

Modelling radiation dose effects to wildlife populations

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ABSTRACT

A continuous, dual life stage, logistic model for generic populations of wildlife is presented in order to assess the non-stochastic effects of radiation on repairable radiation damage, reproductive ability and mortality. Population change is modelled as a function of survival, fecundity, natural mortality and small density 'Allee' effects. Radiation-induced damages in young and adult life stages are modelled by means of a recovery compartment representing the organism's repairing system. Direct effect of radiation on fecundity is also incorporated in the model.

The model is tested against radiation effects data for freshwater fish and small mammal populations, predicting approximately the observed mortality, morbidity and reproductive changes for fish and mice populations at various doses of γ -radiation. Experimental doses at which effects were observed and those for which the model predicts the same effect are well correlated and observed no-effect doses tend to coincide with doses at which model predictions are in the order of a few percent. Limited data for low-energy β -exposures in mammals suggests that the same model may also be applicable in that situation.

Taken together, the results suggest that for small mammal and fish populations, dose rates less than 2×10^{-2} Gy d⁻¹ are not generally predicted to be fatal to the population. Model tests carried out for large mammals indicate that chronic exposure at this level is predicted to be harmful. The long-term effects on the survivability of populations are predicted to be negligible for exposure rates similar to the ERICA screening value for non-human biota (2.4×10^{-4} Gy d⁻¹), supporting the appropriateness of this value for use in environmental assessments.

Keywords: Logistic model, Population Model, Radiation Effects, Repair Mechanism

1. Introduction

Assessing the degree of environmental protection from radiation requires the evaluation of exposure in relation to effects. The ERICA methodology has proposed a benchmark at the ecosystem level of 2.4×10^{-4} Gy d⁻¹ (Beresford et al. 2007; Brown et al. 2008), further endorsed by the EU PROTECT project (Andersson et al. 2009), with expectation that the earliest effects are observed no less than one order of magnitude above this level. However, it is impossible to treat all biota species in a radiological assessment using a single benchmark level. Responses to radiation exposure are highly variable depending on the biological species., since the 50% lethal dose (LD_{50/30}) varies greatly from ~ 10³ Gy for simple unicellular organisms to ~ 1 Gy for large mammals (Bytwerk 2006; Garnier-Laplace et al. 2004; Garnier-Laplace et al. 2006; UNSCEAR 2008).

In order to assess the level of protection for the population (rather than the individual of the species), models are necessary to predict the actual population dynamics of a generic species. There are many examples of these models in the literature, e.g. Leslie Matrix or logistic approaches, both of which have been applied in an ecotoxicology context (Chandler et al. 2004; Doi et al. 2005). These models cover the range from 1 to more than 10 age classes. However, the available genomics data indicates that, in most cases, it is sufficient to consider the population as composed of two age classes. Our approach therefore adopts a system of first-order differential equation with self-limiting growth according to the logistic equation (Verhulst 1838, 1845).

The effect of radiation can be incorporated into a population model and there are many ways to deal with this. The simplest is to assume that the mortality rate is proportional to the dose rate. More sophisticated models include the effect of radiation on reproduction. Even more advanced models consider a variable effect of radiation in the range from chronic to acute exposures, as the natural radiation damage mechanisms of the body are depleted and the balance between 'healthy' and 'damaged' organisms becomes altered (Kryshev et al. 2006; Kryshev et al. 2008). Lastly, more sophisticated approaches that include the effect of radiation on the dynamic energy budgets of living organisms (DEBTox models) have also been successfully developed to deal with toxicity data (Massarin et al. 2010; Alonzo et al. 2008).

In this study we present the most recent results of a project that has successfully developed a simple, 12-parameter generic model of the observed radiation effects (mortality, fecundity and degree of organism damage) over a range of non-human biota, by considering the action of radiation on the repair mechanism, bridging the gap between chronic and acute effects.

