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Simulation of population response to ionizing radiation in an ecosystem with a limiting resource – Model and analytical solutions

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ABSTRACT

A dynamic mathematical model is formulated, predicting the development of radiation effects in a generic animal population, inhabiting an elemental ecosystem 'population-limiting resource'. Differential equations of the model describe the dynamic responses to radiation damage of the following population characteristics: gross biomass; intrinsic fractions of healthy and reversibly damaged tissues in biomass; intrinsic concentrations of the self-repairing pool and the growth factor; and amount of the limiting resource available in the environment. Analytical formulae are found for the steady states of model variables as non-linear functions of the dose rate of chronic radiation exposure. Analytical solutions make it possible to predict the expected severity of radiation effects in a model ecosystem, including such endpoints as morbidity, mortality, life shortening, biosynthesis, and population biomass. Model parameters are selected from species data on lifespan, physiological growth and mortality rates, and individual radiosensitivity. Thresholds for population extinction can be analytically calculated for different animal species, examples are provided for generic mice and wolf populations. The ecosystem model demonstrates a compensatory effect of the environment on the development of radiation effects in wildlife. The model can be employed to construct a preliminary scale 'radiation exposure-population effects' for different animal species; species can be identified, which are vulnerable at a population level to chronic radiation exposure.

1. Introduction

The general request of the public and regulators in respect to protecting wildlife from undesirable effects of technogenic ionizing radiation is to ensure the sustainable existence of populations and ecosystems now and in the future (Andersson et al., 2009; Bréchignac et al., 2012; ICRP, 2014, 2008; USDOE, 2002). Methodological approaches for assessing radiation risk to non-human biota were developed in the recent decades (ICRP, 2014, 2008). Preliminary 'Derived Consideration Reference Levels' (DCRLs) were suggested by the ICRP for Reference Animals and Plants; DCRL was defined as "a band of dose rate within which there is likely to be some chance of deleterious effects of ionizing radiation occurring to individuals of that type of Reference Animal or Plant, derived from a knowledge of defined expected biological effects for that type of organism" (ICRP, 2008).

Despite of considerable progress in developing the radiation risk assessment methodology for non-human biota, it should be admitted that the proposed screening levels (Garnier-Laplace et al., 2006) and reference levels DCRL (ICRP, 2014), intended to ensure the safety of populations, are actually based on information on radiation effects in individual organisms. There is a need to lift the knowledge about individual radiosensitivity to the level of wildlife populations and ecosystems. The peculiarities of radiation responses in an ecosystem are resulting from the differences between the organization of an individual organism as a system of cells and tissues, and organization of an ecosystem as a community of populations associated with their environment (Bréchignac et al., 2012; Sazykina, 2005; Sazykina, Kryshev, 2006). For the purpose of modelling, an ecosystem is considered as a high level of life organization, which includes a self-maintained community of biological species, inhabiting a bordered patch of a territory, and exploiting limited resources within the inhabitance area (Alekseev et al., 1992). There are many factors, which directly or non-directly modify the radiation effects in a self-maintained wildlife population, such as recovering capacity of population, duration of lifespan, reproductive capacity, mortality, availability of living resources,

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relationships with other species. Experimental investigation of radiation effects directly in the contaminated natural ecosystems is an important, but very long-term and expensive task; also, specific results obtained for a particular ecosystem may be non-applicable to another ecosystem (Sazykina and Kryshev, 2006).

Theoretical studies of population/ecosystem response to ionizing radiation can be performed by developing simulation models, combining both radiobiological and ecological processes. Several model approaches, describing radiation effects in generic populations and simple model ecosystems were developed in the recent years (Alonzo et al., 2008; Kryshev et al., 2008; Kryshev, Sazykina, 2015; Monte, 2013, 2009; Sazykina, Kryshev, 2012; Vives i Batlle, 2012; Vives i Batlle et al., 2012; Woodhead, 2003). The population models employed are of two types: discrete age-structured models based on Leslie matrices (Caswell, 2001), and continuous models based on dynamic differential equations (Haefner, 2005; Schoen, 2006; Alekseev et al., 1992). There are also various approaches how to treat radiation effects in populations from simple linear dose-effect response to more complex models with self-recovery of organisms.

In our previous papers, two dynamic approaches to modelling radiation effects in animal populations were formulated – 'a generic population with self-recovery' (Kryshev, Sazykina, 2015; Kryshev et al., 2008), and 'a generic population in a limiting environment' (Sazykina and Kryshev, 2012).

