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Time to establishment success for introduced signal crayfish in Sweden – a statistical evaluation when success is partially known

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Summary

1. The signal crayfish *Pacifastacus leniusculus* is an invasive species in Sweden, threatening the red-listed nobel crayfish *Astacus astacus* through spreading the crayfish plague. Time-to-event models can handle censored data on such introduced populations for which the state (successful or not) is only partially known at the last observation, but even though data on introduced populations most often are censored, this type of model is usually not used for likelihood-based inference and predictions of the dynamics of establishing populations.

2. We specified and fitted a probabilistic time-to-event model to be used to predict the time to successful establishment of signal crayfish populations introduced into Sweden. Important covariates of establishment success were found by the methods of 'model averaging' and 'hierarchical partitioning', considering model uncertainty and multi-colinearity, respectively.

3. The hazard function that received the highest evidence based on the empirical data showed that the chances of establishment were highest in the time periods immediately following the first introduction. The model predicts establishment success to be $< 50\%$ within 5 years after first introduction over the current distributional range of signal crayfish in Sweden today.

4. Among covariates related to temperature, fish species and physical properties of the habitat, the length of the growing season was the most important and consistent covariate of establishment success. We found that establishment success of signal crayfish is expected to increase with the number of days when growth is possible, and decrease with the number of days with extremely high temperatures, which can be seen to approximate conditions of stress.

5. *Synthesis and applications*. The results demonstrate lower establishment success of signal crayfish further north in Sweden, which may decrease the incentives of additional illegal introductions that may threaten the red-listed noble crayfish *Astacus astacus*. We provide a fully probabilistic statistical evaluation that quantifies uncertainty in the duration of the establishment stage that is useful for management decisions of invasive species. The combination of model averaging and hierarchical partitioning provides a comprehensive method to address multi-colinearity common to retrospective data on establishment success of invasive species.

Key-words: censored data, failure-time model, hazard function, hierarchical partitioning, likelihood-based method, model averaging, probabilistic risk analysis, quantitative assessment

Introduction

Recurrent introductions of alien species pose a threat to ecological systems over the world. The outcome of a biological invasion depends on the properties of the invading species and of the biotic and abiotic properties of the donor and recipient systems, as well as on the propagule pressure (Lodge *et al.* 2006; Catford, Jansson & Nilsson 2009). Data on invasions is usually retrospective and observational, giving rise to statistical problems of inference, something which further complicates predictions. Risk analysis, in which uncertainties are specified

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and quantified, is a necessary tool to support the management of invasive species (McNeely *et al*. 2001; Lodge *et al*. 2006).

It is difficult to predict the outcomes of introductions of alien species. Besides measurement errors, two major uncertainties are variability, an intrinsic property of the quantity at interest and model uncertainty, arising when there is no true or best model to describe reality (Burgman 2005). A straightforward way to quantify variability is to use probabilistic models, regarding model output as a random variable, for which model inference and predictions are based on the likelihood of the model. Model uncertainty can then be approached by inference over a set of models where the likelihoods are used to estimate the probability that a model is true (the Bayesian paradigm) or the relative support of a model (the 'information theoretic' paradigm) (Burnham & Anderson 2002).

In order to predict impact – e.g. the ecological or socio-economic harm caused by alien species – it is necessary to predict the probability that species will become successfully established (Colautti, Grigorovich & MacIsaac 2006; Jerde & Lewis 2007). Models of establishment success quantify uncertainty by the probability of establishment success (e.g. Kolar & Lodge 2002; Drake & Lodge 2006) or by the time from introduction to successful establishment (e.g. Leung, Drake & Lodge 2004; Drake, Baggenstos & Lodge 2005; Drury *et al*. 2007; Jerde & Lewis 2007; Caley, Groves & Barker 2008). The probability of establishment success is sensitive to time since introduction, e.g. some species need a lag phase or are dependent on recurrent introduction events before establishing successfully. Since introduced species usually are observed for different amounts of time, this is an important confounder when analysing establishment success. Further, classifying a species as successful or not at the time of the final observation may prove to be difficult and in many cases such uncertainty leads to the removal of data from the analysis. Therefore, modelling transition time as opposed to probability may be more advantageous. Time-to-event models can handle the statistical problems, referred to as censoring, related to data on introduced populations for which the state (successful or not) is only partially known during the period of observation.

Time-to-event analyses are often used to define which factors determine when events take place, such as the death of an individual or failure of a technical system (Kalbfleisch & Prentice 1980; Bedford & Cook 2001). Besides survival analyses of individuals, time-to-event models can also be used for survival analyses of populations, such as the analyses of extinction risks (Pimm *et al*. 1993) and of species dynamics (Ozinga *et al*. 2007). Time-to-event analyses have also been used to test the effect of covariates on the time to establishment failure of a population (Drake *et al*. 2005) or time to establishment success (Caley *et al*. 2008). Caley *et al*. (2008) modelled the probabilistic properties of the time variable, while the model used by Drake *et al*. (2005) was semi-parametric not addressing the uncertainty in time per se. However, if we are to use likelihood-based inference, we need fully parametric time-to-event models in which the distribution of the time variable is assigned a functional form.

