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### Life history traits, radiosensitivity and population modeling: methods to extrapolate from individual endpoints to population dynamics

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## Executive Summary

This report describes in details the basic concepts, needs and data treatment for the population modeling approaches that have been implemented under WP-5 dedicated to “ecologically-relevant low doses effects to non-human species” as part of Task 5.1 devoted to the derivation of population-level protection criteria. Two modeling approaches are presented for extrapolating radiation dose effects from individuals to populations of non-human biota.

◇ The first approach, developed as part of the STAR programme, is inspired from methods which are increasingly used in ecotoxicology to address population effects of chemical contaminants. The approach applies Leslie matrix techniques to the case of chronic external gamma irradiation on a range of wildlife species, based on effect data available in the FREDERICA database and interpreted as dose rate response curves. Considered species cover 14 species representing four taxonomic groups (aquatic and soil invertebrates, fish and terrestrial mammals). The strength of the method is its suitability to integrate outcomes of *DEBTox* applications that will be conducted under Task 5.3 as consequences for population dynamics (limited to the few experimentally tested species).

◇ The second approach evolves from a model specifically developed to address radiation effects at the population level in the European lobster and generalised to some mammalian species during the IAEA programme EMRAS II from 2009 to 2011. The model, based on a set of differential equations describing a simplified life history (with two life stages) with logistic functions for reproduction and mortality and a radiation repair mechanism, is reported in this deliverable with its application to fish and mouse.

Results of simulations are compared and discussed underlying the following conclusions:

- (i) Population consequences vary depending on impaired individual endpoints and life history characteristics of exposed species;
- (ii) Populations can be more radiosensitive than the most sensitive individual endpoint, as a result of combined slight effects on several individual endpoints;
- (iii) The scarcity of data for acute and chronic exposure often makes it necessary to rely on highly speculative extrapolations (*e.g.* among species, acute to chronic exposures, among radiation types). This point underlines the need to improve our understanding of the mechanisms underlying radiation toxicity, in order to make better use and interpretation of all the available effect data.
- (iv) One major limit of the present approaches resides in their incapacity to integrate all the molecular, cellular or histological damages described in exposed organisms. This limit is the cause for one main discrepancy between population-level results and those based on the most sensitive individual endpoints taking account of all sub-individual levels of biological organisation.

Future directions include analysing effects using mechanistic concepts in order to make the best possible use of all available data and defining adequate threshold levels assumed to protect species and/or taxonomic groups according to their life history characteristics.



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## 1. Scope and background

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During the last decade, successive EC-funded projects such as FASSET (Williams 2004), ERICA (Larsson 2008) and PROTECT (Howard et al 2010), conceived, applied and promoted methods for ecological risk assessment to examine whether the environment is protected from ionising radiation. The so-called ERICA tiered approach was proposed in accordance with those developed for chemicals. Assessing the degree of environmental protection from radiation requires the evaluation of exposure in relation to effects. One major task of successively ERICA and PROTECT was to derive ecological protection benchmarks for radioactive substances, intended to reflect concentration levels or dose rates assumed to be “safe” and used to screen out exposure scenarios of no ecological concern. These benchmarks were derived on the basis of current knowledge from the FREDERICA database ([www.frederica-online.org](http://www.frederica-online.org), Copplestone et al., 2008), which compiles acute and chronic effects of ionising radiation on four umbrella endpoints (i.e. mortality, reproduction, mutation and morbidity) in 16 wildlife groups. A preliminary analysis was performed to critically screen available raw effect data from experimental radiotoxicity tests against a number of quality criteria and build dose rate-effect relationships to quantify non-human biota responses to chronic external gamma irradiation exposure. These relationships yielded estimates of critical chronic radiotoxicity values, expressed as  $EDR_{10}$  (dose rate values giving 10% effect in comparison with a control), for each wildlife species and endpoints (including survival, reproduction and age at maturity etc.). An estimate of the Hazardous Dose Rate at which maximum 5% of species are affected at a 10% effect level ( $HDR_5$ ) was then obtained by fitting a Species Sensitivity Distribution (SSD) to the set of lowest estimated  $EDR_{10}$  per species. An Assessment Factor (AF) of 2, determined following a multi-criteria weight of evidence approach, was finally applied to the  $HDR_5$  value to derive an ecosystem-level

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Predicted No-Effect Dose Rate of  $10 \mu\text{Gy h}^{-1}$  (Garnier-Laplace et al., 2008; 2010) in accordance with the generic value proposed by ERICA (Beresford et al. 2007; Brown et al. 2008).

An SSD approach using  $EDR_{10}$  adopted two main implicit assumptions that: 1) radiotoxicity at the individual level can be directly compared between different species and between different endpoints, and 2) any selected individual-level endpoint is directly indicative of effects on population. The second point relates to the recognized need of increasing ecological relevancy by considering higher levels of biological organisation such as populations, communities and ecosystems into ecological risk assessment (De Mott et al., 2005). Like in ecological risk assessment for chemical contaminants, one of the most important challenges in radioecology is to extrapolate toxic effects observed on organisms to higher levels of biological organisation (populations, communities...) to avoid inaccurate ecological risk estimates. Effects at the individual level have, in fact, been shown to have variable predicted consequences on populations depending on which endpoint was affected and on life history characteristics of the exposed species (Stark et al., 2004; Raimondo et al., 2006). Life history encompasses a multitude of traits which define life cycles of species (*e.g.*, survival, time to maturity, fecundity, number of reproductive events, life-span). Addressing consequences of ionising radiation at the population level therefore requires modeling approaches which integrate both individual-based dose-response relationships and life history characteristics of the considered species.

In this context, this report describes two modeling approaches for estimating radiation dose effects to populations of non-human biota. The first approach, developed as part of the STAR programme, is inspired from methods which are increasingly used in ecotoxicology to address population effects of chemical contaminants. The approach applies Leslie matrix



techniques to the case of chronic external gamma irradiation on a range of wildlife species, based on effect data available in the FREDERICA database and interpreted as dose rate response curves. The second approach evolves from a model specifically developed to address radiation effects at the population level in the European lobster and generalised to some mammalian species during the IAEA programme EMRAS II from 2009 to 2011 (Vives i batlle et al., in press). The model, based on a set of differential equations describing a simplified life history with logistic growth function and a radiation repair mechanism, is reported in this deliverable with its application to fish and mouse.

## **2. Overview of the methods for estimating population effects for animals and plants**

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### **2.1. Background**

The ERICA and PROTECT methodologies have proposed a generic screening benchmark of  $10 \mu\text{Gy h}^{-1}$  at the ecosystem level, with expectation that the earliest effects are observed no less than one order of magnitude above this level. Case studies have demonstrated that the application of such generic screening value to all organism types may raise problems, as the most exposed organism identified may not necessarily be the organism most at risk (Beresford *et al* 2009). Garnier-Laplace et al. (2010) have discussed that it is desirable to have screening values for as many relevant organism groups as justifiable (probably at the family or class level). Responses to radiation exposure are highly variable depending on the biological species. For example, the 50% lethal dose ( $\text{LD}_{50/30}$ ) varies greatly from  $\sim 10^3$  Gy for simple unicellular organisms to  $\sim 1$  Gy for large mammals (Bytwerk 2006; Garnier-Laplace et al. 2004; Garnier-Laplace et al. 2006; UNSCEAR 2008).

Similarly, chronic EDR<sub>10</sub> values are spread over 6 orders of magnitude (Garnier-Laplace et al., 2010).

In order to assess species protection at the population level rather than at the individual level, population dynamics of generic species under contaminant/radiation exposure has to be modeled. Many examples of population models exist in the literature, such as population matrices or logistic approaches, both of which have been applied in an ecotoxicology context (Chandler et al. 2004; Doi et al. 2005). Other approaches adopt a system of first-order differential equations 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. Other 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). Finally, more sophisticated approaches (both dynamic and mechanistic in their concept) that include the effect of radiation on the dynamic energy budgets of living organisms (DEBTox model) have also been successfully developed to deal with effect data on depleted uranium chemotoxicity (Massarin et al. 2010, 2011). The strength of this approach was found in its adequacy to be combined with Leslie matrices in order to extrapolate consequences of toxic effects for population dynamics (Biron et al., 2012).

The two approaches presented in this report have been successfully used to model observed radiation effects (mortality, fecundity and degree of organism damage) over a range of generic non-human biota, by considering: 1) the action of chronic radiation on life history traits and their combined consequence for the population and; 2) a simplified population

approach based on modeling of a self-repairing function mechanism that most organisms have.

## 2.2. Combining individual dose-response curves using Leslie matrices

In the STAR programme, a different modeling approach was developed to estimate critical radiotoxicity values, namely  $EDR_x$  (Effective Dose Rates yielding  $x\%$  effect compared to control) for the individual net reproductive rate  $R_0$  (number of offspring per individual over a lifetime) and the asymptotic population growth rate  $\lambda$  (dimensionless). The method uses population matrix models such as Leslie matrices (Leslie, 1945; Caswell, 2001). In the past decades, matrix population models have been increasingly used in ecotoxicology for investigating the dynamics of stage- or age- structured populations under exposure to a toxic compound with various effects on life history traits (survival and reproduction).

Leslie matrices allow instantaneous projection of organism performances to the population level by combining dose rate response relationships established for various individual endpoints and life stages as available in the FREDERICA database with data on species life cycles collected from the literature. The method was initially applied to three invertebrate species (Lance et al., 2012) for which sufficient primary effect data on chronic radiotoxicity was available. In the present report, the method is generalized to other representative wildlife species for which some relevant chronic effects are described, including soil invertebrates, fish and terrestrial mammals. For each of the 14 species considered, sensitivity of  $R_0$  and  $\lambda$  to reduction in fecundity, survival and delay in reproduction is analysed to identify the individual endpoints which have the greatest influence. The  $EDR_x$  estimated in each species are compared between the individual and the population levels and their suitability as ecologically relevant protection criteria is discussed.

### 2.2.1. Why matrix population models?

In the Leslie matrix approach, the population is represented as an age-structured vector  $N(t)$  containing the numbers  $n_i(t)$  of individuals in each age class  $i$  at time  $t$ , with  $i$  the individual age ranging from 1 to  $i_{max}$ . All existing age classes instantaneously advance one age class at discrete, equidistant time intervals  $\Delta$ . The number of eggs in  $n_1(t)$  depends on the cumulative reproductive investment of individuals in all cohorts over the time interval  $(t + \Delta, t)$ . The population at  $t + \Delta$  is obtained from the equation  $N(t + \Delta) = A \cdot N(t)$ , where  $A$  is the transition matrix of  $i_{max} \times i_{max}$ . In a Leslie matrix, the elements of the matrix  $A$  are:

- the survival rates  $P_i$  (the probability that an individual of age class  $i$  survives to the next age class over the time the time interval  $t + \Delta, t$ ) arranged on the subdiagonal of  $A$ ;
- the fecundity rates  $F_i$  for each age class  $i$  arranged on the first row of  $A$ .

The model can predict the steady-state, or stable, age structure to which the population tends asymptotically and where it grows at a rate  $\lambda$ , the asymptotic population growth rate. The mathematical and computational convenience of matrix population models brings many advantages including the possibility:

- to represent mathematically the population structure of a biological species and the growth of the population using a relatively simple updating algorithm operating over discrete time intervals.
- to combine observed effects on different endpoints at the individual level (including among several life stages, several generations, several cohorts with different sensitivities to toxicant or different locations and exposure levels) and extrapolate their consequences to the population level (Task 5.1), on a relatively simple mathematical platform that does not require complex numerical integration methods for its resolution;

- to identify key life history traits (and endpoints) for the population through sensitivity analyses (Task 5.1);
- to integrate outcomes of mechanistic approaches such as DEBtox (Task 5.3), including in a multi-contaminant context (connection to WP 4).

Matrix population models provide a common modeling approach for addressing the different objectives in STAR WP4 and WP5.

### 2.2.2. Main demographic endpoints

Depending on model assumptions, various population characteristics can be obtained from mathematical outcomes of a Leslie matrix. Some of them are given in Table 1.

### 2.2.3. Sensitivity analyses

Sensitivity analyses examine how population endpoints, and particularly the asymptotic population growth rate  $\lambda$ , change in relation to vital rates. The sensitivity of any population endpoint to change in any entry  $a_{ij}$  can easily be calculated.

If some factor  $x$  affects any of the entries  $a_{ij}$  of the transition matrix  $A$ , the total derivative of  $\lambda$  can be approximated by:

$$\frac{d\lambda}{dx} \approx \sum_{i,j} \left( \frac{\partial \lambda}{\partial a_{ij}} \cdot \frac{da_{ij}}{dx} \right)$$

In ecotoxicology, the factor  $x$  can refer to an exposure level, such as the concentration of a chemotoxic compound or a dose rate due to a radionuclide. Total sensitivity of  $\lambda$  can be decomposed into several contributions: for example, sensitivity to changes in fecundity rates and sensitivity to changes in survival rates. Hence, matrix population models can be used to identify which endpoint among survival, longevity, fecundity and age at maturity for example, has the most critical influence on population growth for a given species.