2. Materials and methods

The population model used is based on our previous logistic approach for the European lobster (Vives i Batlle et al. 2009), adapted to a population formed of two age-classes including an independent fecundity function and low-density 'Allee' effect, as represented by the following system of 7 first-order differential equations:

$$\begin{aligned}\frac{dN_0}{dt} &= rF\left(1 - \frac{N_0 + Y_0}{K_0}\right)\left(1 - \frac{W}{N_1}\right) + \kappa_0 Y_0 R_0 - (\alpha_0 d_r + s + d_0)N_0 \\ \frac{dY_0}{dt} &= \alpha_0 d_r N_0 - (\kappa_0 R_0 + \varepsilon)Y_0 - (s + d_0)Y_0 \\ \frac{dR_0}{dt} &= r_0 R_0 \left(1 - \frac{R_0}{M_0}\right) - (k_R^0 Y_0 + \alpha_R^0 d_r)R_0 \\ \frac{dN_1}{dt} &= sN_0 + \kappa_1 Y_1 R_1 - (\alpha_1 d_r + d_1)N_1 \\ \frac{dY_1}{dt} &= \alpha_1 d_r N_1 - (\kappa_1 R_1 + \varepsilon)Y_1 + sY_0 - d_1 Y_1 \\ \frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{M_1}\right) - (k_R^1 Y_1 + \alpha_R^1 d_r)R_1 \\ \frac{dF}{dt} &= fF\left(1 - \frac{F}{L}\right) - rF\left(1 - \frac{N_1}{K_1}\right) - \alpha_f^1 d_r F\end{aligned}$$

Where the dynamic variables are the abundances of healthy (N_i) and damaged (Y_i) individuals at time t ($i = 0$ for young and 1 for adult) and the fecundity F , which represents the number of individuals capable of reproducing. The following rate constants underpin the model:

- s , the growth rate from young to adult;
- d_i , the intrinsic rates of population loss for young and adult;
- R , the reproduction rate (number of females produced by each fertile female);
- $K_0 = K_1 \frac{d_1}{s} \left(1 - \frac{s+d_0}{s} \frac{d_1}{r}\right)$ and K_1 , the carrying capacities for juveniles and adults;
- W , the Allee constant indicating how reproduction reduces at low population density ($W \geq 2$).

The effect of radiation manifests itself as repairable radiation damage, reproduction effects and lethal damage (mortality). This is incorporated as the repairing functions R_i for young and adult, an approach grounded on previous literature (Laurie et al. 1972) where $\alpha_i, \alpha_R^i, \alpha_f^i, \varepsilon, \kappa_i, k_R^i, r_i, f$ are parameters for the radiation model described elsewhere (Kryshev et al. 2006; Kryshev et al. 2008; Vives i Batlle in press; Vives i Batlle et al. 2009). For example, The lethality parameter ε is

designed such that at a dose equal to the LD_{50/30} over 30 days 50% of the organisms suffer lethal damages, hence $\varepsilon = 2.3 \times 10^{-2} \text{ d}^{-1}$. M_0 and M_1 are logistic constants for the recovery pool, made equal to K for symmetry reasons, and d_r is the radiation dose rate.

This system of equations was solved numerically by the Gear method, using the modelling software *ModelMaker®* version 4 (Citra 1997; Rigas 2000). The characteristic physiological parameters for the species were taken from the Animal Ageing and Longevity Database (AnAge 2012) and other online resources such as Arkive (www.Arkive.org) and the Fishbase (www.fishbase.org), as described previously (Vives i Batlle in press). To cover for lack of information on the adult mortality rate we interpreted lifespan as the age of the 10% oldest survivors, and an average mortality rate of ln(10)/lifespan was thus derived. Observing that the adult death rate follows an allometric law with mass, we adapted this law to fit the mortality rate for juveniles. The basic model parameters for the various species studied are given in Table 1.

The model was calibrated for various species with LD_{50/30}s of 3 Gy for fish eggs (Gorodilov 1971), 5.78 gy for adult fish (Kryshev et al. 2008) and 11.1 (Gambino et al. 1968; Golley et al. 1965), 10.2 (Pryor et al. 1967), 2.6 Gy (Norris et al. 1968) and 2.3 Gy (Sasser et al. 1971; Von Zallinger and Tempel 1998) for mouse, rabbit, dog and deer (cattle), respectively (assumed to be the same for adult and young due to data unavailability).