Because of the lack of evaluated time-to-event models of establishment of introduced populations, we decided to specify a fully parametric time-to-event model and to evaluate it with an empirical data set on introductions of American signal crayfish *Pacifastacus leniusculus* in Sweden.

The first introductions of signal crayfish in Sweden occurred in 1960. The introductions were deliberate and initially done with the permission of the Swedish Board of Fisheries. The introductions were a consequence of the decline of the native noble crayfish *Astacus astacus,* which suffered from the crayfish plague *Aphanomyces astaci*, which is lethal to the noble crayfish. The signal crayfish has been established in Sweden and has spread to about 25% of possible crayfish habitats in Sweden (Bohman, Nordwall & Edsman 2006). It is now considered an invasive species in Sweden, since it is a vector for the crayfish plague and, following habitat alteration and pollution, it is the main cause of the decline in the abundance and distribution of the red-listed noble crayfish (Skurdal *et al*. 1999).

Introductions of signal crayfish were initially supervised by Swedish authorities (Edsman 2004). Introduced populations were monitored from the start to evaluate the success of introductions. Several of the introductions of signal crayfish into the southern part of Sweden were successful, which increased the commercial interest in the species. Because the signal crayfish was found to spread crayfish plague, no introduction permits for signal crayfish are given into waters not already occupied by the species today. However, due to exaggerated expectations of establishment success and productivity, signal crayfish are introduced illegally to the northern part of Sweden. These introductions have been less successful; nevertheless, they often cause the crayfish plague to spread to waters which have hitherto been spared, and preventing these introduction efforts would be advantageous for the conservation of noble crayfish in Sweden. We believe that by quantifying the uncertainty in establishment success, we can reduce the likelihood of additional illegal introductions.

The first objective of this study was to specify a probabilistic time-to-event model to predict the time to successful establishment of an introduced population for risk analysis and to parameterize the proposed model by using data on establishing populations of signal crayfish in Sweden, addressing both model uncertainty and method reliability. Our second objective is to use the time-to-event model to predict the success of signal crayfish establishments over a larger area of Sweden.

Materials and methods

MODEL

The uncertainty in establishment success was quantified by a time-to-event model. The probability for an establishment to be successful before t years is given by $P(T < t)$ (Jerde & Lewis 2007), where T is time from introduction to successful establishment. We assume an Allée effect on population dynamics, i.e. that population growth at small population sizes is regulated by positive density dependence and that the population cannot be established unless the population size exceeds the so called Allée threshold (Leung *et al.* 2004; Colautti *et al.* 2006). We regarded the transition from introduction to establishment as successful when the population size exceeded a critical threshold n_A.

The true Allée threshold for crayfish populations is unknown. We assumed n_A to have been reached when test fishing resulted in at least one catch per unit effort (CPUE), corresponding to the average number of crayfish caught per trap and day. The number of traps depends on the size of the crayfish habitat. The value of one CPUE was chosen since when this occurs, a population is regarded to have a size large enough to sustain fishery (Söderbäck & Edsman 1998). The data set consisted of populations with a known first introduction time. Populations that did not exceed 1 CPUE before the last observation were regarded as right-censored observations (Kalbfleisch & Prentice 1980).

SPECIFYING THE MODEL

Time to successful establishment was modelled with the accelerated failure time model (Kalbfleisch & Prentice 1980), which is a multiple linear regression of the time to successful establishment for population *i*, where T_i and covariates $x_{i1}, x_{i2},\ldots, x_{ip}$ are given by:

$$\ln T_i = \beta_0 + \beta_0 x_{i1} + \ldots + \beta_p x_{ip} + \sigma\varepsilon_i. \qquad \text{eqn 1}$$

The parameters $\beta_0, \ldots, \beta_p$, and σ are to be estimated, and ε_i is a random term that defines the distribution for *T*. A positive value on β_j means that the covariate x_j delays the time to successful establishment and thereby decreases establishment success.

The distribution of *T* is most easily understood by its hazard function, where the hazard at time *t*, $h(t)$, is the rate at which events occurs at *t* (Kalbfleisch & Prentice 1980). There is a one-to-one relationship between the distribution function and hazard function given by:

$$h(t) = f(t)/P(T > t),$$

where $f(t)$ is the density function for *T*. So-called semi-parametric failure time models, e.g. the well known Cox regression, do not specify a particular hazard function, as the main purpose of the model is to estimate the effects of covariates. However, since the purpose of our model is to predict establishment success we searched for a parametric hazard function and evaluated the evidence for three general shapes of the hazard function.