**Table 1. Calculated population endpoints using matrix population models.**

Name, symbol	Mathematical calculation	Further comments
Asymptotic population growth rate, $\lambda$	Dominant eigenvalue of the transition matrix A	- if $\lambda > 1$ , population grows on the long-term. - if $\lambda < 1$ , population tends toward extinction.
Stable age distribution, $w$	Right eigenvector of A associated to $\lambda$	e.g. the contribution of each age class to population size
Reproductive values, $v$	Left eigenvector of A associated to $\lambda$	e.g. the contribution of each age class to population growth
Individual net reproductive rate, $R_0$	$R_0 = \sum_i f_i \cdot l_i$	where $l_i$ is the probability to survive until age $i$ : $l_i = \prod_{j=1}^{i-1} S_j$
Probability of extinction	$P(\lambda < 1)$	when a distribution of $\lambda$ values is calculated for a considered exposure scenario
Time to extinction, $T_\varepsilon$	$(A)^{T_\varepsilon} \cdot N_0 \leq \varepsilon \cdot N_0$	lapse time required for a population with $\lambda < 1$ to decline from $N(t_0)$ to a target fraction $\varepsilon$ of $N(t_0)$
Delay in population growth index, $\lambda$	$\delta = t_x - t$ <p>where</p> $\begin{cases} N(t) = (A_0)^t \cdot N(t_0) \\ (A_x)^{t_x-1} \cdot N(t_0) < N(t) \\ (A_x)^{t_x} \cdot N(t_0) \geq N(t) \end{cases}$ <p>with <math>A_0</math> and <math>A_x</math> the transition matrices of the control and exposed populations.</p>	lapse time required for an exposed population (with $\lambda > 1$ ) to grow from $N(t_0)$ to a target size $N(t)$ compared to the unexposed control
Relative changes in carrying capacity, $\frac{K_X}{K_0}$	with $K_0$ and $K_X$ the asymptotic sizes of the control and exposed populations.	only in density-dependent populations

#### 2.2.4. Population response to ionising radiation

Toxicity is widely known to alter different life history traits of organisms at different life stages, suggesting that the population response to a toxicant depend on the combined responses of every affected endpoint and life stage. Expressing matrix entries as functions of exposure concentration or dose rate is particularly well adapted to evaluate more precisely how exposure to radionuclides influences population dynamics. The model simply writes:

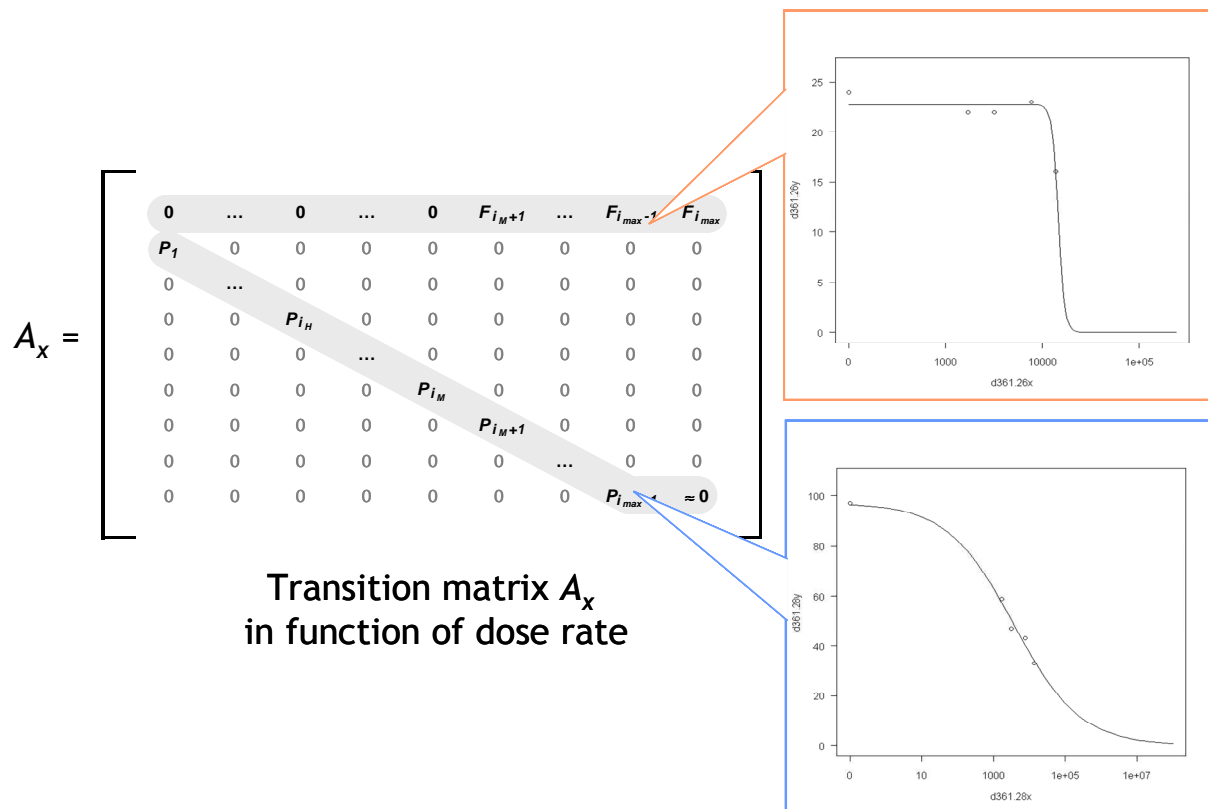
$$N(t+1) = A_x \cdot N(t)$$

with  $A_x$  the exposure-dependent transition matrix.

Exposure-response relationships can be used to link matrix entries  $a_{ij}(x)$  to any exposure condition  $x$  and extrapolate population growth rate  $\lambda$  as a function of  $x$ . Responses to toxicity are expressed as reduction coefficients, which apply to each impaired vital rate (Fig. 1). Such dose rate-response relationships are available from the FREDERICA database, including polynomial, log-logistic, Probit or Weibull models. Additional relationships can be fitted based on newly acquired experimental data. All details are given in Part 3.

### **2.3. A dual age-class model associated with radiotoxic effects assumptions**

The second method based on the logistic approach, evolved from a recent study for the European lobster (Vives i Batlle et al., 2010), adapted to a population formed of two age-classes including an independent fecundity function and low-density 'Allee' effect. The approach uses a system of continuous (in respect of time), non-linear differential equations to describe the population behavior at any point in time. Its specific purpose was to develop a model capable of predicting dynamic long-term effects of chronic exposures on a simplified, dual age class population structure. The logistic model was recently used to run an inter-



**Fig. 1. Extrapolation approach proposed for predicting population-level response**

using dose rate-effect relationships derived from chronic toxicity data (experiments or FREDERICA database) and age-structured population matrix (based on demographic data from the literature).

comparison benchmark scenario “Population response to chronic radiation exposure” with generic population models of seven mammalian species. In this study, life history parameters for mouse, hare/rabbit, wolf/wild dog and deer were defined using the Animal Ageing and Longevity Database (AnAge 2012) as reported in Vives i Batlle et al. (in press).

The effect of radiation in the continuous model is represented as acting upon repairable radiation damage, reproduction effects and lethal damage (mortality). This is incorporated as the repairing functions  $R_i$  for young and adult, an approach that follows previous work to evaluate cell survival to radiation exposures to selected endpoints (Laurie et al., 1972; Kappos and Pohlit, 1972), attempting to extrapolate it to higher levels of organization. The parameters for the radiation model are described elsewhere (Kryshev et al. 2006, 2008; Vives i Batlle et



al., 2010, in press). The full description of the model, extracted from a recent publication (Vives i Batlle, in press), is given in Part 4.

## 2.4. Species selection

### 2.4.1. Species addressed with the Leslie matrices

The approach based on Leslie matrices aims to combine chronic effects of gamma radiation found in the FREDERICA database for different endpoints. The database covers chronic effects at the individual and sub-individual levels including 1) morbidity, 2) mortality, 3) reproductive capacity and 4) mutations. Genetic, biochemical or histological damages cannot be used directly in the extrapolation from individual effects to population dynamics. The primary/main focus is therefore given to species for which at least one chronic gamma effect on survival, fecundity or hatching is described. The selected species cover several taxonomic groups including aquatic and soil invertebrates (i.e. mollusks, annelids and arthropods) as well as fish and terrestrial mammals. Some additional species for which no relevant chronic effect data were available are also included in the study (i.e. *Lumbricus terrestris*, *Rattus norvegicus* and *Sus scrofa*). The earthworm *L. terrestris* was included to explore how the difference in life history characteristics compared to a closely related species (i.e. *Eisenia fetida*) influence population responses, assuming the same individual radiosensitivity with respect to reproduction endpoints. For the two mammalian species (*R. norvegicus* and *S. scrofa*) for which only genetic, biochemical or histological damages are described, effects on survival and fecundity are predicted from extrapolations as described in paragraph 2.6.2.

#### 2.4.2. Species addressed with the dual age class model

The logistic model with radiation repair mechanism only included species of freshwater fish and mice, which are the ones for which the FREDERICA database has relevant data. Life history parameters for the freshwater fish species considered (common grass and silver carp, loach, tilapia, Siberian roach, goldfish and pike) were averaged to create a single model for generic freshwater fish. It is of course difficult to include additional species due to the scarcity of effects information in databases such as FREDERICA, most of which is of the form “no effect observed” or “minor/some/major” loss of fecundity, survival or healthy individuals, without giving numerical information.

#### 2.4.3. ICRP “Reference Animals and Plants”

Considering the huge diversity of living organisms, it is impossible to consider all species of flora and fauna as part of an environmental impact assessment, and to enhance consistency with the existing radioprotection system for human beings. In this context, ICRP has promoted the concept of “Reference Animals and Plants” (RAP): a RAP “is defined as a hypothetical entity, with the assumed basic characteristics of a specific type of animal or plant, as described to the generality of the taxonomic level of Family, with precisely defined anatomical, physiological, and life-history properties that can be used for the purposes of relating exposure to dose, and dose to effects, for that type of living organism”. This limited set of pre-defined reference organisms is composed of 12 species: deer, rat, duck, frog, trout, flatfish, bee, crab, earthworm, pine tree, wild grass, and brown seaweed. These RAPs are documented in terms of dosimetric models to convert exposure to radionuclides into dose (rate), life history traits and qualitative dose (rate) – response relationships.

The methods we propose in this deliverable are applicable to any of these RAPs provided that dose rate – response relationships can be mathematically processed on the basis of

existing effects data and/or that assumptions for inter-species extrapolation can be reasonably adopted.

#### 2.4.4. Vascular plants, phytoplankton, bivalves

Several taxa have not yet been modeled, but are under consideration for future model development. These will extend the range of life history types and phylogenetic groups considered and further test the applicability of the modeling approach. Candidate species for future model development include the following species:

- ***Lemna minor***: Initially, a population model for *Lemna minor* (Driever et al. 2005) has been tested to analyse uranium effects on growth. Model modifications are considered by adopting different functional responses for reproduction rate and mortality to test its suitability for analysing effects of chronic gamma exposure.

- ***Poa annua***: At present cold tests are performed to evaluate the life cycle of a grass, *Poa annua*, under greenhouse conditions. Tests are set up to see if and how we can influence life cycle seed-to-seed in field is 6 weeks; under greenhouse conditions 12 weeks). Once set up is optimized, gamma exposure experiments will be established to assess growth related parameters and reproduction (time to reproduction, number of viable seeds, post-radiation growth). These can then be used as input data to the population modeling.

- **Marine bivalves** (*Mytilus edulis* and *Crassostrea gigas*) are under consideration as candidates for future model development. Marine bivalves are ecologically important, are abundant in coastal areas, and are often consumed by humans. Their life histories provide an interesting comparison with the previously modeled species and good life history data is available. Adults are either hermaphroditic (*Crassostrea gigas*) or unisexual (*Mytilus edulis*). After fertilization, large numbers of offspring pass through different pelagic larval stages over

the course of several weeks, before settling on to the substrate and metamorphosing into small sessile juveniles. Juvenile stage varies widely between species according life history strategies and environmental conditions such as temperature, food availability and substrate availability. Age at maturity varies is usually one to a few years. Most bivalves can in principle live for decades, but early mortality, especially during the larval stage, is high. Irradiation effect data is less readily available. Extrapolation and/or complementary experiments will need to be carefully considered.

- **Phytoplankton** forms the base of the majority of aquatic food webs and is thus interesting to consider from an ecological perspective. In addition, most have a relatively simple life cycle, dominated by vegetative reproduction, though sexual reproduction and resting stages may also occur. Preliminary data searches have found that most irradiation effects data are presented for cultures rather than individual cells, and thus dose rate response curves are established at the population level, without further population modeling required.

## **2.5. Collecting information on species life history parameters**

### 2.5.1. Life history parameters for the Leslie matrices

Life history data for aquatic and soil invertebrates and one fish species (i.e. Medaka) were obtained from the literature and served as the basis for estimating average parameter values to be used in the Leslie Matrix models describing the control populations. In order to limit the variability due to differences in experimental conditions among studies, we considered only values measured under optimal temperature and light conditions. Parameters for aquatic invertebrates, soil invertebrates and Medaka are given in Tables 2, 3, and 4, respectively. Parameters for which only one study was available are reported without standard deviation.

In fish (except Medaka) and terrestrial mammals, values for life history parameters in the Leslie matrices are derived from online databases including the Animal Ageing and Longevity Database (AnAge 2012, <http://genomics.senescence.info/species/>) and Fishbase ([www.fishbase.org](http://www.fishbase.org)). Parameters are given in Tables 4 and 5.

#### 2.5.2. Inferring life history parameters for the dual age class model

The logistic differential equations model with repair serves to illustrate well the problem of inferring life traits from physiological parameters. The primary characteristic physiological information for the species are taken from the AnAge Database (AnAge 2012) and other online resources such as Arkive ([www.Arhive.org](http://www.Arhive.org)) and the Fishbase ([www.fishbase.org](http://www.fishbase.org)), as described previously (Vives i Batlle, in press). When knowledge is scarce or limited (e.g. missing data for some critical life stage of the organism development) it is necessary to carry out various interpolations and extrapolations to cover data gaps in life history parameters. The method used to cover these data gaps where direct data is not available on reproduction rate, growth rate, natural mortality rates in the environment under the effect of predation or organism sizes are fully described in Part 4, also quoting a previous publication (Vives i Batlle, in press).

#### 2.5.3. Dealing with gaps of knowledge

It is recognized that there is a significant uncertainty concerning the results of the many studies performed to assess the response of wild populations to radiation. The main issues and limitations identified in these previous studies, which can aid their evaluation for application to radiological assessment, relate to extrapolating model predictions to natural populations. This is because population dynamics depend on many environmental factors such as the presence of limiting resources, fluctuating trophic conditions and temperature, predation

pressure, density-dependence and exposure to mixtures of toxicants, among others. Another factor often not well understood is interactions among species in a community-level context (Wilson et al. 2009). Those limitations have been recently discussed by Garnier-Laplace et al. (2012), underlying the discrepancy between laboratory or controlled conditions in ecotoxicity tests and chronic field exposure conditions in the Chernobyl Exclusion Zone data.

