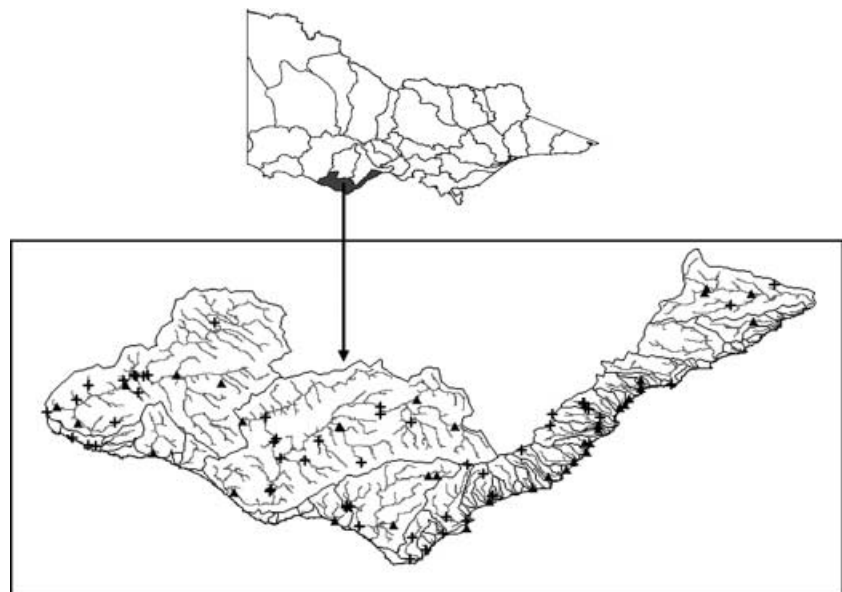


Figure 3 The distribution of *Potamopyrgus antipodarum* in the Otways catchment. The 64 basins and the digital elevation model-derived streams are shown. + = absent, ▲ = present.

events is strongly related to catchment invasion status. A naïve interpretation of this result, especially when combined with anecdotal evidence that stocking is a major vector of this species in the USA (Hosea & Finlayson, 2005), would be that stocking has been a historically important vector of *P. antipodarum* in Victoria. Our second test, which included time-series information, shows that this relationship is more complex than indicated by the first analysis, and that fish stocking may not be a major vector. Spatial autocorrelation was not an important factor in either of these models. At a smaller spatial scale, the Otways catchment analysis was consistent with the statewide time-series result. Hence, in both heterogeneous and relatively homogenous landscapes the same relationship was found.

A simple way to determine the patterns of spread of invading species is to take a snapshot survey and compare invaded sites to uninvaded sites based on indicators of vector movement and/or habitat suitability (e.g. Capelli & Magnuson, 1983). While this approach is often the best possible — especially for cryptic species that are rarely noticed unless specifically sought — there are many limitations, one of which is clearly demonstrated by the difference in results between our two tests for the importance of fish stocking as a vector of *P. antipodarum*. If our data set had been based on a snapshot survey of current distribution we would have erroneously concluded that the number of fish stocking events is strongly related to *P. antipodarum* distribution. Our time-series data show that the number of fish stocking events is probably not driving the snail's distribution even though the total number of stocking events was correlated to invasion status. Analyses of snapshot survey data are limited because it is only possible to say that invasion occurred before the date of sampling. This compromises the statistical analysis by allowing the intensity of the vector (in our case, number of stocking events) to increase after the site was invaded. In turn, this can bias the result towards finding a significant relationship.

Using the same methods as for the first stocking analysis, we showed that catchment invasion status is positively related to angling activity. This analysis suffers from the same problem as for stocking, but because there are no time-series data for angling activity to allow the more detailed analysis, the positive relationship between catchment invasion status and angling activity must be treated cautiously. While catchments with high angling activity were more likely to be invaded, we cannot say whether this is an effect of angling itself or of a factor correlated with angling activity. Anecdotal evidence from the USA suggests that *P. antipodarum* has been spread extensively as 'hitchhikers' on angling equipment (Hosea & Finlayson, 2005). A detailed monitoring scheme of angler movements among Victorian water bodies would help to establish the degree to which such movements facilitate current *P. antipodarum* spread.

Vectors other than stocking and angling have been suggested for *P. antipodarum* in Victoria, but data were not available to explore how they relate to the snail's spread. *P. antipodarum* is a small snail (< 6 mm high) that is easily dispersed passively by birds and fish (Haynes *et al.*, 1985). It has been observed in the mud on the bill of ducks (Coates, 1922), and in continental Europe its first appearance was in the Western Baltic on a migra-

tion flyway (Lassen, 1975). Hence, its spread among Victorian catchments may be facilitated by waterfowl. It can survive passage in the guts of fish such as trout, perch, and roach, so its movement within catchments may be assisted by fish, especially upstream (Haynes *et al.*, 1985).

The analysis of the spread of *P. antipodarum* is not only important for Australia, but also for other invaded regions. In Europe, *P. antipodarum* was first reported from the Thames Estuary, England, in 1859. Within 40 years, it had spread throughout southern England (Boycott, 1936), with its dispersal probably facilitated by the canalization of England's waterways. It had spread to continental Europe by 1887, and is now reported from most European countries (Lassen, 1975; Zaranko *et al.*, 1997). The snail was first reported in the USA in 1987 (Bowler, 1991), and in the first 10 years of invasion it colonized 640 km of the Snake River and its tributaries and continued its spread across the North American continental divide into the Madison River and Missouri River basin. A separate invasion in the Great Lakes was discovered in 1991 (Zaranko *et al.*, 1997). By the start of 2005, *P. antipodarum* had been reported from all of the western states except New Mexico (MSU, 2005). Similar to the pattern we found for *P. antipodarum* spread in Victoria, the rate of range expansion in the USA has accelerated over time (MSU, 2005).

In the USA, *P. antipodarum* has spread over a larger area in a shorter time than the Victorian invasion. This may be a result of greater average flow of human vectors in the USA compared to Victoria over the last century. We note that the USA has a stronger angling culture and a much larger human population, which may have been important factors. Based on the current rate of spread in the USA and the history of invasion in Victoria over a long time period, we expect to see greater rates of spread in the USA in the future.

Each of our results underlines the role that long-term historical data have to play when investigating the spread of non-indigenous species. Such data usually are not available; we were fortunate in this case that scientists at the Australian Museum spent much time and effort confirming the presence or absence of *P. antipodarum* in archived samples. Without these time-series data, detailing both presences and absences, it would have been easy to conclude that fish stocking itself was the principal vector for this species. The management implications from such an erroneous conclusion could be costly and may have had little effect on the spread of *P. antipodarum* in Victoria.

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