When the *T* follows a Weibull distribution, the corresponding hazard function is either decreasing or increasing and is given by:

$$h(t) = \lambda p(\lambda t)^{p-1}, \qquad \text{eqn 2}$$

which relates to the parameters in eqn 1 as $p = 1/\sigma$ and $\lambda = e^{-\beta X}$. The hazard function increases with time when $\sigma < 1$, is fixed when $\sigma = 1$, and decrease when $\sigma > 1$. By adding a denominator to eqn 2 as:

$$h(t) = \lambda p(\lambda t)^{p-1}/[1 + (\lambda p)^p]. \qquad \text{eqn 3}$$

we get the second hazard function, which is valid when *T* follows a log-logistic distribution. This so called log-logistic hazard function decreases when $\sigma \geq 1$, and increases and then decreases when $\sigma < 1$. In a situation where *T* is log-normally distributed, but when many observations are censored, the log-logistic hazard function is preferred (Kalbfleisch & Prentice 1980).

A third alternative for the hazard, common when studying real systems, is a U-shaped hazard function, where the hazard initially is large, then decreases and then increases. Here we defined such function as a mixture of two Weibull hazard functions as:

$$h(t) = \lambda p_0(\lambda t)^{p0-1} \text{ when } t < t' \text{ and } \lambda p_1(\lambda t)^{p1-1} \text{ when } t > t', \qquad \text{eqn 4}$$

where t' is a cutoff time. We used this function as it was easy to implement in a general statistical package by letting the cutoff time t' be fixed separating observed populations with a known state before t' from the others into different strata (Kalbfleisch & Prentice 1980). Since t' is not estimated we selected the best hazard function for different possible values on the cutoff times $t' = 1{\cdot}5, 2{\cdot}5, 3{\cdot}5$ and $4{\cdot}5$.

DATA ON ESTABLISHMENTS

The data consisted of 165 signal crayfish populations legally introduced by the Swedish Fishery Council into 134 lakes and 31 running waters during the years 1968–1985. The introductions were carried out in a geographical area (Fig. S1, Supporting information) covering a large part of southern Sweden where signal crayfish are now successfully established (Swedish Board of Fisheries Database of Crayfish Occurrences). The introductions were monitored during periods of 1–18 years and more than 60% of the introduced populations were inspected on more than one occasion after the first introduction (Fig. 1).

PROPAGULE PRESSURE

Every population resulted from one or more intentional introductions. However, detailed data on introduction events were only available for 42 (26%) populations (Fig. S2, Supporting information), and are too sparse to be considered as useful. We assumed periods of observation to be independent of introduction effort and catches and the introduction effort to be independent of the covariates specified below (Fig. S2).

COVARIATES OF ESTABLISHMENT SUCCESS

Crayfish population growth is affected by temperature (Reynolds 2002; Olsson *et al.* 2010). Individual growth is possible above a certain temperature and reproduction is successful after a period of time with a temperature above a certain level (Abrahamsson 1971). High temperatures may be stressful to crayfish development and behaviour (Jonsson & Edsman 1998; Verhoef & Austin 1999). We quantified the yearly influence of temperature as the numbers of days with an average air temperature above 5°C and the number of days with an

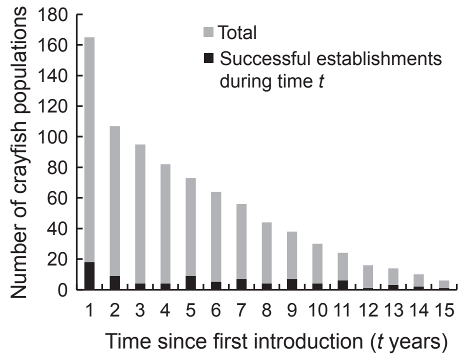

Fig. 1. The total number of observed crayfish populations and the number of populations becoming successful in establishing during different years after first introduction.

average air temperature above 20°C (Table S1, Fig. S3, Supporting information). The former which we called *D5*, approximates duration of the growth season (or the inverse of the length of the winter period) and the latter, which we called *D20*, approximates the occurrence of high temperatures in the crayfish habitat. The influence of temperature on establishment success was alternatively approximated by altitude (*Altitude*) or the geographical coordinates in the South-North (*ycoord*) and West – East (*xcoord*) directions (Georef RT90) (Fig. S3, Supporting information). The latter two covariates may also capture a combination of *Altitude*, *D5* and *D20*.

Systems without a predator are believed to be easier to invade and predator presence is therefore a plausible covariate of establishment success (Lodge *et al*. 2006). The abundance of signal crayfish has been shown to decrease in the presence of fish predating on eggs or juvenile crayfishes (Nyström 2002). We approximate predator presence at the time of the introductions in the data set from surveys of predatory fish carried out by the Swedish Board of Fisheries from the period 1980–1990 (Table S1, Supporting information).

There are several reasons why establishment success differs between lakes and running water (Pursiainen & Erkamo 1991; Nyström *et al*. 2006) and between habitats of different sizes. Predation pressure may be higher in running waters compared to lakes, as fish spend longer in the pelagic zone in lakes; on the other hand, running water offers fewer substrata for crayfish refuge (Nyström *et al*. 2006). The qualities of the habitats also influence population monitoring – crayfish catching methods differ between lakes and running waters, which is likely to affect the relationship between CPUE and the true abundance of crayfish. For these reasons, we included the type of habitat (lake or running water) as a nuisance factor in all models.