Our previous model 'a population with self-recovery' (Kryshev, Sazykina, 2015; Kryshev et al., 2008), described internal processes of radiation damage in animal organisms, and self-recovery of organisms due to the repairing mechanisms and the biosynthesis of new biomass; the ecosystem factors were not considered in this model. The model was formulated as a set of non-linear differential equations, which were too complicated to be solved analytically.

The other previous model 'a population in a limiting environment' (Sazykina and Kryshev, 2012) represented an elementary ecosystem, consisting of a population, limited by a single living resource. Population characteristics, such as mortality and growth rates were constructed as empirical functions of radiation dose rates. This model was described by a set of non-linear differential equations, which provided an analytical dependence of population size from dose rates of chronic exposure, including threshold for population extinction. The limitation of this model is the lack of knowledge about radiation dose-effect curves for growth, reproduction, and mortality rates, which are known only for few animal species (mice, dogs) well-studied in radiobiology (UNSCEAR, 1982).

The scope of the present paper is formulation of an ecological model for radiation effects in a generic animal population, inhabiting a patch of a territory with a single limiting resource.

2. Model description

2.1. An ecological model 'population-resource' with self-recovery

Let us start with a simple ecological model 'population – resource', describing a generic population, inhabiting a patch of a territory (habitat patch) with a limiting amount of living resource. The growth of gross population biomass in this simple ecosystem is simulated by the modified Verhulst's logistic growth model (Alekseev et al., 1992; Sazykina et al., 2000; Sazykina, Kryshev, 2012). The size of population is characterized by its gross biomass (M); the biomass growth is restricted by a single limiting resource, which total amount in a habitat patch is constant. Some part of the limiting resource is occupied by the population proportionally to its gross biomass ($h_0 \cdot M$), the remaining part (S) of the resource is freely available in the habitat patch. According to the Liebig's 'law of the minimum', the biomass growth rate is proportional with saturation to the amount S of the limiting resource freely available in the habitat patch.

The equations for biomass growth in a limiting environment are the following:

$$\frac{dM}{dt} = M\left(-\varepsilon_0 + \mu_0 \times F \times \frac{S}{SAT + S}\right); \qquad S + h_0 \times M = RES = const; \tag{1}$$

where M-is the gross population biomass; S – is the amount of limiting resource freely available in the habitat patch; SAT – is the constant of half-saturation in the limiting resource; h_0 – is the amount of the limiting resource, required to support a unit of biomass. For simplicity, a unit of the living resource is assumed to support a unit of biomass, i.e. $h_0 = 1$.; also SAT value is assumed to be $SAT = 1$. For simplicity, the term of resource saturation is approximated by a linear function of S at $S/(SAT + S) < 2/3$, and 1 in other cases. RES – is the total amount of the limiting resource in a given habitat parch; ε_0 – is the natural intrinsic rate of biomass losses due to mortality, metabolism and predation, day^{-1}; μ_0 – is the intrinsic maximal rate of biomass biosynthesis, including reproduction, day^{-1}; F – is the growth factor, describing the state of the reproduction/biosynthesis system in organisms.

The dynamic behaviour of the population biomass (1) follows the logistic growth formula (Alekseev et al., 1992; Sazykina et al., 2000; Sazykina, Kryshev, 2012).

Without radiation stress, both the population size M^0_{st}, and the amount of residual resource S^0_{st} reach steady state values described by analytical formulae:

$$M^0_{st} = RES - \frac{\varepsilon_0}{\mu_0 \times F_0}; \qquad S^0_{st} = \frac{\varepsilon_0}{\mu_0 \times F_0}. \tag{2}$$

2.1.1. Equation for the growth factor and the self-repairing capacity of population

The state of reproduction/biosynthesis capacity of population biomass is described by a growth factor F (for simplicity it may be imagined as an aggregate of 'growth hormones'). Without radiation stress, the concentration of the growth factor F in the gross biomass is self-regulated by a simple logistic equation:

$$\frac{dF}{dt} = F\{\mu_F(1 - F)\}; \tag{3}$$

where

$F(t)$ – is the current relative concentration of the growth factor per unit of biomass; μ_F – is the intrinsic rate for reproducing the growth factor in the biomass.

In the control (without radiation stress), the steady state value of the growth factor is normalized to 1 (100% of the control value): $F = F_0 = 1$.

2.1.2. Equation for the self-repairing capacity of population

In addition to the equations for biomass growth and growth factor, the model considers an internal 'self-repairing system', existing in the living biomass, which repairs non-lethal damages caused by various stressors, including ionizing radiation (for simplicity it may be imagined as an aggregate of 'repairing substances' in tissues). Without radiation stress, the relative concentration of the self-repairing capacity per unit of the living biomass, R (so called intrinsic 'repairing pool') (Kryshev and Sazykina, 2015)