## **2.6. Collecting information on species radiosensitivity**

### 2.6.1. Chronic dose rate response curves for Leslie matrices

For the Leslie matrices, dose response curves from the FREDERICA database were selected and only included effects on survival, fecundity and hatching, as already mentioned in paragraph 2.4.1. There were few species for which all the chronic radiation effect data needed for the population dynamic modeling was present, and therefore a number of assumptions and extrapolations had to be performed as described in the next paragraph. The original references from which raw data were collected, the FREDERICA database dose response curve identification number, and the type of extrapolations (if needed) are specified in Table 6.

### 2.6.2. Extrapolation rules

When knowledge on chronic data was scarce or even non-existent in a species, effects were estimated using extrapolations rules. Scientifically grounded extrapolations were proposed in the case of chemicals, such as, for example, transformations based on species sensitivity distributions establishing acute to chronic ratios for different substances (Duboudin et al., 2004). Such meta-analysis has never been achieved in the case of ionising radiation and would require a considerable amount of work. Simple extrapolations rules were employed at

this preliminary stage to overcome the problem of untested individual endpoints in some species, although we are aware that these represent a weakness in our approach.

- **Extrapolation among life stages (within the same species):**

Effects of gamma radiation on survival during one life stage (juvenile or adult) or one age class were considered to be representative of the entire juvenile and adult stages. This assumption might underestimate toxicity because critically sensitive life stages might exist although their radiosensitivity has not been investigated. In egg carrying species, such as *Porcellio scaber*, survival rates of eggs were considered equal to that of the adult.

- **Extrapolation from acute to chronic exposure (within the same species):**

Effect on survival in *Neanthes arenaceodentata*, *Eisenia fetida*, *Lumbricus terrestris* and effects on hatching and fecundity in *Oryzias latipes* were only examined after acute short-term irradiation. An extrapolation from acute to chronic exposures was performed assuming that an equal effect level results from chronic low dose rate as from acute irradiation, depending only on the cumulated dose. With respect to adult mortality, this assumption might be conservative because most data would suggest that dose protraction increases the LD<sub>50</sub> value due to compensating repair mechanisms and replacement of killed cells through proliferation of survivors, which can take place at low dose rates (UNSCEAR, 2008). On the other hand, exposure of critically sensitive life stages, for which there are less data, complicate the extrapolation from acute to chronic exposures (ECRR, 2010).

- **Extrapolation among taxonomically close species:**

Radiosensitivity in one species was considered to be representative of another species in few taxonomically close cases only (within a same suborder, family or genus), namely:

- Chronic effects on hatching and fecundity: from the red worm *Eisenia fetida* to the common earthworm *Lumbricus terrestris*, two species of the Lumbricidae family (Annelids, Oligochaetes);
- Acute effects on survival: from the common pill woodlouse to *Armadillium vulgare* to the common rough woodlouse *Porcellio scaber*, two species of the oniscid suborder (Crustaceans, Isopods);
- Acute effects on survival: from the mosquitofish *Gambusia affinis* to the guppy *Poecilia reticulata*, two fish species of the poeciliid family (Teleosts, Cyprinodontiformes);
- Acute effects on survival and chronic effects on fecundity: from the Chinook salmon *Oncorhynchus tshawytscha* to the rainbow trout *Oncorhynchus mykiss*, two fish species of the salmonid family (Teleosts, Salmoniformes).

- **Extrapolation among radiation types:**

No effect of chronic or acute gamma radiation on survival was available for the earthworm *L. terrestris* and for the rainbow trout *Oncorhynchus mykiss*. In these cases, chronic survival was extrapolated from acute exposure to X-rays respectively in *Oncorhynchus tshawytscha* and *L. terrestris*.

- **Extrapolation based on allometry (among mammal species):**

In terrestrial mammals, chronic radiosensitivity of life history traits was particularly well described in the mouse *Mus musculus*. Studies were much scarcer in larger species, with chronic dose response curves available only for reproduction in the goat *Capra hircus* and for mortality in the dog *Canis familiaris*. To overcome knowledge gaps, allometric relationships were established so as to estimate parameters of the missing dose response curves. This was achieved after survival was expressed on the same time unit in different species. By analogy



to the approach proposed by Bytwerk (2006), parameters  $\theta$  of dose rate response curves (EDR<sub>50</sub> or slope parameter) were expressed as functions of body mass  $M$ :

$$\theta = a \cdot M^b$$

This extrapolation was also applied to two additional species for which no relevant chronic effect data were available (i.e. *Rattus norvegicus* and *Sus scrofa*).

### 2.6.3. Inferring 30-day lethal dose for the dual age class model

Although the fundamental mechanisms that cause radiation damage apply similarly to all species, responses to radiation exposure are extremely variable depending on type of radiation, the intensity of the exposure (acute versus chronic), biological endpoint (mortality, morbidity or reproduction), life stage and, above all, species. The 50% lethal dose, that is, the dose of radiation expected to cause death to 50 percent of an exposed population within 30 days (LD<sub>50/30</sub>) varies greatly among wildlife, from  $\sim 10^3$  Gy for simple unicellular organisms to  $\sim 1$  Gy for large mammals. This highlights the higher radiation sensitivity of organisms having a larger level of biological organization (Garnier-Laplace et al. 2004; Bytwerk 2006; Garnier-Laplace et al. 2006; UNSCEAR 2008), not to mention individual variability within the same family (Tsyusko et al. 2011).

In light of the above, gaps of knowledge across and within species are difficult to address. For this reason, it is always recommended to use experimentally-derived 50% lethality effect doses for the juvenile and adult of the species under consideration, as done for most of the considered species in the dual-age class model. When there are no direct experimental values available, a method was devised for inferring LD<sub>50/30</sub> from allometric relationships. This method uses the mass-dependent allometric equation based on Bytwerk (2006) and Highley and Bytwerk (2007):

$$\alpha = \frac{\ln 2}{LD_{50}} = 0.0961 \times m(\text{kg})^{0.1297}$$

This work compiled LD<sub>50/30</sub> values for acute exposure in covering many phyla, for the adult of each species. Authors stated that this allometric relationship only applies to the adult members of each species. For offspring, if no experimental data is available, a value at least as low as that for the adult is used to avoid an underestimation of radiosensitivity.

A challenge of the approach is that LD<sub>50/30</sub> values have long been known to be dependent on test conditions such as dose rate and exposure duration. The exact relationship is inadequately understood, though the 50% lethal dose is likely to be higher when spreading the exposure over longer times (Bytwerk 2006). This means that, in practice, calibrating the model with allometrically-derived LD<sub>50/30</sub> is likely to result in a conservative estimation of threshold values at which effects on mortality occur under chronic exposure.

#### 2.6.4. Validation of the model with fish effect data from the EPIC study

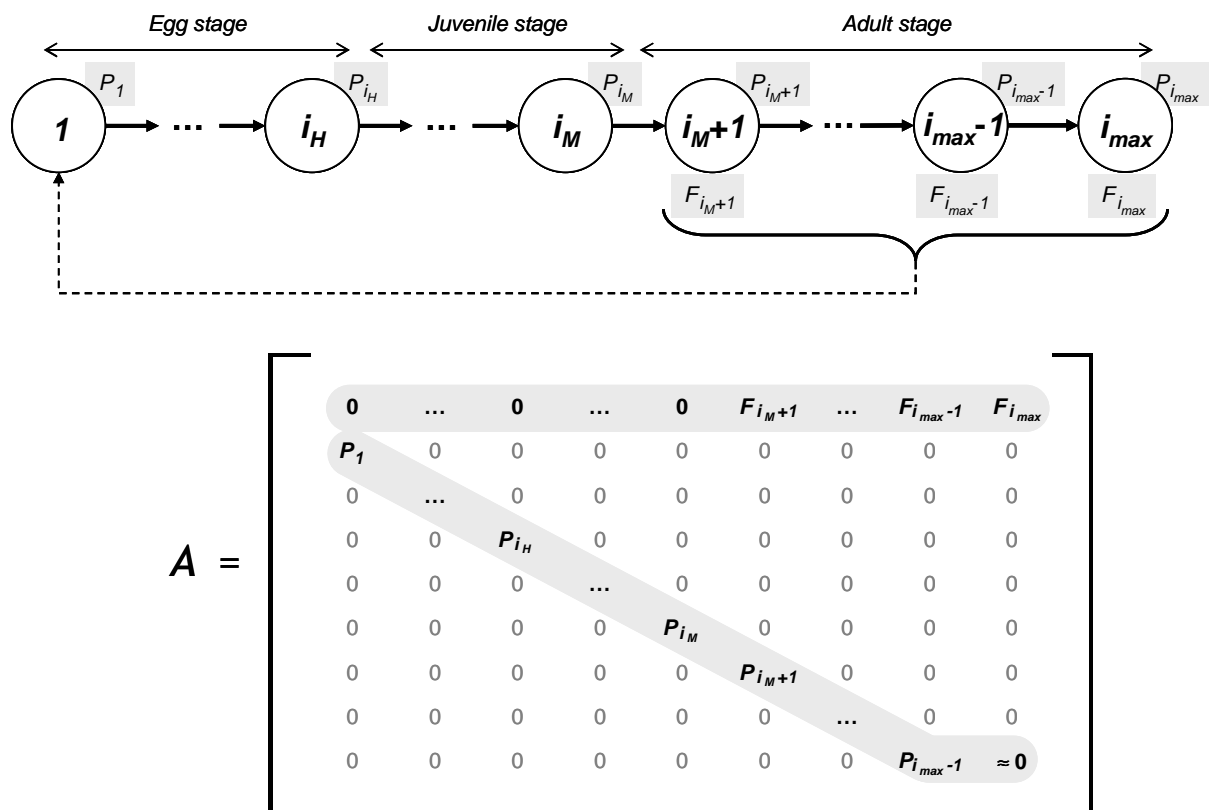
In order to provide validation data for radiation effects in adult fish, we consulted the effect data on chronic radiation in fish from the EPIC study ( Sazykina and Kryshev 2003). These data have already been used to calibrate a single-age population model for fish (Kryshev et al. 2008). The EPIC study also includes information on dose-effect relationships for salmon and pike eggs (Kryshev and Sazykina 2005) previously used in modeling (Kryshev et al. 2006). The assembled comparison dataset is established in these two publications, which also give a point of comparison with a previous, single age class population model (Kryshev et al. 2006; 2008).

### 3. Combining dose rate-response curves using Leslie matrices

#### 3.1. Mathematical formulation

##### 3.1.1. Modeling life history

Time units are expressed in weeks, months or years depending on species longevities. Three different life stages, namely the egg, the juvenile and the adult stages, were defined over the species life cycles (Fig. 2), considering age at hatching  $i_H$ , age at maturity  $i_M$  (e.g. at first reproduction) and species longevity  $i_{max}$  (in time units). Survival rates  $P_i$  (per time unit) at age  $i$  were calculated in the different life stages as:



**Fig 2. Life cycle graph and associated Leslie matrix  $A$**

with egg, juvenile and adult stages. Ages expressed in weeks with  $i_H$  at hatching,  $i_M$  at first reproduction, and  $i_{max}$  the species lifespan and  $P_i$  the survival rate (proportion of survival per week) and  $F_i$  the fecundity rate (number of offspring per week) in age class  $i$  (Caswell, 2001).

$$P_i = (H)^{1/i_H}$$

in the egg stage (e.g. with  $1 \leq i \leq i_H$ ) with  $H$  the proportion of hatching eggs;

$$P_i = (S_{obs})^{1/t_{obs}}$$

in the juvenile and adult stages (e.g. with  $i_H < i \leq i_M$  and  $i_M < i < i_{max}$  respectively), with  $S_{obs}$  the proportion of survivors after a period  $t_{obs}$  (specific of each life stage if available or common to the juvenile and adult stages otherwise). Individuals of age  $i_{max}$  were assumed to die of old age, so  $P_{i_{max}} \approx 0$ .

In fish and mammals, age-specific survival rates are obtained based on the Gompertz function (Finch, 1990; Strehler, 1999) which is the simplest, most widely used method to describe the increase in mortality rates  $M_i$  (per time unit) with age  $i$  in vertebrates:

$$P_i = 1 - M_i = 1 - IMR \cdot 2^{\frac{i-i_M}{MRDT}}$$

with  $IMR$  the initial mortality rate (per time unit) at maturity and  $MRDT$  the mortality rate doubling time (in time unit).

Reproduction occurred only in the adult stage. Fecundity rates at age  $i$  (average eggs per adult per time unit) were calculated as:

$$F_i = p_R \cdot R_i$$

where  $p_R$  is the proportion of reproducing adults, and  $R_i$  is the reproduction rate (eggs per reproducing adult per time unit).

### 3.1.2. Modeling individual $R_0$ and population $\lambda$

Population dynamics were studied using Leslie matrices (Caswell, 2001). Each matrix model described a theoretical age-structured population, assuming a closed system with no immigration or emigration, no seasonal change in survival and fecundity rates, no density-

dependence, no competition, parasitism or predation pressure. Leslie matrices were constructed with a number of age classes and time steps (i.e. in weeks, months or years) in accordance with species longevities (Fig. 2). As an example, Leslie matrices for *O. diadema*, *N. arenaceodentata* and *P. heterostropha* were constructed with 15, 31 and 22 one week age classes respectively. Leslie matrices were used to calculate the asymptotic population growth rate  $\lambda$  as the dominant eigenvalue of the matrix (Caswell, 2001). Values of  $\lambda$  provided information regarding population sustainability,  $\lambda$  below 1 indicating a long-term decline in population size ultimately leading to extinction. The net reproductive rate  $R_0$  were calculated as an integrated index of individual reproductive performance allowing comparisons of sensitivity between the individual and the population levels:

$$R_0 = \sum_i F_i \cdot \prod_{j=1}^{i-1} P_j$$

where  $\prod_{j=1}^{i-1} P_j$  is the probability to survive until age  $i$ , and  $F_i$  and  $P_i$  are the age specific fecundity and survival rates respectively. Matrix computations were performed using the software MATLAB (MathWorks, Inc).