The time it takes to exceed the Allée threshold n_A could be shorter in smaller habitats due to a lower true value of n_A. The size of the habitat could also influence the time to successful establishment due to differences in temperature regimes between small and large lakes. To remove a possible bias, the size of the habitat given by the logarithm of lake area was included as a second nuisance factor in all models.

Models

Model inference addressing model uncertainty was made in a likelihood-based framework (Fig. 2) consisting of 'model selection' and 'model averaging' (MA) (Burnham & Anderson 2002). Observational and retrospective data often give multi-colinear variables (Quinn & Keough 2002) and the method of inference may have an effect on the results. To overcome these problems we also derived the effects of covariates with the method of 'hierarchical partitioning' (HP, Chevan & Sutherland 1991)

Model selection and model averaging. The Akaike weight for model k in the set of candidate models $j = 1,\ldots,R$ were calculated as

$$w_k = exp(-1/2\Delta_k)/\Sigma_j exp(-1/2\Delta_j), \qquad \text{eqn 5}$$

where $\Delta_k = AICc_k - AICc_{min}$ is the Akaike difference based on the Akaike information criterion corrected for small sample size (Burnham & Anderson 2002). For each choice of hazard function we fitted the model containing all covariates in the multiple regression, i.e. the global model. Evidence for the hazard function was the ratio between the Akaike weights from the hazard function with the highest weight and the weight of that hazard function as

$$ER_k = \max_j w_j/w_k. \qquad \text{eqn 6}$$

The goodness-of-fit was evaluated by comparing the estimated parametric hazard functions to the non-parametric hazard function derived by Cox regression, i.e. the semi-parametric failure time model where the hazard is estimated for each time interval where no events occur in the original data (Kalbfleisch & Prentice 1981). A good fit of the global model justifies its use in MA, since we can be sure that at least one combination of covariates result in an acceptable model (Burnham & Anderson 2002).

We selected the hazard function with the lowest evidence ratio and fitted all models made up from all possible combinations of covariates. Models within two Akaike difference units from the best model had a substantial support in data (Burnham & Anderson 2002) and provided a small subset of models to be studied in more detail.

The relative importance (*RI*) of a covariate was calculated as the sum of the Akaike weights of the models containing that covariate. For each covariate we calculated its *RI* value, the model averaged parameter estimate β_{av}, based on the models with that variable only and the unconditional standard deviation $s(\beta_{av})$ (Burnham & Anderson 2002).

Hierarchical partitioning. With hierarchical partitioning, it is possible to estimate the contribution that each predictor value gives to the improvement in goodness-of-fit, both independently and together with other covariates (Chevan & Sutherland 1991; Mac Nally & Walsh 2004). The independent contribution of a covariate was calculated by averaging the improvement in the measure of goodness-of-fit, here the log likelihood, over all possible models with and without that covariate.

The joint effect is derived from the differences between the summed goodness-of-fit values from models of variables separately and the summed goodness-of-fit values from models with the covariates jointly (Chevan & Sutherland 1999). This difference is positive in models with multi-colinear covariates and negative in models with covariates with a strong interaction. A covariate's joint effect is then the average over all these differences, which can include both positive

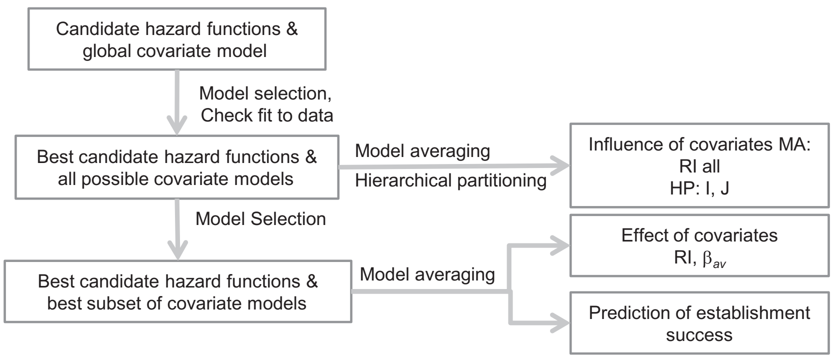

Fig. 2. Flowchart showing the procedure for model inference and prediction.

and negative values if there is both multi-colinearity and interaction effects among the covariates.

The accelerated failure time model was fitted with the function *survreg* and Cox regression was done with the function *coxph*, both found in the survival package in R v.2.8.1 (R Development Core Team 2005). The HP was carried out with functions modified from the *hier* package in R (Mac Nally & Walsh 2004).