A key feature of the model calibration is the equation for the reversibly damaged population which contains the terms $\alpha_i d_r N_i - (\varepsilon + \kappa_i R_i) Y_i$ factorising loss due to lethal damages plus repaired damages (for chronic doses of radiation, R can be approximated to R_{max}). If the ratio “lethal damages / total (lethal + repaired) damages” expressed as $\rho = \frac{\varepsilon}{\varepsilon + \kappa R_{max}}$ is known, then a certain relationship exists

between k and R_{max} : $\kappa = \frac{\varepsilon}{R_{max}} \left(\frac{1}{\rho} - 1 \right)$. For low-LET irradiation f is low, no more than 2% (Kryshev et al. 2006; Kryshev et al. 2008) which for $\varepsilon = 2.3 \times 10^{-2} \text{ d}^{-1}$ gives $\kappa \approx \frac{1}{R_{max}}$.

For high-LET irradiation the ratio of lethal to total damages is high, no less than 90% (Vives i Batlle et al. 2009) giving

$\kappa \approx \frac{1}{400R_{max}}$. In both cases $\kappa_R \approx 1.5\kappa$. For low-energy beta radiation, we adopted an intermediate f value of 0.25 (chosen by judgment to be closer to the low-LET than the high-LET case), which gives $\kappa \approx \frac{1}{15R_{max}}$.

In this paper we tested for the first time the applicability of both high- and low-LET approximations to a combined dataset of radiation effects (mortality, morbidity, reproduction) in mammals and fish derived from the ERICA (Brown et al. 2008) and the EPIC (Sazykina and Kryshev 2003) radiation effects databases. The mortality, morbidity and reproduction effect endpoints assessed were modeled as changes in the adult (or, in the case of fish eggs, juvenile) age classes at the indicated post-exposure time, expressed mathematically as $1 - \frac{N_0 + Y_0}{K_1}$, $1 - \frac{R}{K_1}$ and $1 - \frac{F}{K_1}$, respectively.

3. Results and discussion

3.1. Fish and small mammals - Low LET radiation

We consulted the information on the effects of chronic radiation in fish and fish eggs established by other authors (Kryshev et al. 2008; Kryshev et al. 2006). For small mammals (mouse/vole) we used the effects data from the ERICA tool (Coppleson et al. 2008), which also contained additional data for fish. Not all the data could be used - a limitation of our study is that the radiation repair approach is not mechanistic, and therefore cannot cover the whole range of teratogenic, genetic, developmental and behavioral effects observed in biota, such as hormetic effects, specific genetic, blood composition effects or changes in size or lifespan.

In general, the model was found to predict successfully most of the experimental observations for loss of fecundity/survival/repair. The mean absolute differences between prediction and observation for fish and mice were 13% (77% of the data within $\pm 20\%$) and 22% (75% of the data closer than $\pm 30\%$), respectively. We then calculated the dose rates at which the model predicts the same effects on mortality, morbidity or reproduction as observed experimentally for the reported observation periods. The 49 theoretical versus model-predicted dose rates for fish and mammals were combined in order to obtain a larger dataset, and the results were graphically analyzed, as shown in figure 1. The two sets of data were found to be linearly correlated: Modelled dose rate = $0.98 \times$ Experimental dose rate; close to a 1:1 relationship with a coefficient of determination $R^2 = 0.88$ over a wide dose rate interval from 10^{-4} to 1 Gy d^{-1} . The data subsets for fish (EPIC), fish (ERICA) and mice (ERICA) are similarly correlated.

There are some limitations to our validation. For fish egg there was a single anomaly in that practically total mortality of eggs is predicted for a dose rate of $9.4 \times 10^{-1} \text{ Gy d}^{-1}$ applied over 14 days. With a LD_{50/30} of 3 Gy d^{-1} the model cannot reproduce this result because it implies a higher LD_{50/30} for acute doses. Likewise, for mice a single data point corresponding to an acute dose of 7.7 Gy applied over a 20-minute period could not be modelled for the same reason. These problems can nevertheless be

avoided by optimizing the radio-sensitivity parameters α_i to values somewhat different from the actual LD_{50/30}.