### 3.1.3. Sensitivity of individual $R_0$ and population $\lambda$ to changes in individual endpoints

Sensitivity of population  $\lambda$  and individual  $R_0$  to reduction in fecundity, reduction in survival and delay in reproduction were examined in all species. To do so, effect  $x$  (ranging from 0 to 100% compared to the control) was applied to fecundity rates  $F_i$  or survival rates  $P_i$  as follows:

- 1)  $x$  % decrease in  $F_i$  in all age classes;

2)  $(x)^{1/2i_M}$  % decrease in  $P_i$  in all age classes so as to obtain  $x\%$  decrease in survival after  $2i_M$  (with  $i_M$  the age at first reproduction);

3) a delay  $\delta$  in reproduction of  $x\%$  relative to  $i_M$  obtained by shifting fecundity rates so that:

$$F_{i+\delta} = F_i$$

In the semelparous species (the marine polychaete *N. arenaceodentata* and the fish *O. mykiss*) in which death occurred straight after reproduction, delaying reproduction led to increasing age class number in the Leslie matrix, whereas delay in reproduction did not change age class numbers in the iteroparous species. After the effect was applied,  $\lambda(x)$  and  $R_0(x)$  were calculated as above and reductions in  $\lambda$  and  $R_0$  were expressed as percent relative to the values  $\lambda(0)$  and  $R_0(0)$  in the control population.

#### 3.1.4. Effects of external gamma radiations

Dose rate-effect relationships in each species were described with log-logistic or Brain-Cousens models (Garnier-Laplace et al., 2008; 2010) and effective dose rates  $EDR_x$  causing  $x = 10, 20$  or  $50\%$  effect on hatching, fecundity and survival were calculated. Effects of gamma radiation were combined and propagated to the population level using Leslie matrices. To do so, effects on hatching, fecundity and survival at a dose rate  $dr$ ,  $x_H(dr)$ ,  $x_F(dr)$  and  $x_S(dr)$  respectively, were applied uniformly to the survival and fecundity rates  $P_i(0)$  and  $F_i(0)$  in the control matrices assuming that: 1) reduction in hatching applied to survival in the egg stage; 2) reduction in survival after a time  $t_{obs}$  applied to the juvenile or adult stage (specific of each life stage if data is available or common to the juvenile and adult stages otherwise); 3) reduction in fecundity applied to the adult stage. Thus:

$$\begin{cases} P_i(dr) = P_i(0) \cdot [x_H(dr)]^{1/i_H} & \text{with } 1 \leq i \leq i_H \\ P_i(dr) = P_i(0) \cdot [x_S(dr)]^{1/t_{obs}} & \text{with } i_H \leq i < i_M \quad \text{or } i_M \leq i < i_{max} \\ F_i(dr) = F_i(0) \cdot x_F(dr) & \text{with } i_M \leq i < i_{max} \end{cases}$$

with  $P_i(dr)$  and  $F_i(dr)$  the survival and fecundity rates in age class  $i$  at a dose rate  $dr$ . Effects on survival time were translated to effects on survival rates assuming that survival time represented the time required to reduce a population to 10% of its initial size, *i.e.*:

$$x_S(dr) = (0.1)^{\left[ \frac{1}{t_{dr}} - \frac{1}{t_0} \right]}$$

with  $t_0$  and  $t_{dr}$  the survival times in the control and at the dose rate  $dr$  respectively.

Values of  $\lambda(dr)$  and  $R_0(dr)$  were calculated as explained above and expressed as percent reduction relative to the control  $\lambda(0)$  and  $R_0(0)$  for  $dr$  ranging from 0 to  $10^8 \mu\text{Gy h}^{-1}$ . Effective dose rates  $R_0\text{-EDR}_x$  and  $\lambda\text{-EDR}_x$  causing  $x = 10, 20$  or  $50\%$  effect on  $R_0$  and  $\lambda$  respectively and extinction dose rates ( $Ex\text{-EDR}$ ) causing the extinction of the population ( $\lambda \leq 1$ ) were calculated.

### 3.1.5. Building and propagating uncertainty

Uncertainty and confidence intervals (95%) were built using a parametric bootstrap method. To do so, datasets were simulated for each endpoint and species by randomly sampling residual values from a normal distribution. Sampling was achieved within a range from  $-3\sigma$  to  $3\sigma$ , where  $\sigma$  was the standard deviation of observed residuals to avoid extreme values while exploring 99% of the distribution. A dose rate response curve was adjusted to each sampled data set and the procedure was repeated to obtain 10,000 parameter sets for each endpoint (hatching, fecundity and survival). Sometimes, the parameter estimation process apparently failed to converge, leading to aberrant parameter values. Such cases were

not included in the analysis. Bootstrap and fitting were performed using the R software (R Development Core Team, 2010) with the *drc* and *boot* packages (Ritz & Streibig, 2005).

Uncertainty was propagated:

- **To the population level.** In each species, we randomly combined dose response curves using Leslie matrices to obtain 10,000 response curves of  $\lambda(dr)$  and  $R_0(dr)$  over the range of dose rates.
- **Among mammal species.** Randomly pairing dose rate response curves between the mouse and the goat for fecundity and between the mouse and the dog for survival allowed establishing 10,000 allometric relationships with body mass and estimate 10,000 new parameter sets (EDR50 and slope parameter) for all additional mammalian species.

#### 3.1.6. Lowest significant effects

This point aimed to estimate dose rate thresholds (hereafter referred to as  $R_0$ -loEDR and  $\lambda$ -loEDR) above which  $R_0(dr)$  and  $\lambda(dr)$  became significantly lower than their respective control values  $R_0(0)$  and  $\lambda(0)$ . To achieve this estimation, the 10,000 response curves of  $R_0(dr)$  were used to calculate 5,000 random values of  $\Delta R_0(dr) = R_0(dr) - R_0(0)$  (with  $R_0(0)$  and  $R_0(dr)$  based on independent parameter sets).  $R_0$ -loEDR was defined as the dose rate where the frequency of  $\Delta R_0(dr) > 0$  in this distribution went below  $f = 0.05$ . Other target frequency values were tested ( $f = 0.01$  and  $0.001$ ). The same approach was conducted with the 10,000 response curves of  $\lambda(dr)$  to estimate  $\lambda$ -loEDR. Values of  $R_0$ -loEDR and  $\lambda$ -loEDR were approached by dichotomy (to a precision of  $\pm 0.25 \mu\text{Gy h}^{-1}$ ). Confidence intervals (95%) were constructed by randomly pairing  $R_0$  or  $\lambda$  response curves to build  $n = 2500$  or  $5000$  distributions of  $\Delta R_0(dr)$  and  $\Delta\lambda(dr)$ .



## 3.2. Life history parameters

Considered species, for which data on chronic effects of external irradiation on survival of main life stages (*i.e.*, eggs, juveniles and adults) and on fecundity were available in the FREDERICA database, included the following species covering four taxonomic groups.

### 3.2.1. Aquatic invertebrates

Aquatic invertebrates (Table 2) were represented by two marine polychaetes, *Neanthes arenaceodentata* and *Ophryotrocha diadema*, and a freshwater gastropod, *Physa heterostropha*. The polychaetes *N. arenaceodentata* and *O. diadema* are important members of benthic marine communities and one of the major food resources for fish and crustaceans (Akesson, 1983). The gastropod *P. heterostropha* (syn. *P. acuta* and *integra*) lives and feeds in the water column (*e.g.*, on sediments, stones, macrophytes) and might be the most widespread freshwater gastropod in the world (Dillon et al., 2002).

Further life cycle specificities are given below:

1) *N. arenaceodentata* is a unisexual polychaete with a sex ratio of 50%. The species is semelparous and short-lived because females die soon after reproduction (Pesch et al., 1991).  $P_{repro}$  is determined by the proportion of males and females establishing pairs between 11 and 14 weeks of age (88%) and the proportion of pairs producing fertilized eggs (86%) (Oshida et al., 1981; Pesch et al., 1991; Moore and Dillon, 1993; Harrison and Anderson, 1994; Bridges et al., 1996).

2) *O. diadema* is an iteroparous hermaphroditic polychaete. Fecundity is age-dependent, with reproductive output reaching maximum (30-40 eggs day<sup>-1</sup>) four weeks after maturity. Cocoons are released at intervals of about 3 days with an average lifetime total of  $14 \pm 1$  cocoons and  $313 \pm 15$  eggs produced per adult (Akesson, 1983; Premolli and Sella, 1995; Knowles and Greenwood, 1994; 1997; Sella and Lorenzi, 2000).

**Table 2. Life-history parameters for aquatic invertebrates.**

Data from the literature are reported as mean ( $\pm$  standard deviation when available). Age-specific values depend on age  $i$  (week).

	<i>Neanthes arenaceodentata</i>	<i>Ophryotrocha diadema</i>	<i>Physa heterostropha</i>
% hatching $H$	54.6 $\pm$ 2.5	75.0 $\pm$ 1.2	90.4 $\pm$ 2.0
Age (weeks)			
Hatching $i_H$	3	2	1
Maturity $i_M$	14	5	7
Lifespan $i_{max}$	15 (death after reproduction)	31	22
Survival rates $P_i$ (week <sup>-1</sup> )			
Egg	0.82 $\pm$ 0.01	0.87 $\pm$ 0.01	0.90 $\pm$ 0.02
Juvenile	0.96 $\pm$ 0.01	0.97 $\pm$ 0.01	$i < 4$ : 0.75 $\pm$ 0.01 $i = 4$ : 0.92 $\pm$ 0.01 $i > 4$ : 0.93 $\pm$ 0.01
Adult	0.96 $\pm$ 0.01	0.97 $\pm$ 0.01	0.93 $\pm$ 0.01
		declining by 0.03 per week for $i > 13$	
% reproducing adults $p_R$	38	95	91
Reproduction rates $R_i$ (eggs week <sup>-1</sup> )			
	330 $\pm$ 6	increasing from 30 $\pm$ 1 ( $i = 6$ ) to 60 $\pm$ 3 ( $i = 9$ )	varying from 27 $\pm$ 3 ( $i = 9$ ) to 165 $\pm$ 7 ( $i = 15$ )
		declining by 10% per week for $i > 12$	21 $\pm$ 3 for $i > 15$
References	Oshida et al., 1981; Pesch et al., 1991; Moore & Dillon, 1993; Harrison & Anderson, 1994; Bridges et al., 1996	Akesson, 1983; Premolli & Sella, 1995; Knowles & Greenwood, 1994; 1997; Sella & Lorenzi, 2000; Lorenzi et al., 2006	De Witt, 1967; Ravera, 1967; Cooley & Miller, 1971; Cooley, 1973; Fujita & Egami, 1984; Wethington & Dillon, 1997; Monsutti-Grecescu, 1998; Jarne et al., 2000; Henry, 2002; Escobar et al., 2008; Auld & Relyea, 2010

3) *P. heterostropha* is a hermaphroditic gastropod which preferentially outcrosses (Wethington and Dillon, 1997, Jarne et al., 2000). The species lays egg capsules, typically containing a few ten eggs (Jarne et al., 2000; Henry, 2002). Fecundity is age-dependent reaching maximum between 8 and 15 weeks of age (De Witt, 1967; Ravera, 1967; Cooley and Miller, 1971; Cooley, 1973; Fujita and Egami, 1984; Monsutti-Grecescu, 1998; Henry, 2002; Auld and Relyea, 2010).

### 3.2.2. Soil invertebrates

Soil invertebrates (Table 3) were represented by two terrestrial oligochaetes belonging to the earthworm family Lumbricidae, *E. fetida* and *L. terrestris*, and the common woodlouse, *P. scaber* (Latreille 1804), which is a terrestrial crustacean. Earthworms contribute to soil formation and maintenance of soil structure and fertility and increase the nutrient availability for plants and other organisms (Edwards, 2004). They also constitute a major food source for many soil and terrestrial invertebrate and vertebrate species. The woodlouse *P. scaber* has a key role in the organic matter decomposition in soils (Lemos et al., 2010). The life cycle characteristics described below are mainly obtained from experiments performed at ~20, 15 and 15-20 °C for *E. fetida*, *L. terrestris*, and *P. scaber*, respectively.

1) *E. fetida* is an epigeic earthworm species which typically lives in compost or manure heaps. It is one of the most frequent used species in standard soil toxicity testing (OECD, 2004; Spurgeon et al., 2003) due to the ease with which it can be obtained and experimented upon, its high reproductive capacity and short life-cycle. *E. fetida* is a hermaphrodite characterized by reciprocal crossover fertilization (Cluzeau et al., 1992). At constant temperature (~20°C), it will be a continuous breeder producing from 2 to 5 cocoons per worm per week. The hatchability of cocoons is generally high (90-100%) (e.g. Heckmann et al., 2011; Hertel-Aas et al., 2007, 2011) and an average of around 3 hatchlings emerge per cocoon

**Table 3. Life-history parameters for soil invertebrates.**

Parameters at optimal temperatures of 20-25 °C for *E. fetida* and 10-15 °C for *L. terrestris* (reviewed by Lowe and Butt, 2007). Data from the literature are reported as mean ( $\pm$  standard deviation when available). Age-specific values depend on age  $i$  (month).

	<i>Eisenia fetida</i>	<i>Lumbricus terrestris</i>	<i>Porcellio scaber</i>
% hatching $H$	96	71	79
Age (months)			
Hatching $i_H$	1	3	1
Maturity $i_M$	3	7	13
Lifespan $i_{max}$	20	31	30
Survival rates $P_i$ (month <sup>-1</sup> )			
Egg	0.96	0.892	0.79
Juvenile	0.985	0.988	$i < 4$ : 0.8426 $i \geq 4$ : 0.9828
Adult	0.899	0.968	0.9388
% reproducing adults $p_R$	100 (hermaphroditic)	100 (hermaphroditic)	50 (unisexual)
Reproduction rates $R_i$ (eggs month <sup>-1</sup> )	increasing from 24.1 ( $i = 4$ ) to 28.8 ( $5 \leq i \leq 17$ ) declining for $i > 17$ 21.6 ( $i = 18$ ) 10.1 ( $i = 19$ ) 0.7 ( $i = 20$ )	increasing from 1.2 ( $i = 8$ ) 1.8 ( $i = 9$ ) to 2.9 ( $10 \leq i \leq 20$ ) declining by 2% per month for $i > 20$ to 0.55 ( $i = 31$ )	1 <sup>st</sup> reproductive period 10.1 ( $i = 14$ ) 2.4 ( $i = 15$ ) 6.9 ( $i = 16$ ) 4.4 ( $i = 17$ ) Non productive period ( $18 \leq i \leq 26$ )  2 <sup>nd</sup> reproductive period 20.3 ( $i = 27$ ) 5.1 ( $i = 28$ ) 15.2 ( $i = 29$ ) 10.1 ( $i = 30$ )
References	Hertel-Aas et al. 2007; Hertel-Aas et al. 2011; Spurgeon & Hopkin, 1996; Michon, 1954 cited in Gates, 1972; Venter & Reinecke, 1988	Svendsen et al., 2005; Butt, 1993; Butt et al., 1994	Sutton et al., 1984; Warburg et., 1984; Donker et al., 1993a,b; Whittington et al., 1993; Van Brummelen et al., 1996; Zimmer & Topp, 1997; Zimmer, 2002; Kolar et al., 2008; Lemos et al., 2009, 2010;

(e.g. Edwards and Bohlen, 1996; Hertel-Aas et al., 2007; 2011). The embryonic development takes from 3 to 4 weeks and the juveniles reach the adult stage 7 to 12 weeks after hatching (Edwards and Bohlen, 1996; Hertel-Aas et al., 2007, 2011; OECD, 2004; Spurgeon and Hopkin, 1996). The average and maximum life expectancy have been reported to be approximately 21 months (Michon, 1954 cited in Gates (Gates, 1972) and 54 to 60 months (Herlant-Meewis, 1967 cited in Gates 1972), respectively.