Prediction. To predict establishment success in Sweden, we use the parameterized model, with which we derive the probability of a successful establishment t years after the first introduction, where $t < 10$ and percentiles of the time to successful establishment. The probability of establishment success within t years after introduction was calculated with MA over the set of best models (see Appendix S1, Supporting information), where the uncertainty in these predictors was quantified as bootstrapped CI.

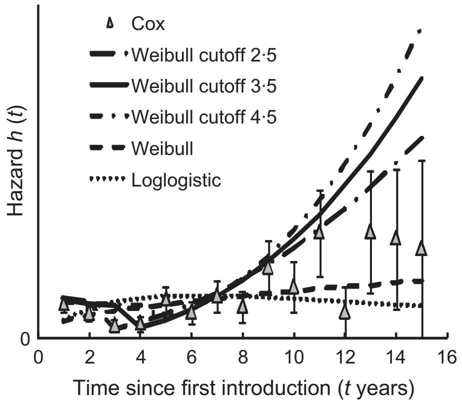

Fig. 3. Estimated parametric hazard functions (Table 1) compared to the semi-parametric hazard function from Cox regression.

Results

MODEL SELECTION OF THE HAZARD FUNCTION

The accelerated failure time model is a possible fully parametric alternative for statistical analysis of censored data on establishing populations. Models with a U-shaped hazard function had the highest support in data (Table 1) and showed, for the time within 10 years from introduction, a similar pattern as crude hazards estimated from a semi-parametric model (Fig. 3). The highest evidence (*ER*, eqn 6) was given by the stratified Weibull hazard function with a cutoff $t' = 3{\cdot}5$ and we used this hazard function below.

Model averaging

Models within two Akaike units from the best model received 55% of support in the data (Table 2). These eight models were assumed to include the major part of the model uncertainty related to the accelerated failure time model. Any common model selection procedure, such as stepwise regression, is likely to end up with a model from this subset of best models.

The relative importance of the covariates were in falling order *D20*, *D5*, *ycoord*, *Altitude*, *xcoord* and *Predator* (Fig. 4a). When we only considered the subset of best models, there was only a slight change in the relative importance of covariates (Fig. 4a). All covariates were represented at least once in the subset of best models (Table 2). The number of days with a temperature above 20°C (*D20*) was represented in all of the

Table 1. Evidence for the different candidate hazard functions

Candidate hazard function	Ln	d.f.	AICc	Δ	*w*	*ER*
Weibull	−257·9	10	537·2	60·7	0%	1·52E13
Weibull cutoff 1·5	−238·3	11	500·3	23·8	0%	147267
Weibull cutoff 2·5	−230·1	11	483·9	7·4	2%	40
Weibull cutoff 3·5	−226·4	11	476·5	0·0	80%	1
Weibull cutoff 4·5	−227·9	11	479·5	3·0	18%	4
Log-logistic	−263·7	10	548·8	72·3	0%	5·02E15

eight best models (Table 2), which suggests that this is a strong predictor of establishment success. The covariate with the second strongest support was the closely related number of days when temperature is above 5°C (*D5*). The third strongest covariate was either the north–south direction (*ycoord*), seen over all possible models, or altitude (*Altitude*), seen over the eight best models (Table 2).

The time to successful establishment increased with the number of days with an average temperature above 20°C (*D20*), and in the presence of a predator on crayfish (*Predator*) (Table 2 and Fig. 5). Establishment occurs earlier in locations with a greater number of days above 5°C (*D5*) or in habitats at a higher altitude (*Altitude*). The sign of the coefficients was the same in these models and models where the covariate was the only variable. We can therefore conclude that the estimated effects are not an artefact from the correlation to other covariates in the analysis.

Hierarchical partitioning

The number of days with a temperature above 5°C and 20°C (*D5* and *D20*), and the South–North direction (*ycoord*) had significant independent effects on the time to successful establishment ($P < 0{\cdot}05$, 500 randomizations). All covariates had large positive joint effects (Fig. 4b), suggesting that the effects of multi-colinearity among covariates were stronger than the effects of interactions (Chevan & Sutherland 1991).

Comparison of model averaging and hierarchical partitioning

Model averaging (MA) and HP gave similar results: the three covariates with a significant effect in HP (Fig. 4b) also received the highest relative importance using the full *RI* from the MA (Fig. 4a) and had the most influential coefficients in the regression (Fig. 5). The two methods reveal different aspects on possible interactions; HP shows that there exists strong multi-colinearity (but not between which covariates) and that the effect of multi-colinearity is

Table 2. The eight best models based on the Weibull hazard function with a cutoff 3·5 and the information needed to arrive at the model averaged estimates of model parameters. For each model we show the log likelihood (Ln), number of parameters (d.f.), Akaike information criteria corrected for small sample size (AICc), Akaike difference (diff), Akaike weight seen over the eight models (w) and the cumulative Akaike weight seen over all possible combinations of the covariates (w.cum all)