We verified mathematically that survival, fecundity and repairing pool have a quasi-sigmoidal dose-response relationship with an initial low-effect region followed by large variation over a narrow interval around a tipping value, whereupon the dose-response curve decreases to 0% effect (Figure 2). The most sensitive endpoint seems to be morbidity, followed by fecundity and effect on survival. At a population (rather than individual) level, the mouse appears more radiosensitive than fish despite the lower LD_{50/30} for the latter, with an earlier onset of fecundity loss for the former organism. We attribute this to the combined effect of greater longevity and reproduction rates for freshwater fish compared with mice. A general effects threshold value in the order of $(2 - 3) \times 10^{-2}$ Gy d⁻¹ can be deduced for both species. We also found that for fish and small mammals the adult mortality fraction f_m correlates approximately with the cumulative dose D_c as in $f_m = 1 - e^{-kD_c}$. The parameter k is species-dependent, being 3.5×10^{-2} Gy⁻¹ (modelled data) vs. 3.1×10^{-2} Gy⁻¹ (experimental data) for mammals, and 5×10^{-2} Gy⁻¹ (modelled data) vs. 1.1×10^{-1} Gy⁻¹ (experimental data) for fish.

3.2. Higher LET radiation

We studied the relative difference in effect of adopting a “lethal damages / total damages” ratio of 0.02 (γ -radiation) or 0.90 (α -radiation). Whilst for small mammals (mice) a low-LET radiation dose rate of 10⁻² Gy d⁻¹ induces a 2.1% loss of survival (mortality) after 10³ days, an equivalent α -radiation dose rate of 7×10^{-4} Gy d⁻¹ is required to generate the same effect in the model. This suggests a radiation quality factor of 14 for high-LET α -radiation, resembling the factor of 10 - 20 often adopted in non-human biota dose assessments (Brown et al. 2008; Vives i Batlle et al. 2004). With $\rho = 25\%$ (the intermediate < 10 keV β -radiation case) the equivalent dose rate is 2.2×10^{-3} Gy d⁻¹ which gives a radiation quality factor of 4.5, resembling the factor of 3 for low-energy β -radiation adopted in non-human biota dose assessments by analogy to ³H dosimetry. For fish, the model-predicted radiation quality factors are 25 for α - similar to the value of 30 calculated in our previous work (Vives i Batlle et al. 2009) - and 7.5 for < 10 keV β -radiation. These higher values result from an asymmetric population effect on species that have a very high fecundity but a very low survival from egg to adult.

The ERICA database contains only 5 records of quantifiable effects (mainly fecundity) of < 10 keV β -radiation to small mammals which can be interpreted on the basis of our model (Table 2). Some of the records are for rat rather than mice species; hence model runs for those data were adapted for the different LD_{50/30} of 7.5 Gy for the rat (Casarett 1968; Hall 1973) to avoid reducing the dataset.

The model tends to give somewhat lower estimates of loss of survival and fecundity (differences < 20%), but successfully predicts zero-to-moderate effects on fecundity at doses $< 5 \times 10^{-3}$ Gy d⁻¹ and significant effects at doses in the order of 2×10^{-2} Gy d⁻¹, a factor of ~ 3 below the doses at which low-energy β -radiation produces significant effect on reproduction. Without adjusting the LD_{50/30}, a single acute effect in mice fecundity at 1.7×10^{-2} Gy d⁻¹ in 30 d (equivalent to a dose of 0.5 Gy) cannot be reproduced by the model – a similar problem as that encountered previously for acute doses. However, the remaining results show an acceptable linear correlation between experimental dose and 'same effect' modelled dose ($y = 1.6731x$; $R^2 = 0.97$). This provisional result needs to be revisited when further effects data for low-energy β radiation on mammals and other species becomes available.

3.3. Predictions for larger mammals

Theoretical 5-year model predictions for larger mammals (mouse, rabbit, wolf and deer) exposed to chronic low-LET radiation with dose rates of 0 to 5×10^{-2} Gy d⁻¹ suggest that whilst for small mammals exposed to dose rates ≤ 0.02 Gy d⁻¹ populations reach a stable level some 10% below controls, while for larger animals (dog, deer) populations become extinct at lower dose rates. Overall, these results tend to confirm the ERICA benchmark value of 2.4×10^{-4} Gy d⁻¹ being a dose rate below which adverse effects are not expected, with the first observable effects on mammals occurring typically one order of magnitude above. A potential relationship: bigger animals = more longevity = slower reproduction rate = more radiation effect can be hypothesized from this analysis (Vives i Batlle in press).