2) *L. terrestris* is an anecic earthworm which occurs in pasture land where it lives in deep vertical burrows within the soil (Edwards and Bohlen, 1996). It is considered as a more ecologically relevant species than *E. fetida* and the reproductive capacity is much lower. *L. terrestris* is also a reciprocal hermaphrodite and it produces approximately 0.5 to 0.75 cocoons per week (Butt et al., 1992; Svendsen et al., 2005). The hatchability of cocoons is lower than for *E. fetida*, varying from 56 to 84 % (Butt, 1993; Butt et al., 1994; Daniel., 1992; Svendsen et al., 2005). The embryonic development lasts for at least 13 weeks and only one hatchling emerge from each cocoon. It reaches sexual maturity after approximately 5 months, and a median adult survival time of 21.5 months has been estimated (Svendsen et al 2005).

3) *P. scaber* is unisexual and the sex ratio in the field is about 1 throughout the year (Donker et al., 1993a). They have distinct reproductive periods and females will probably have two broods during their lifetime. After fertilization, the eggs are stored in the brood pouch for 26 to 30 days (Lemos et al., 2010; Whittington et al., 1993), and the newly hatched mancae (larvae) is kept there for several days after which they are released from the female (Whittington et al., 1993). The number of embryos in the brood depends on the size of the female with an average of around 20 mancae delivered following one pregnancy (Donker et al., 1993b; Lemos et al., 2010; Zimmer and Topp, 1997). The juveniles become sexually matured after approximately one year and the maximum life-span was reported to be 30 months (Sutton et al., 1984).

### 3.2.3. Fish

Fish (Table 4) are represented by two freshwater species, the Japanese medaka *Oryzias latipes* and the guppy *Poecilia reticulata*, and a freshwater salmonid, the rainbow trout *Oncorhynchus mykiss* (replaced in future modeling developments by the Chinook salmon *Oncorhynchus tshawytscha* as more effect data are available for this species). Fish are important members of the aquatic communities, as low trophic level consumers (herbivorous or planktivorous species) or higher trophic level predators (piscivorous species). Life cycle specificities are given below ([www.fishbase.org](http://www.fishbase.org)):

1) Rainbow trout and steelhead trout are freshwater resident and ocean-going forms of the same salmonid species *Oncorhynchus mykiss*. Native to tributaries of the North Pacific Asia and America, the species has been introduced to all continents. Like salmon, steelheads are anadromous: they return to their original freshwater hatching ground to spawn after two to three years at sea (fecundity of 3000 to 5000 eggs). The species is capable of iteroparity if it can return to the ocean after spawning and has very slow ageing, with a maximum recorded life-span of 11 years. High mortality in streams has also been reported, suggesting that the species may be considered as semelparous (although the iteroparous reproduction could also be taken into account).

2) Japanese medaka, *Oryzias latipes*, native of freshwaters and brackish waters of East Asia, is a widely used organism in biological investigations because of its high fecundity, small adult size, and ease of husbandry. Every few days, females spawn a cluster of 15-20 externally fertilized eggs attached to the female before deposition onto vegetation or the bottom. A mean proportion of hatching eggs of 73% has been reported, with egg development of 10 days and species longevity of 347 to 485 days.

3) The guppy *Poecilia reticulata* is native of the Amazonian area and has been introduced to

**Table 4. Life-history parameters for fish.**

Data from the literature are reported as mean ( $\pm$  standard deviation when available). Age-specific values depend on age  $i$  (month).

	<i>Oryzias latipes</i>	<i>Poecilia reticulata</i>	<i>Oncorhynchus mykiss</i>
% hatching $H$	75	n.a. (ovoviviparous)	n.d.
Age (months)			
Hatching $i_H$	0.5	0 (ovoviviparous)	1
Maturity $i_M$	4.5	2.6	34
Lifespan $i_{max}$	20	28	35 (death after reproduction)
Survival rates $P_i$ (month <sup>-1</sup> )			
Early life stages	0.84 0.95	0.9	0.77 0.95
Initial mortality rate (year <sup>-1</sup> )	0.1	0.7	0.9
Mortality rate doubling time (year)	0.2	0.4	2
% reproducing adults $p_R$	50 (unisexual)	50 (unisexual)	50 (unisexual)
Reproduction rates $R_i$ (offspring year <sup>-1</sup> )	10 broods month <sup>-1</sup> 45 eggs per brood $R_i = 175$ ( $i = 5$ ) $R_i = 350$ ( $i > 5$ )	1 brood month <sup>-1</sup> 30 eggs per brood $R_i = 21$ ( $i = 3$ ) $R_i = 30$ ( $i > 4$ )	1 spawning trip 5000 eggs $R_i = 5000$ ( $i = 35$ )
References	Man and Hodgkiss (1981); Egami (1971); Balon (1990); Howard et al. (1998); Teather et al. (2000); Davis et al. (2002); Dhillon & Fox (2004); Iwamatsu (2004); Leaf et al. (2011)	Animal Aging and Longevity Database <a href="http://genomics.senescence.info/species/">http://genomics.senescence.info/species/</a>  FishBase Database <a href="http://www.fishbase.org">http://www.fishbase.org</a>	

many countries on all continents, as one of the most popular freshwater aquarium species. It is a small member of the Cyprinodontiformes, with a longevity of 2 years and like all other members of the Poeciliid family is ovoviviparous (*i.e.* live-bearing). Males possess a modified tubular anal fin, the *gonopodium*, used to inseminate female guppies. The gestation period is on average of 28 days, varying with water temperature. Broods are on average of 28 free swimming fry which reach maturity within three to four months. After giving birth, the female is ready for mating within only a few hours.

#### 3.2.4. Terrestrial mammals

Terrestrial mammals (Tables 5-1&2) are represented by two muroid rodents, the house mouse *Mus musculus* and the brown rat *Rattus norvegicus*, and three larger species, the domestic dog *Canis familiaris*, the domestic goat *Capra hircus* and wild boar *Sus scrofa*. Life cycles are detailed below (AnAge database, <http://genomics.senescence.info/species/>):

1) The house mouse *Mus musculus* lives mainly associated with humans as a wild animal. As the laboratory mouse, the species is one of the most important model organisms in biology and medicine research. Breeding occurs throughout the year (however, animals living in the wild do not reproduce in the colder months, even though they do not hibernate). The gestation period is about 19–21 days. One female can have five to 10 litters per year, of six to eight young, so the mice population can increase very quickly. Males reach sexual maturity at about six weeks and females at about eight weeks, but both can breed as early as five weeks. House mice usually live under a year in the wild, due to a high level of predation and exposure to harsh environments. In captivity, however, they often live two to three years.

2) The brown rat (street rat, Norwegian rat) *Rattus norvegicus* is one of the largest muroids. This rodent has spread to all continents, making it the most successful mammal on the planet after humans. Indeed, with rare exceptions, the brown rat lives wherever humans live,



particularly in urban areas. *R. norvegicus* has also become the laboratory rat, an important model organism in biological research. As a true omnivore, the brown rat consumes almost anything, with cereals forming a substantial part of its diet. The brown rat can breed throughout the year if conditions are suitable, with a female producing up to five litters a year. The gestation period is only 21 days, and litters number seven young on average. Rats reach sexual maturity in about five weeks. The maximum life span is up to three years, although

**Table 5-1. Life-history parameters for terrestrial mammals.**

Data from the literature are reported as mean ( $\pm$  standard deviation when available). Age-specific values depend on age  $i$  (month, = 4 weeks).

	<i>Mus musculus</i>	<i>Rattus norvegicus</i>
Mass (g)	20.5	300
Age (months)		
Maturity $i_M$	1.4	3.25
First birth	2	4
Gestation time	0.6	0.75
Lifespan $i_{max}$	28	38
Survival rates		
Initial mortality rate (year <sup>-1</sup> )	0.01	0.002
Mortality rate doubling time (year)	0.3	0.3
% reproducing adults $p_R$	50 (unisexual)	50 (unisexual)
Reproduction rates $R_i$ (offspring month <sup>-1</sup> )	5.4 litters year <sup>-1</sup> 7 offspring per litter $R_i = 2.9 (i > 2)$	3.7 litters year <sup>-1</sup> 9.9 offspring per litter $R_i = 3.8 (i > 4)$
References	Animal Aging and Longevity Database <a href="http://genomics.senescence.info/species/">http://genomics.senescence.info/species/</a>	

most barely manage one. A yearly mortality rate of 95% is estimated, with predators and interspecies conflict as major causes.

3) The domestic dog *Canis lupus familiaris* (*Canis familiaris*) is a subspecies of the gray wolf (*Canis lupus*). The species is a member of the Canidae family. The dog may have been the first animal to be domesticated, as working, hunting, and companion animal in human history. Unlike obligate carnivores, dogs can adapt to a wide-ranging diet. In domestic dogs, sexual

**Table 5-2. Life-history parameters for terrestrial mammals.**

Data from the literature are reported as mean ( $\pm$  standard deviation when available). Age-specific values depend on age  $i$  (year).

	<i>Canis familiaris</i>	<i>Capra hircus</i>	<i>Sus scrofa</i>
Mass (kg)	40	61	180
Age (years)			
Maturity $i_M$	1.4	1.1	0.9
First birth	1.6	1.5	1.25
Gestation time	0.2	0.4	0.3
Lifespan $i_{max}$	14	14	18
Survival rates			
Initial mortality rate (year <sup>-1</sup> )	0.02	0.02	0.02
Mortality rate doubling time (year)	3	3	4
% reproducing adults $p_R$	50 (unisexual)	50 (unisexual)	50 (unisexual)
Reproduction rates $R_i$ (offspring year <sup>-1</sup> )	1.5 litters year <sup>-1</sup> 6 offspring per litter $R_i = 3.6 (i = 2)$ $R_i = 9 (i > 2)$	1 litters year <sup>-1</sup> 1.5 offspring per litter $R_i = 0.75 (i = 2)$ $R_i = 1.5 (i > 2)$	1.5 litters year <sup>-1</sup> 7 offspring per litter $R_i = 7.9 (i = 2)$ $R_i = 10.5 (i > 2)$
References	Animal Aging and Longevity Database <a href="http://genomics.senescence.info/species/">http://genomics.senescence.info/species/</a>		

maturity happens around age six to twelve months for both males and females. Dogs bear their litters for an average of 63 days, although the length of gestation can vary. An average litter consists of about six puppies. The aging profile of dogs varies according to their adult size (often determined by their breed): smaller dogs often live over 15–16 years, medium and large size dogs typically 10 to 13 years.

4) The domestic goat *Capra aegagrus hircus* (*Capra hircus*) is a domesticated subspecies of the wild goat of southwest Asia and Eastern Europe. The goat is a member of the family Bovidae. Goats are one of the oldest domesticated species, and have been used for their milk, meat, hair, and skins over much of the world. Goats are browsing animals, like deer, preferring to feed on vines, shrubbery and on weeds, not grazers like cattle and sheep. Goats reach puberty between three and 15 months of age, depending on breed and nutritional status. Breeding season varies with regions and climates. Gestation length is approximately 150 days. Twins are the usual result, with single and triplet births also common. Life expectancy is between 15 and 18 years.

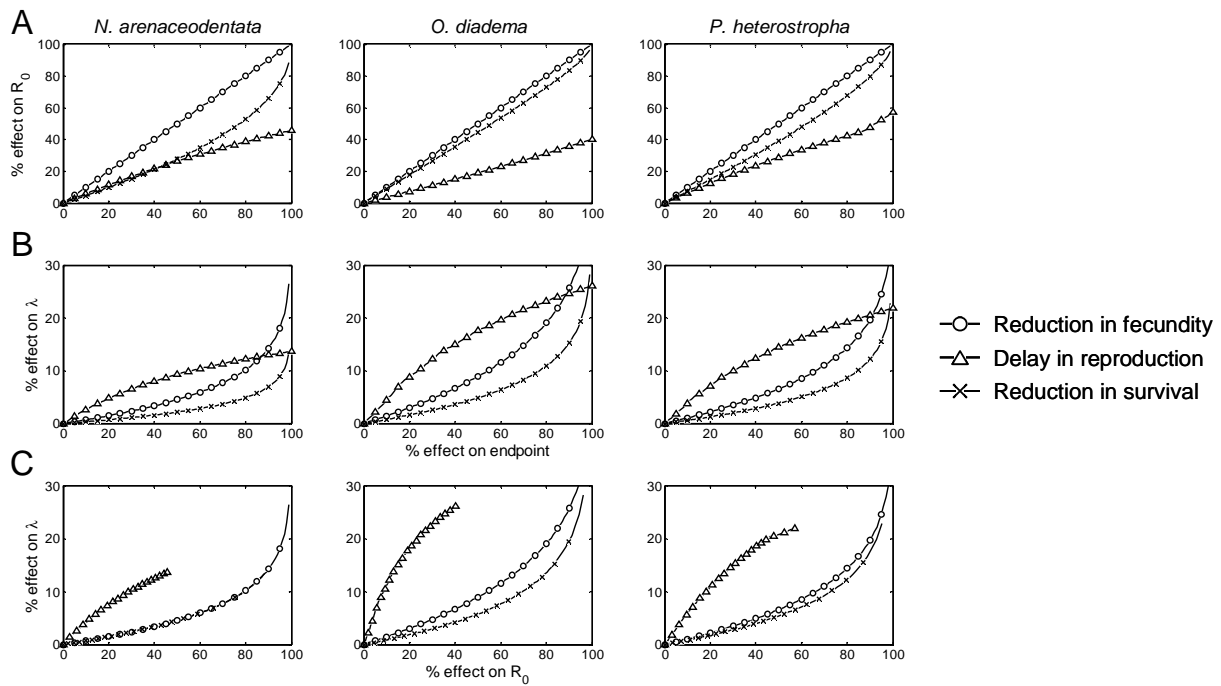
5) Wild boar *Sus scrofa* (*Sus scrofa*), also known as wild pig, is a species of the family Suidae. Native across much of Europe and much of Asia, populations have been artificially introduced in other parts of the world, most notably the Americas and Australasia. The age of puberty for sows ranges from 8 to 24 months of age depending on environmental and nutritional factors. Gestation lasts approximately 115 days, giving birth to a litter typically of 4–6 piglets.