Model no.	1	2	3	4	5	6	7	8
Ln	−227·1	−228·5	−227·7	−227·7	−227·8	−226·7	−226·9	−229·2
d.f.	8	7	8	8	8	9	9	7
AICc	471·1	471·8	472·3	472·4	472·6	472·6	472·9	473·0
diff	0·0	0·7	1·1	1·3	1·4	1·5	1·8	1·9
w (%)	22	16	12	12	11	10	9	8
w.cum all (%)	12	21	27	34	40	46	50	55

Model parameters		Model specific estimates								MA estimate
ycoord	Est		0·18		0·18	0·12				0·16
	SE		0·04		0·04	0·07				0·22
xcoord	Est			0·09				0·04		0·07
	SE			0·05				0·07		0·15
Altitude	Est	−0·11					−0·11	−0·09		−0·11
	SE	0·05					0·05	0·07		0·14
Predator	Est				0·11		0·08			0·10
	SE				0·09		0·09			0·21
D5	Est	−0·20		−0·21		−0·10	−0·19	−0·20	−0·23	−0·19
	SE	0·05		0·05		0·09	0·05	0·05	0·05	0·14
D20	Est	0·20	0·17	0·25	0·17	0·22	0·20	0·20	0·29	0·21
	SE	0·07	0·05	0·06	0·05	0·07	0·07	0·07	0·06	0·07
Intercept	Est	2·62	2·65	2·64	2·59	2·63	2·58	2·63	2·61	2·62
	SE	0·13	0·13	0·13	0·14	0·13	0·14	0·13	0·14	0·13
Size	Est	−0·05	−0·01	0·02	0·02	0·00	−0·02	−0·03	0·00	−0·01
	SE	0·10	0·09	0·10	0·09	0·09	0·11	0·10	0·10	0·10
Type	Est	−0·26	−0·32	−0·29	−0·33	−0·28	−0·27	−0·27	−0·25	−0·29
	SE	0·13	0·14	0·14	0·14	0·14	0·14	0·14	0·14	0·14
log σ_0	Est	−1·22	−1·22	−1·19	−1·23	−1·21	−1·22	−1·22	−1·15	−1·21
	SE	0·10	0·10	0·10	0·10	0·11	0·10	0·10	0·10	0·11
log σ_1	Est	0·15	0·15	0·15	0·15	0·14	0·15	0·15	0·14	0·15
	SE	0·12	0·12	0·12	0·12	0·12	0·12	0·12	0·12	0·12

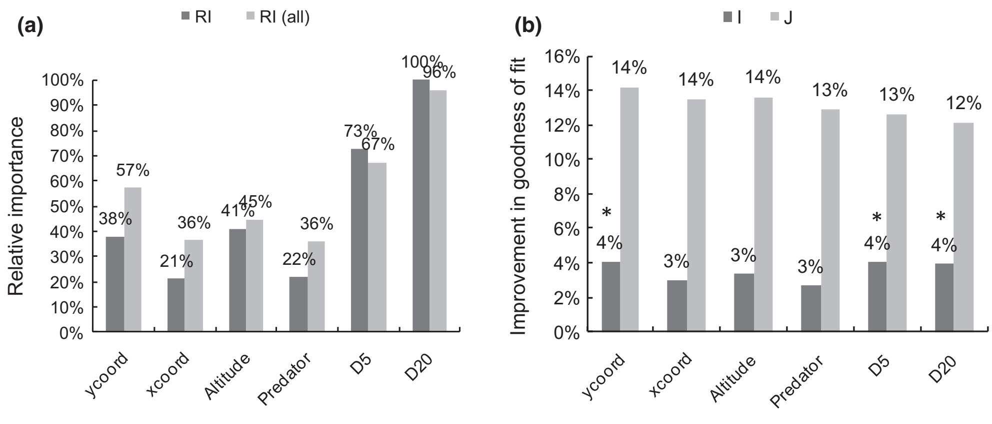

Fig. 4. The influence of the covariates expressing geographical coordinates (*ycoord* and *xcoord*), altitude (*Altitude*), the presence of a predator (*Predator*), and the number of days above 5 (*D5*) and 20°C (*D20*), on the time to successful establishment shown as (a) the relative importance from the eight best models (*RI*) or all models (*RI* all), and (b) independent (I) and joint (J) effects from a hierarchical partitioning. These figures are based on an underlying failure time model with a stratified Weibull hazard function and the cutoff at $t' = 3{\cdot}5$. Significant independent effects on the 5% level in the HP are denoted with a star.

stronger than possible strong interaction effects (which would have appeared as negative values). However, the covariate with the smallest joint effect, *D20*, was also the covariate with the highest relative importance seen by MA (*RI* = 96%; Fig. 4a). An explanation for the relatively low joint effect for *D20* (Fig. 4b) could be strong interaction effects between *D20* and some other covariates, since that would increase the goodness-of-fit value for models where *D20* is combined with these covariates. We conclude that the strong interaction effect for *D20* would not have been