4. Conclusions

A logistic population model was calibrated with life history data for dual age-class populations representing fish and mammals. Radiation effects were modeled using the concept of a recovery pool representing the effect of radiation on the repair system, as well as direct effect on fecundity. The key radiation parameters driving the model are the LD_{50/30}'s for young and adult, to which the model calibration is connected for acute effects.

In most cases, the model gives reasonable results in predicting the observed mortality, morbidity and reproductive changes for fish and mice populations at various doses of γ -radiation (differences typically within $\pm 20\%$). Experimental doses at which effects were observed and those for which the model predicts the same effect are well correlated and observed no-effect doses tend to coincide with doses at which model predictions are in the order of a few percent. Limited data for low-energy β -

exposures in mammals suggests that the same model may also be applicable by recalibrating a single parameter (ρ).

Our modeling results cannot be interpreted as final model validation because an independent extensive set of data for chronic irradiation in natural conditions is not yet available. However, our approach offers a practical way to approach the problem, suggesting a way to treat more complex situations at the foodweb/ecosystem level with a relatively simple formalism.

5. References

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Table 1: Population model parameters

Symbol	Description	Freshwater fish ¹	Mouse	Hare/rabbit	Wolf/dog	Deer
d ₀	Juvenile death rate (d ⁻¹)	1.23E+00	2.74E-05	1.34E-05	9.68E-06	5.80E-06
m ₀	Mass for juvenile (kg)	1.78E-06	1.90E-03	8.25E-02	4.50E-01	6.71E+00
d ₁	Adult death rate (d ⁻¹)	8.85E-04	1.42E-03	6.40E-04	3.15E-04	2.93E-04
m ₁	Mass for adult (kg)	4.94E+00	2.32E-02	3.00E+00	3.33E+01	1.49E+02
s	Growth rate(d ⁻¹)	1.14E-04	4.12E-02	2.10E-02	2.11E-02	4.87E-03
r	Reproduction rate (d ⁻¹)	7.53E+02	2.98E-02	1.99E-02	7.39E-03	1.60E-03

¹Average of data for Common carp, Grass carp, Loach, Tilapia, Siberian roach, Goldfish, Silver carp and Pike

Table 2: Effects of low energy (< 10 keV) β-radiation to small mammals interpreted as % loss of survival/fecundity.

Endpoint	Species	Dose rate (Gy d ⁻¹)	Time (d)	Effect	Survival/fecund. loss		Dose for same effect
					Observed	Predicted	
Mortality	Mice	3.6E-03	7.2E+02	No effect on lifespan	0%	2.9%	1.3E-03
Fecundity	Rats	4.8E-03	4.1E+01	Moderate effect in female reproductive organs (oocytes)	30%	11%	1.4E-02
Fecundity	Mice	1.7E-02	3.0E+01	Severe effect in female reproductive organs (oocytes)	93%	20%	N/A
Fecundity	Rats	3.0E-02	4.3E+01	Reduction in sperm content. No effects in females	77%	56%	5.0E-02
Fecundity	Rats	3.0E-02	2.3E+01	Major decrease of fecundity	60%	40%	5.0E-02