### 3.3. Sensitivity analyses to changes in individual endpoints

#### 3.3.1. Aquatic invertebrates

Due to their relatively short longevities, population dynamics of aquatic invertebrates were described with one week as a time step. Contrasting life histories among the three tested species (Table 2) yielded different net reproductive rates  $R_0$  of 44, 237 and 317 offspring produced over a lifetime and different asymptotic population growth rates  $\lambda$  of 1.29, 1.63 and 1.92, respectively in *N. arenaceodentata*, *P. heterostropha* and *O. diadema*. The marine polychaete *N. arenaceodentata* was the slowest growing species, due to a relatively long juvenile stage and a very short reproductive period due to semelparity.

Net reproductive rate  $R_0$  was most sensitive and directly proportional to changes in fecundity independent of life history strategies (Fig. 3A). Response of  $R_0$  to changes in other life history traits differed among species and was most sensitive to changes in survival in *O. diadema* than in *N. arenaceodentata*. Delay in reproduction showed the smallest influence on  $R_0$  independent of the species. Conversely, asymptotic population growth rate  $\lambda$  was most sensitive to delay in reproduction (except for reductions in fecundity above 90%) in every species (Fig. 3B). Population  $\lambda$  showed greater variations in fast growing *O. diadema* than in the slow growing *N. arenaceodentata*. Reducing  $\lambda$  by 10% was obtained through strong reductions in fecundity (by 50 to 80%) or survival (by 80 to 95%). Comparing sensitivity between  $R_0$  and  $\lambda$  (Fig. 3C) highlighted delay in reproduction (e.g. measuring changes in age at maturity) as a highly relevant ecotoxicological endpoint for individual-to-population extrapolations.

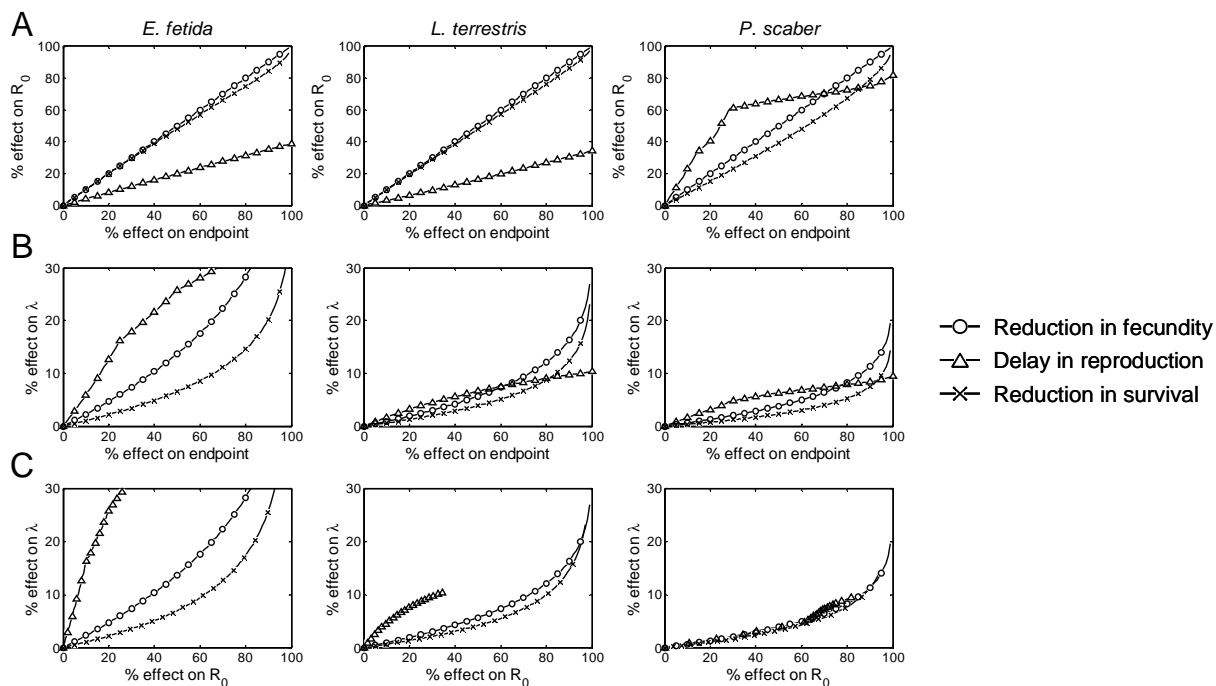


**Fig 3. Sensitivity analyses for three aquatic invertebrate species *N. arenaceodentata*, *O. diadema* and *P. heterostropha***

as responses of (A) net reproductive rate  $R_0$  (offspring per individual over a lifetime), (B) asymptotic population growth rate  $\lambda$  and (C) compared sensitivity of  $\lambda$  and  $R_0$ , to reduction in fecundity, delay in reproduction and reduction in survival (respectively expressed as % reduction in fecundity rates, % increase in age at first reproduction and % reduction in survival at twice the age at first reproduction).

### 3.3.2. Soil invertebrates

Due to relatively long lifespans in soil invertebrates (Table 3), population dynamics were described with one month (4 weeks) as a time step. Different net reproductive rates  $R_0$  of 10.6, 27.0 and 208 offspring produced over a lifetime and different asymptotic population growth rates  $\lambda$  of 1.13, 1.27 and 2.48 were obtained for *P. scaber*, *L. terrestris* and *E. fetida*, respectively. The woodlouse *P. scaber* was the slowest growing species due to a long juvenile stage and only two short reproductive periods during the lifetime. The influence of similar percentage changes of the three endpoints on the individual net reproductive rate  $R_0$  was very similar for *E. fetida* and *L. terrestris* (Fig. 4A).  $R_0$  was equally sensitive and directly



**Fig 4. Sensitivity analyses for three soil invertebrate species *E. fetida*, *L. terrestris* and *P. scaber***

as responses of (A) net reproductive rate  $R_0$  (offspring per individual over a lifetime), (B) asymptotic population growth rate  $\lambda$  and (C) compared sensitivity of  $\lambda$  and  $R_0$ , to reduction in fecundity, delay in reproduction and reduction in survival (respectively expressed as % reduction in fecundity rates, % increase in age at first reproduction and % reduction in survival at twice the age at first reproduction).

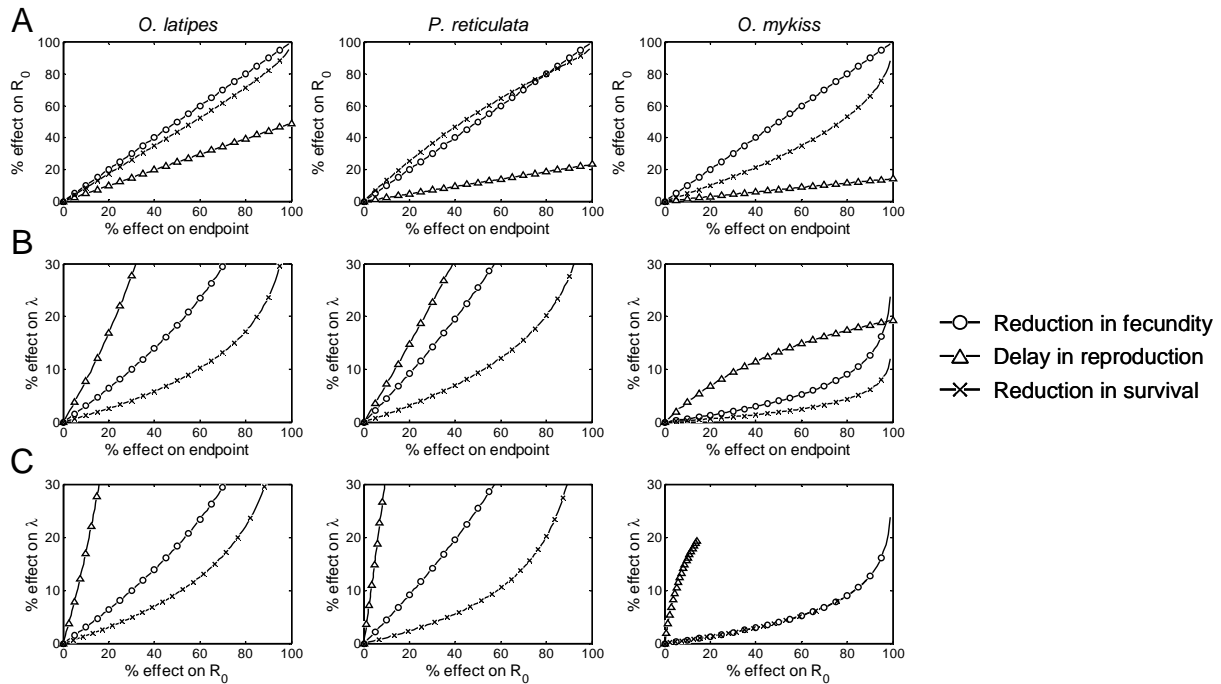
proportional to changes in fecundity and mortality in the two earthworm species, whereas delays in reproduction had smaller influence on  $R_0$ . The net reproductive rate in *P. scaber* was, on the other hand, most sensitive to delay in reproduction at effect values below 70%, whereas it became most sensitive to reduction in fecundity at higher values. The asymptotic population growth rate  $\lambda$  was most sensitive to delay in reproduction and least sensitive to effects on mortality in the prolific fast growing ( $\lambda = 2.48$ ) *E. fetida* (Fig. 4B): A 10% reduction of  $\lambda$  was obtained either by a ~12% delay in reproduction, 40% reduction in fecundity or a 70% reduction in survival. The asymptotic population growth rate was less sensitive and showed less variation in response to similar effects on the different endpoints in the slow growing *L. terrestris* ( $\lambda = 1.27$ ) and *P. scaber* ( $\lambda = 1.13$ ) (Fig 4B). A 10% reduction

of  $\lambda$  for *L. terrestris* and *P. scaber* was first obtained after either large reductions in fecundity (70 and 85%, respectively) or survival (85 and 90%, respectively) or a large delay in reproduction (85 and ~100%, respectively). Comparing sensitivity between  $R_0$  and  $\lambda$  (Fig. 4C) showed that delay in reproduction is an important ecotoxicological endpoint for *E. fetida* and *L. terrestris* populations. The situation was different in *P. scaber* where any change in  $R_0$  was associated with one effect level on population  $\lambda$  independent of the impaired individual endpoint.

### 3.3.3. Fish

Time steps of 8 weeks were chosen to describe population dynamics in the three fish species (Table 4). With population  $\lambda$  of 5.42 and 5.23, *Oryzias latipes* and *Poecilia reticulata* are much higher reproductive fish than the slow growing *Oncorhynchus mykiss*. The latter species exhibits a smaller population  $\lambda$  (1.52) in spite of its  $R_0$  of 1250.9 offspring per fish (equivalent to that of 1332.6 offspring per fish in *O. latipes* and much greater than 252.9 offspring per fish calculated in *P. reticulata*) due to semelparity and a relatively long juvenile stage.

Individual  $R_0$  in oviparous species is most affected by changes in fecundity whereas  $R_0$  in the ovoviviparous *P. reticulata* appears most sensitive to changes in survival (Fig. 5, A). As observed in aquatic invertebrates, individual  $R_0$  is relatively less sensitive to changes in survival in the slow growing semelparous species than in fast growing iteroparous species. Similarly again, population  $\lambda$  (most affected by delay in reproduction in all species) is less sensitive to changes in individual endpoints in the slow growing semelparous *O. mykiss* than in fast growing iteroparous *O. latipes* and *P. reticulata* (Fig. 5, B).



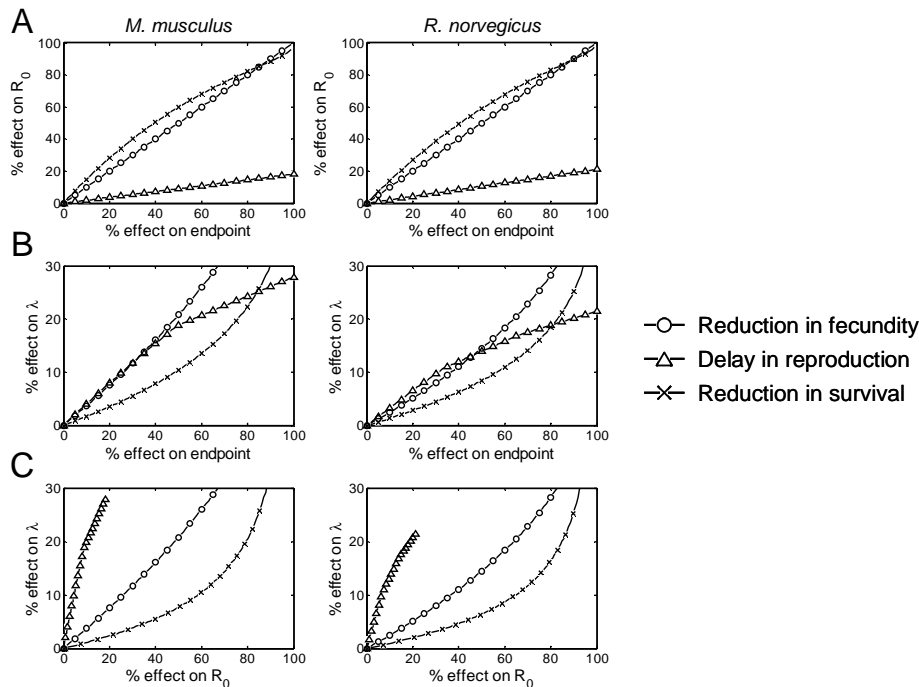
**Fig 5. Sensitivity analyses for three fish species *O. latipes*, *P. reticulata* and *O. mykiss***

as responses of (A) net reproductive rate  $R_0$  (offspring per individual over a lifetime), (B) asymptotic population growth rate  $\lambda$  and (C) compared sensitivity of  $\lambda$  and  $R_0$ , to reduction in fecundity, delay in reproduction and reduction in survival (respectively expressed as % reduction in fecundity rates, % increase in age at first reproduction and % reduction in survival at twice the age at first reproduction).