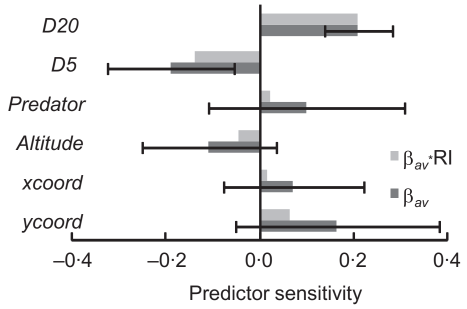

Fig. 5. Predictor sensitivity derived as the standardized parameter estimates of the coefficients in the multiple regression term in the model of the time to successful establishment. Predictor sensitivities are based on model averaging over the eight best models directly (β_{av}) and weighted by the relative importance of each model ($\beta_{av}{\cdot}RI$). Bars represent one SD based on both parameter and model uncertainties.

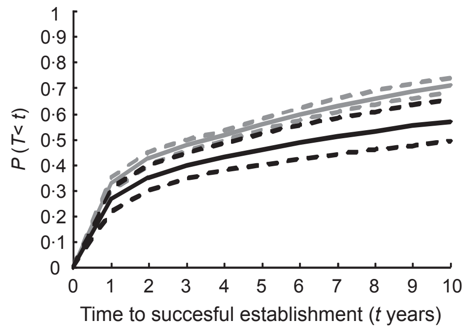

Fig. 6. Predicted probability of successful establishment before t years (solid line) with bootstrapped 90% CI (dashed lines), for the most northern (black) and southern (gray) populations in the data set, given the best three best models in Table 2.

seen by the MA only, while the strong predictive power of *D20* was not seen in the HP by itself.

Predictions

We derive predicted value of establishment success for the observed populations in the data set using the three best models, in which the covariates *D5*, *D20*, *ycoord*, *xcoord* and *Altitude* are represented at least once (Table 2). We found the choice of threshold n_A reliable; a sensitive analysis showed that changing the threshold from 1 to 0·5 or to 2 CPUE did not affect the choice of hazard function, nor the covariate with consistent high support (see Appendix S2, Supporting information).

The probability of success was in general predicted to between 25% and 30% 1 year after, and between 55% and 70% 10 years after introduction (Fig. 6). By comparing the width of the 90% CI we see that the uncertainty was larger for the northernmost lake than for the southernmost lake in the data set (Fig. 6).

We used geo-referenced values on covariates *ycoord*, *xcoord*, *Altitude*, *D5* and *D20* for a large geographical area of Sweden representing the current distributional region of signal crayfish today and thus in which we know that establishment is possible. Predictions using MA gave a probability of establishment success within 5 years after introduction of between 25% and 45% (Fig. 7a). Thus, the probability of successful establishment after 5 years is less than 50%. We then compared the 30th percentile of the time to successful establishment, which is the maximum time to establishment found with a probability of 30%. Over the current distributional range of signal crayfish in Sweden the 30th percentile of time to successful establishment is between 2 and 7 years (Fig. 7b).

Discussion

Management strategies to mitigate the impact of introduced alien populations should be based on predictions of establishment success. In this study we derive and evaluate a parametric time-to-event model which is an unusual application of a common model within the domain of risk analysis (Bedford & Cooke 2001). Time-to-event models are used for probabilistic analysis of the duration of stages in an invasions process (Jerde & Lewis 2007; Caley *et al.* 2008). In this application a successful establishment of an introduced population is the hazardous event, while earlier applications of time-to-event models on populations most commonly use the failed persistence of a population following introduction as the hazardous event (e.g. Drake *et al.* 2005, but see Drury *et al.* 2007). Failed persistence may not be a permanent state, since establishment success may follow from several introduction events (Drake & Lodge 2006) and time to successful establishment is not necessarily the same as time to population extinction. We define time to successful establishment as the time from first introduction to the time when the introduced population size exceeds a predefined Allée threshold, i.e. when population growth does not exhibit positive density dependence due to low population size.

Modelling time instead of single events makes it possible to study the processes of establishment near to and far from the introduction, by for example considering lag phases and time dependent effects (Newman & McCloskey 1996). A time-to-event analysis reflects the nature of the data on newly introduced populations, primarily characterized by censoring. Data on establishing populations are censored in different ways. Introduced populations may be observed during time periods of different length and the time for the first introduction may be unknown. By handling censoring it becomes possible to consider more information which increases the power of methods for inference.

To ensure robust results we used two different statistical approaches of multiple regression, namely Model Averaging, which assigns a weight for every model under consideration and gives predictions by weighting the predictions from each model, and hierarchical partitioning, which measures the effect of covariates only, however not deriving a predictable function per se (MacNally & Walsh 2004). One advantage of MA is that it gives a more sensitive measure of a covariate's importance in models and predictions and handles model uncertainty at the same time (Fig. 5). One advantage of HP is the derivation of a covariate's independent effect, which can be tested for. Both for MA and HP, the relative importance and independent effect of a covariate are relative to the other variables included.