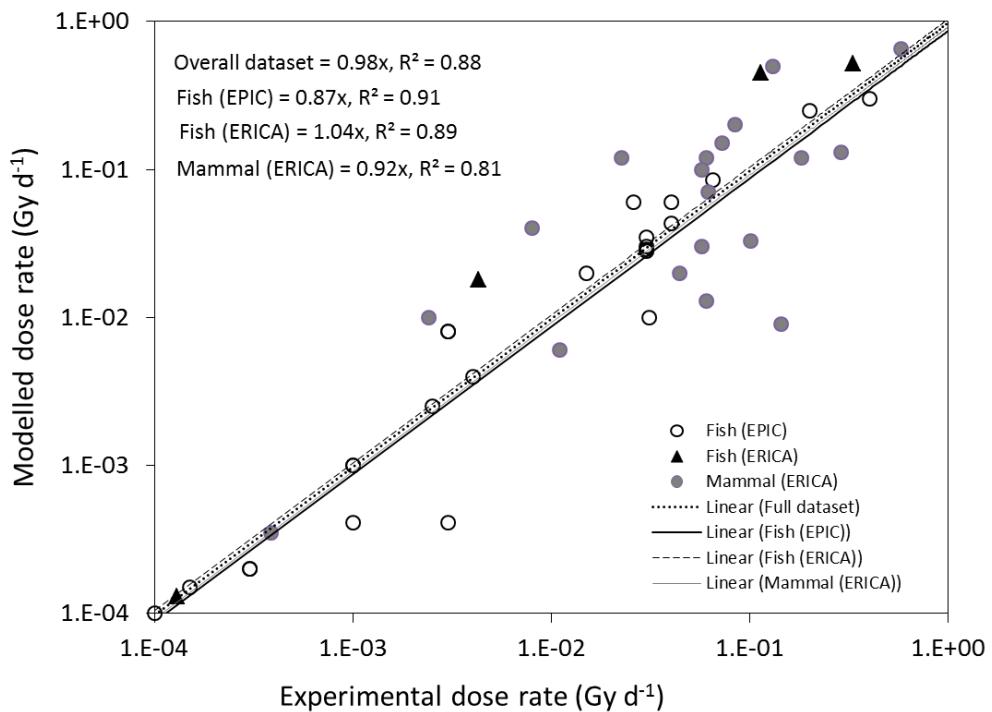


Figure 1: Comparison of experimental dose rates for different effects with model-predicted dose rate needed to obtain the same observed effect in (combined data for mice, fish and fish eggs from EPIC and ERICA).

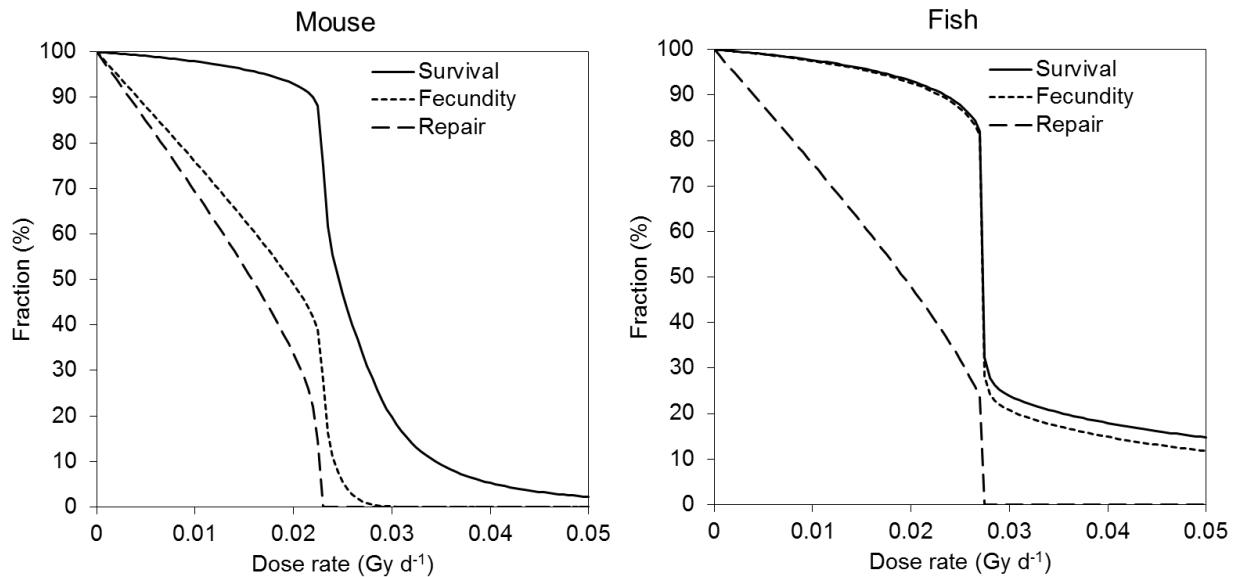


Figure 2: Survival, fecundity and repair pool of the adult mouse (left) and fish (right) as a function of dose rate.