### 3.3.4. Terrestrial mammals

Considered mammals are characterized by moderate individual  $R_0$  ranging from 40-46 (*Rattus norvegicus* and *Sus scrofa*) to 32-33 (*Mus musculus* and *Canis familiaris*) and 5.5 (*Capra hircus*) offspring per individual. Population dynamics in small mammalian species (*M. musculus* and *R. norvegicus*) with short longevities are described with time steps of 8 weeks (Table 5.1) and are therefore easier to compare to those of fish. Rodents show population  $\lambda$  of 2.27 and 1.83, which range as intermediate values between fast growing and slow growing fish. Longevities are expressed in years in larger mammal species (Table 5.2). Population  $\lambda$  in *Capra hircus*, *Canis familiaris* and *Sus scrofa* (respectively 1.39, 2.26 and 2.61 when 1 year is considered as a time step) must be re-adjusted relative to a common time



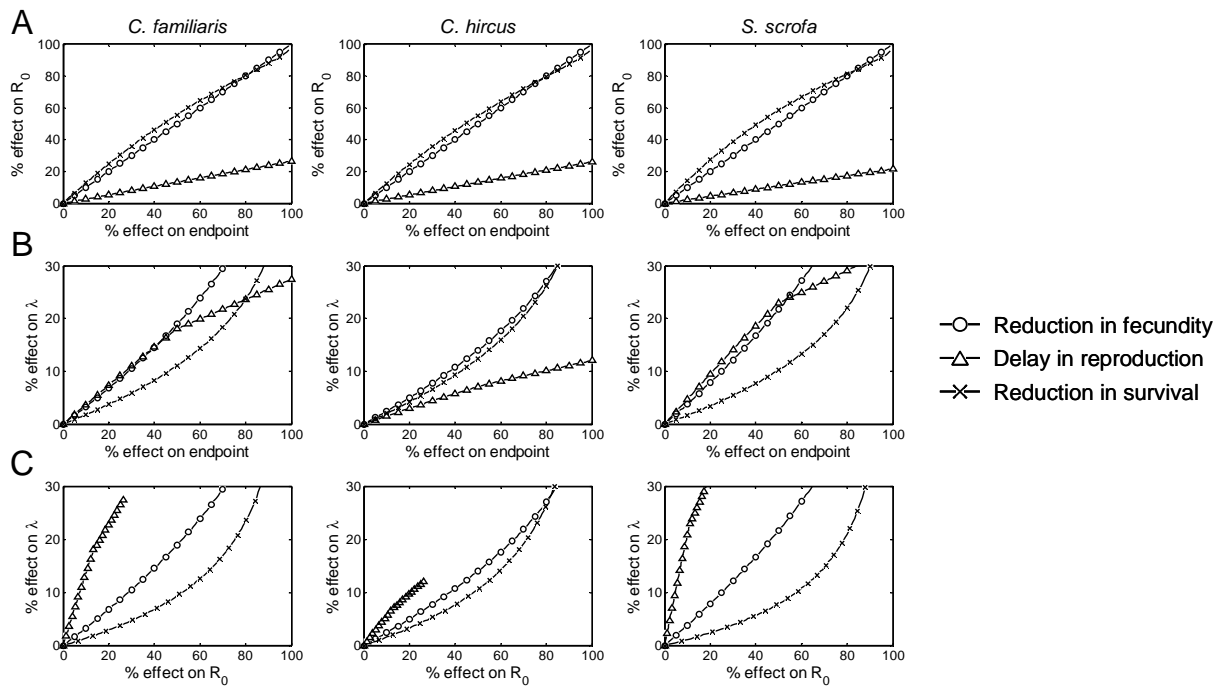


**Fig 6-1. Sensitivity analyses for two terrestrial mammalian species *M. musculus* and *R. norvegicus***

as responses of (A) net reproductive rate  $R_0$  (offspring per individual over a lifetime), (B) asymptotic population growth rate  $\lambda$  and (C) compared sensitivity of  $\lambda$  and  $R_0$ , to reduction in fecundity, delay in reproduction and reduction in survival (respectively expressed as % reduction in fecundity rates, % increase in age at first reproduction and % reduction in survival at twice the age at first reproduction).

step (becoming 1.05, 1.06 and 1.16 with time steps of 8 weeks) to be compared to that of fast growing rodents.

Individual  $R_0$  is most affected by changes in survival in all mammal species, a common feature to viviparous species and the ovoviviparous fish *P. reticulata* (Figs. 6.1 & 6.2, A). Mammals are characterized by a small  $i_M$  due to their short juvenile stage relative to longevity. As a consequence, delay in reproduction (expressed relative to  $i_M$ ) has an apparent moderate influence on population  $\lambda$  (Figs. 6.1 & 6.2, B). Delay in reproduction remains, however, a critical endpoint, considering its compared influence on  $R_0$  and  $\lambda$  (Figs. 6.1 & 6.2, C).



**Fig 6-2. Sensitivity analyses for three terrestrial mammalian species *C. familiaris*, *C. hircus* and *S. scrofa***

as responses of (A) net reproductive rate  $R_0$  (offspring per individual over a lifetime), (B) asymptotic population growth rate  $\lambda$  and (C) compared sensitivity of  $\lambda$  and  $R_0$ , to reduction in fecundity, delay in reproduction and reduction in survival (respectively expressed as % reduction in fecundity rates, % increase in age at first reproduction and % reduction in survival at twice the age at first reproduction).

### 3.4. Effects of ionising radiation on individual endpoints

The amount of available data on survival and reproduction effects of chronic gamma radiation strongly varies among species (Tables 6-1&2). Knowledge gaps were dealt with using extrapolations as described in paragraph 2.6.2. In the case of the mouse, several studies address chronic survival and provide complementary knowledge. In this case, effect data are merged together after survival rates are translated to the same time basis. Effects on reproduction are also particularly well described in the mouse, through reductions in litter size, number of litter and proportion of reproducing females. Resulting effect is considered to be the combination of the three endpoints.

**Table 6-1. FREDERICA dose response curves selected for aquatic and soil invertebrates.**

Effect description and identity number in the FREDERICA database. Extrapolations are indicated by letters: A, from acute to chronic; L, among life stages; S, among taxonomically close species; X, among radiation types.

Species and endpoints	Database ID num.	Effect description and extrapolations		Reference
<i>Neanthes arenaceodentata</i>				
Hatching	358-6	Percent hatching broods		Harrison & Anderson, 1994
Fecundity	358-13	Embryos per brood		
Survival	357-27/28	Juvenile survival to day 100	A	Anderson et al., 1990
<i>Ophryotrocha diadema</i>				
Hatching	361-23	% hatching eggs		Knowles & Greenwood, 1994
Fecundity	361-31	Eggs per worm		
Survival	361-28	Survival to day 62		
<i>Physa heterostropha</i>				
Hatching	326-6	% hatching eggs		Cooley & Nelson, 1970
Fecundity	326-5	Eggs per snail		
Survival	326-3	Adult survival		
<i>Eisenia fetida</i>				
Hatching	Hertel-1	F0 hatching - week 9 to 12		Hertel-Aas et al., 2007
Fecundity	Hertel-2	F0 total hatchlings per adult		
Hatching	Hertel-5	F1 hatching - week 12 to 16		
Fecundity	Hertel-3	F1 total hatchlings per adult		
Survival	755-14	Survival rate at day 80	A	Suzuki & Egami, 1983
<i>Lumbricus terrestris</i>				
Survival	764-3	Survival to day 67	AX	Hancock, 1962
<i>Porcellio scaber</i>				
Hatching	772-7	Female survival to day 40	L	Nakatsuchi & Egami, 1981
Fecundity	247-12	Number of offspring per tank		Hingston et al., 2004
Survival	772-7	Female survival to day 40	AS	Nakatsuchi & Egami, 1981

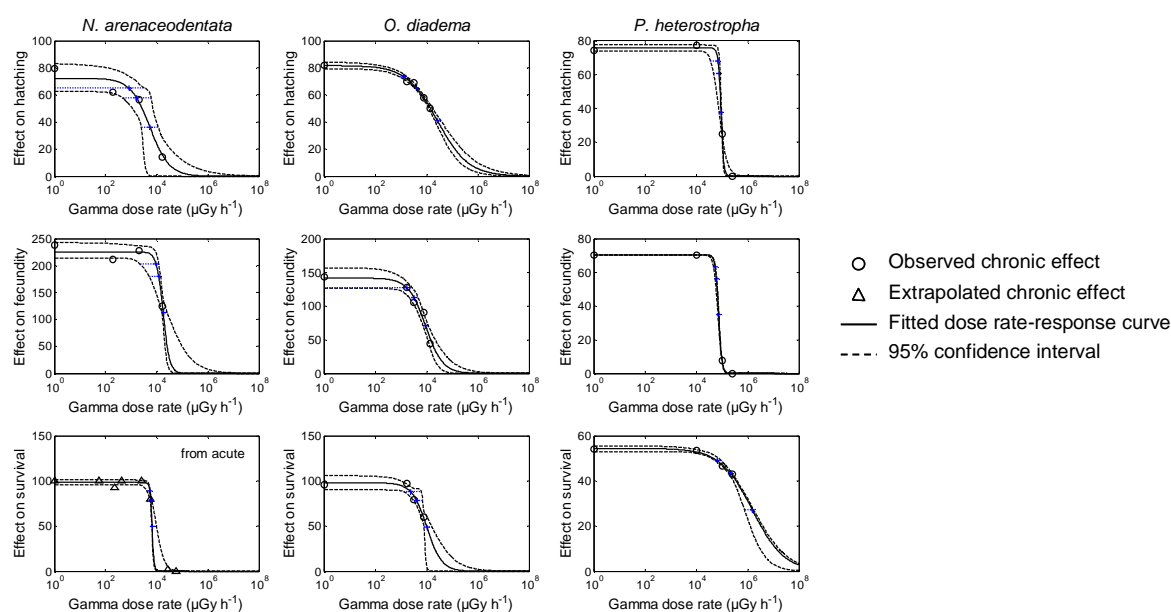
**Table 6-2. FREDERICA dose response curves selected for fish and terrestrial mammals.**

Effect description and identity number in the FREDERICA database. Extrapolations are indicated by letters: A from acute to chronic; L, among life stages; S, among taxonomically close species; X, among radiation types; M, among mammals based on allometry.

Species and endpoints	Database ID num.	Effect description and extrapolations		Reference
<i>Oryzias latipes</i>				
Hatching	16-14	Relative male hatching rate	A	Egami et al., 1983
Fecundity	16-10	Relative hatching rate	A	
Survival	204-3	Fish lifespan		Egami & Hama-Furukawa, 1980
<i>Poecilia reticulata</i>				
Fecundity	74-2/3	Mean infertility / Fecundity		Woodhead, 1977
Survival	88-1	Survival to day 30	AS	Blaylock & Mitchell, 1969
<i>Oncorhynchus mykiss</i>				
Hatching	61-1	Frequency of viable eggs	A	Newcombe & McGregor, 1972
Fecundity	170-1	Percent undifferentiated sex	S	Bonham & Donaldson, 1972
Survival	65-4	Fingerling survival to day 90	ASX	Bonham et al., 1948
<i>Mus musculus</i>				
Fecundity	{	624-4/5	Litter size	Rönnbäck, 1967
		616-1/4	Fertility span /Litter number	Rönnbäck, 1983
		624-1/2	Percent reproducing	Rönnbäck, 1967
Survival	{	618-8/10	Survival time	Mole & Thomas, 1961
		619-1	Lifespan reduction	Spalding et al., 1964
		1027-6	Survival time	Thomson & Grahn, 1989
		Tanak-19	Female survival time	Tanaka et al., 2007
<i>Canis familiaris</i>				
Fecundity		Extrapolated fecundity effect	M	Allometry with m = 40 kg
Survival	630-1	Survival at day 540		Raabe et al., 1981
<i>Capra hircus</i>				
Fecundity	622-1	Offspring over 5 litters		Austin & Hupp, 1969
Survival		Extrapolated survival effect	M	Allometry with m = 60 kg
<i>Rattus norvegicus</i>				
Fecundity		Extrapolated fecundity effect	M	Allometry with m = 300 g
Survival		Extrapolated survival effect	M	Allometry with m = 300 g
<i>Sus scrofa</i>				
Fecundity		Extrapolated fecundity effect	M	Allometry with m = 180 kg
Survival		Extrapolated survival effect	M	Allometry with m = 180 kg

#### 3.4.1. Aquatic invertebrates

Comparing radiosensitivity of individual endpoints among the three species (Fig. 7, Table 7) suggested that *N. arenaceodontata* was slightly more radiosensitive than *O. diadema*, with lowest  $EDR_{10}$  respectively of 832 and 1288  $\mu\text{Gy h}^{-1}$  respectively. In both species, hatching was the most sensitive individual endpoint although  $EDR_{10}$  confidence intervals reported for hatching overlapped with those reported for fecundity. *P. heterostropha* appeared to be the least sensitive species with a lowest  $EDR_{10}$  of 54954  $\mu\text{Gy h}^{-1}$  for fecundity, *i.e.* one order of magnitude greater than those calculated for the other species (Table 7). With the exception of *N. arenaceodontata* survival which was extrapolated from acute irradiation, all dose rate response curves were obtained from chronic exposures, making aquatic invertebrates the best described taxonomic group in terms of chronic radiosensitivity.