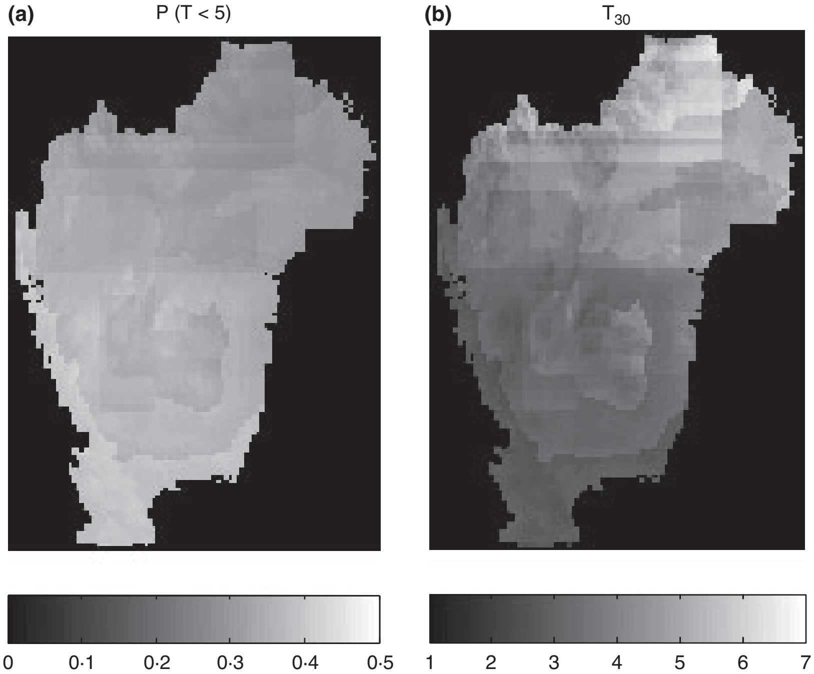

Fig. 7. Predictions made on geo-referenced data on (a) the probability of successful establishment 5 years after first introduction, and (b) the 30th percentile for the time to a successful establishment of an introduced population of signal crayfish. The maps cover the southern part of Sweden where signal crayfish are occurring today.

Adding or removing important covariates changes the results from both MA and HP, while adding or removing unimportant covariates will not. Combining the results from MA and HP provided a comprehensive analysis of covariate effects. An approach to identify a best subset of models by MA and only keep those models having only covariates with significant independent effects would result in selection of models 1, 2, 5 and 8 in Table 2 for prediction.

We expected colinearity among covariates, as the majority of the covariates are (more or less) related to temperature. Differences in establishment success were reduced by the length of the winter as well as by the number of days with an average temperature above 20°C. The latter was the most important covariate due to a strong interaction with other covariates. One reason could be that it approximates the temperature regime differently than the other temperature covariates. An increment of the number of days with high temperatures reduces establishment success, while all other temperature variables are positively related to establishment success. Although a high temperature promotes growth, it also is a stress factor. Signal crayfish cultured at 15°C, 18°C and 21°C obtained the fastest growth at 21°C but survival was greater at 15°C (Mason 1979). The occurrence of or duration of high temperatures during the growing season have been shown to delay mating and increase mortality (Jonson & Edsman 1998). Long periods of high temperatures may also lead to oxygen deficit in shallow lakes and thus cause lower survival. To sum up, the strongest covariates reducing the uncertainty in establishment success of signal crayfish were variables approximating when conditions for population growth are favourable (*D5*) and extreme (*D20*).

In our analysis the years immediately after the first introduction were characterized by high chances of establishment success that descended with time from introduction. The majority of established populations of signal crayfish were successfully established during the 2 or 3 years following the first introduction. Predictions of the time until the population size exceeds a certain threshold can alternatively be used to explore the possibilities of harvesting following introductions of signal crayfish. In fact, our choice of Allée threshold at one CPUE is the same as a rule of thumb for determining when a crayfish population is in a productive state (Söderbäck & Edsman 1998).

Conclusion

Likelihood-based methods of predicting invasion risk can provide a rigourous quantification of uncertainties, but this requires validated probabilistic models of the various stages in biological invasions. Methods for inference and prediction must be able to deal with sparse data being observational and suffering from multi-colinearity. We demonstrate how censored data could be treated using time-to-event analysis as an instrument to increase the information in data and to quantitatively analyse the transition between and the duration of stages in a biological invasion. Using this approach, we were able to evaluate establishment success of the signal crayfish and demonstrate a lower success in more northerly areas, which potentially could reduce the motivation for illegal introduction which are currently threatening the red-listed nobel crayfish.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Predictions of establishment success using MA.

Appendix S2. Sensitivity analysis of the Allée threshold.

Table S1. Covariates used in the analysis.

Fig. S1. Observations and area for prediction.

Fig. S2. Data on introduction effort.

Fig. S3. Geo-referenced values of covariates.

Fig. S4. Sensitivity of MA to the Allée threshold.

Fig. S5. Sensitivity of HP to the Allée threshold.

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