**Fig 7. Effects of chronic gamma radiation on individual endpoints of three aquatic invertebrate species *N. arenaceodontata*, *O. diadema* and *P. heterostropha***

as responses of hatching (% success), fecundity (number of offspring produced) and survival (% survival) on a range of dose rates. Datasets from tested chronic exposure (open circles) or from extrapolations (open triangles) as detailed in each graph. Dose rate-response curves fitted using the log-logistic model (95%-confidence intervals based on a parametric bootstrap with 10,000 resampled datasets).  $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as horizontal blue dotted lines.

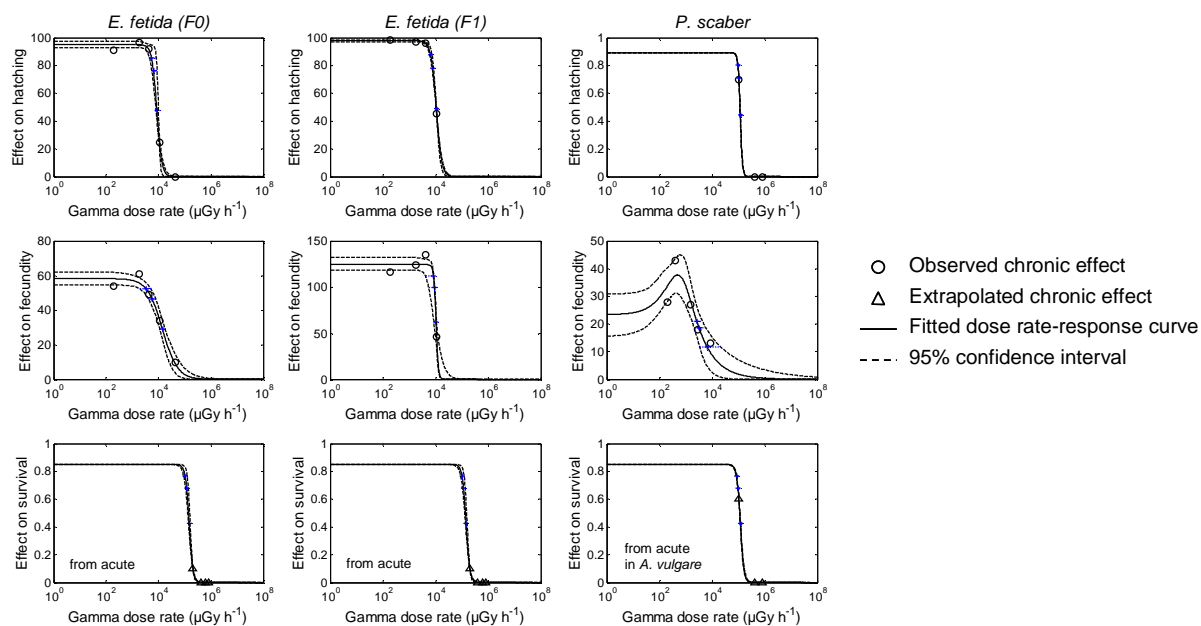
**Table 7. Effective dose rates for individual endpoints in aquatic invertebrate species.**

$EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  inducing 10%-, 20%- and 50%-effect on hatching, fecundity and survival of each studied species as derived from log-logistic dose response curves. Confidence intervals (95%) presented into brackets built using parametric bootstrap with 10,000 resampled datasets.

Endpoint and $EDR$ ( $\mu\text{Gy/h}$ )	<i>Neanthes arenaceodentata</i>	<i>Ophryotrocha diadema</i>	<i>Physa heterostropha</i>
<b>Hatching</b>			
$EDR_{10}$	832 [0 - 3631]	1288 [851 - 1738]	70795 [36308 - 81283]
$EDR_{20}$	1660 [468 - 6026]	3890 [3311 - 4571]	77625 [47863 - 85114]
$EDR_{50}$	5495 [2570 - 12023]	26915 [21379 - 36308]	93325 [77625 - 95499]
<b>Fecundity</b>			
$EDR_{10}$	9550 [2291 - 12303]	1738 [0 - 2818]	54954 [47863 - 56234]
$EDR_{20}$	12303 [5012 - 14125]	3162 [2042 - 4677]	61659 [54954 - 63096]
$EDR_{50}$	18197 [16218 - 26915]	9120 [7413 - 11749]	74131 [69183 - 75858]
<b>Survival</b>			
$EDR_{10}$	5495 [4266 - 5623]	2399 [1288 - 6310]	66069 [56234 - 97724]
$EDR_{20}$	5888 [5495 - 6607]	4074 [3090 - 7079]	208930 [177828 - 239883]
$EDR_{50}$	6761 [6457 - 10233]	10233 [7943 - 16218]	1513561 [758578 - 1737801]

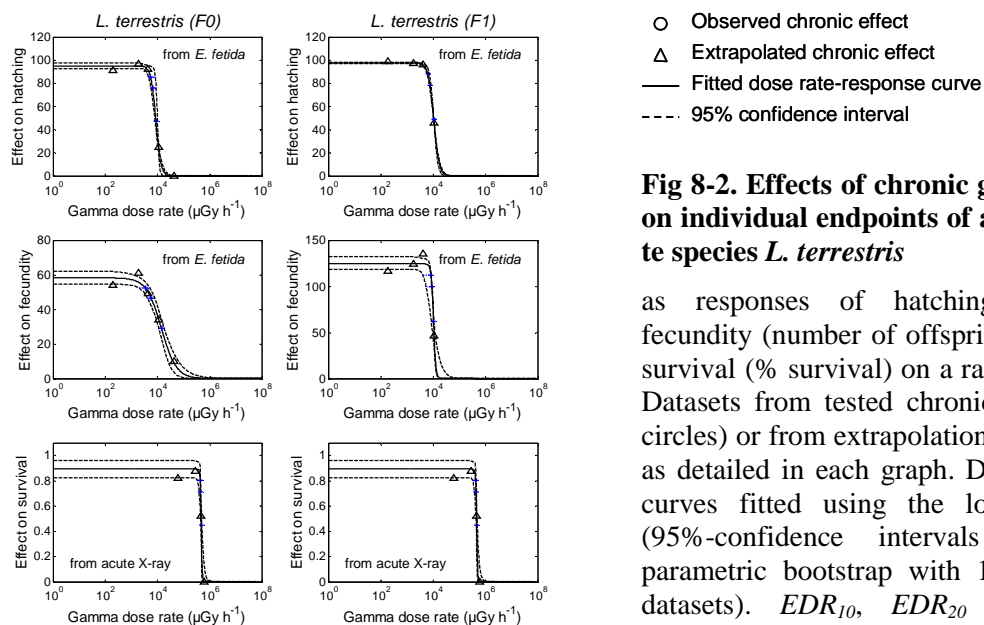
### 3.4.2. Soil invertebrates

Few individual endpoints were studied under chronic exposure in soil invertebrates. With a lowest  $EDR_{10}$  for fecundity of  $2630 \mu\text{Gy h}^{-1}$  in *Porcellio scaber* (Figs. 8-1&2, Table 8), the woodlouse appears to be more radiosensitive species than *Eisenia fetida*. The dose response curve for *P. Scaber* fecundity was, however, best fitted to the data using the Brain-Cousens's model (Brain and Cousens, 1989), indicating slightly increased fecundity compared to



**Fig 8-1. Effects of chronic gamma radiation on individual endpoints of two soil invertebrate species *E. fetida* and *P. scaber***

as responses of hatching (% success), fecundity (number of offspring produced) and survival (% survival) on a range of dose rates. Datasets from tested chronic exposure (open circles) or from extrapolations (open triangles) as detailed in each graph. Dose rate-response curves fitted using the log-logistic and Brain-Cousens models (95%-confidence intervals based on a parametric bootstrap with 10,000 resampled datasets).  $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as horizontal blue dotted lines.



**Fig 8-2. Effects of chronic gamma radiation on individual endpoints of a soil invertebrate species *L. terrestris***

as responses of hatching (% success), fecundity (number of offspring produced) and survival (% survival) on a range of dose rates. Datasets from tested chronic exposure (open circles) or from extrapolations (open triangles) as detailed in each graph. Dose rate-response curves fitted using the log-logistic model (95%-confidence intervals based on a parametric bootstrap with 10,000 resampled datasets).  $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as horizontal blue dotted lines.

controls at lower dose rates. Compared to aquatic invertebrates, *P. scaber* is more radiosensitive than the freshwater gastropod *Physa heterostropha* and more radioresistant than the marine polychaetes *N. arenaceodentata* and *O. diadema* (Table 7). In the earthworm *Eisenia fetida*, two successively exposed generations F0 and F1 yielded lowest  $EDR_{10}$  for fecundity of 3388 and 6457  $\mu\text{Gy h}^{-1}$  respectively. This observation suggested that effects were

**Table 8. Effective dose rates for individual endpoints in soil invertebrate species.**

$EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  inducing 10%-, 20%- and 50%-effect on hatching, fecundity and survival of each studied species as derived from log-logistic and Brain-Cousens dose response curves. Confidence intervals (95%) presented into brackets built using parametric bootstrap with 10,000 resampled datasets.

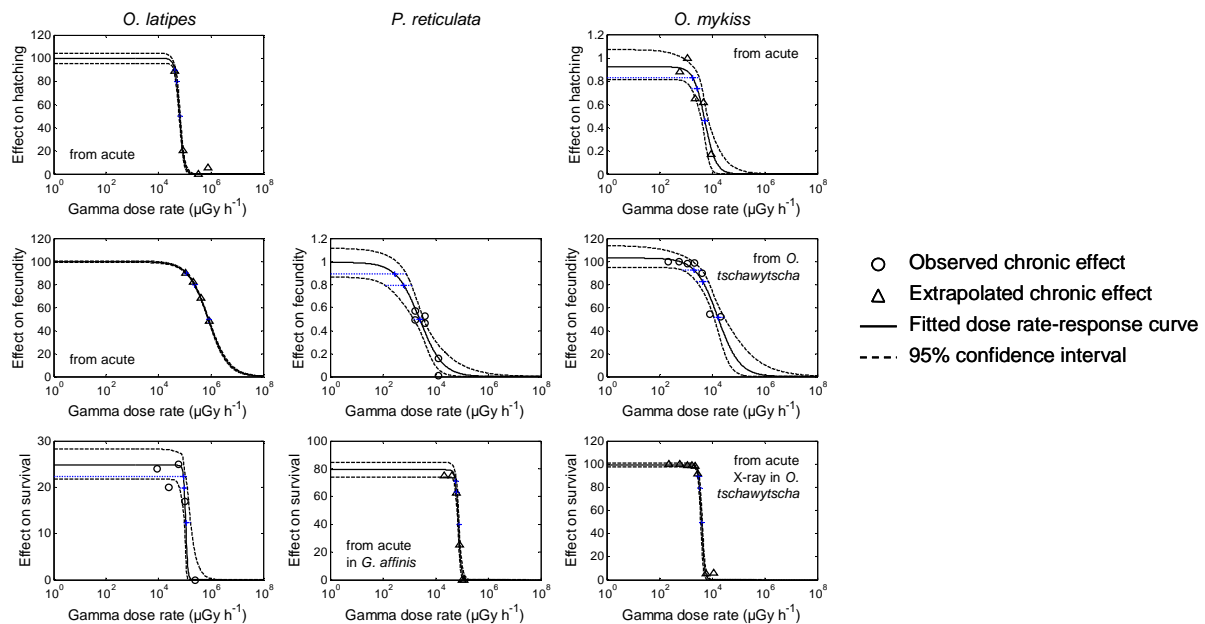
Endpoint and $EDR$ ( $\mu\text{Gy/h}$ )	<i>Eisenia fetida</i> F0	<i>Eisenia fetida</i> F1	<i>Porcellio scaber</i>
<b>Hatching</b>			
$EDR_{10}$	5495.0 [4570.5 - 8317.5]	6456.5 [6025.5 - 7413.0]	95499.0 [95499.0 - 95499.0]
$EDR_{20}$	6606.5 [5754.0 - 9119.5]	7762.0 [7413.0 - 8511.0]	104712.5 [104712.5 - 104712.5]
$EDR_{50}$	8912.0 [8128.0 - 10232.5]	510714.5 [10714.5 - 10964.5]	120226.0 [120226.0 - 120226.0]
<b>Fecundity</b>			
$EDR_{10}$	3388.0 [1949.5 - 5247.5]	8317.5 [4168.5 - 8709.0]	2630.0 [1737.5 - 4265.5]
$EDR_{20}$	5754.0 [4168.5 - 7943.0]	9119.5 [5495.0 - 9332.0]	3162.0 [2089.0 - 5888.0]
$EDR_{50}$	14454.0 [11481.5 - 18196.5]	10471.0 [8709.0 - 10964.5]	6606.5 [3388.0 - 21877.0]
Endpoint and $EDR$ ( $\mu\text{Gy/h}$ )	<i>Eisenia fetida</i>	<i>Lumbricus terrestris</i>	<i>Porcellio scaber</i>
<b>Survival</b>			
$EDR_{10}$	102329.0 [91201.0 - 123026.5]	436515.5 [338843.5 - 457088.0]	85113.5 [85113.5 - 87096.0]
$EDR_{20}$	117489.5 [107151.5 - 138038.0]	446683.5 [389045.0 - 467735.0]	97723.5 [97723.5 - 97723.5]
$EDR_{50}$	147910.5 [138038.0 - 162180.5]	5478630.0 [467735.0 - 501187.0]	120226.0 [120226.0 - 123026.5]



slightly stronger in the F0 than in the F1 generations. However, the difference was not significant, when comparisons were based on the same endpoint between the two generations. The radiosensitivity of the two earthworm species could only be compared with respect to survival, due to lack of reproduction data for *L. terrestris* (Table 8, Fig. 8-2), indicating that *E. fetida* was slightly more sensitive than *L. terrestris* with chronic  $EDR_{10}$  survival values of 102329  $\mu\text{Gy/h}$  and 436516  $\mu\text{Gy/h}$ , respectively. Both values were, however, based on extrapolations from acute exposures.

### 3.4.3. Fish

The lowest observed  $EDR_{10}$  values varied among the different fish species (Fig. 9, Table 9), ranging from 282  $\mu\text{Gy h}^{-1}$  for *P. reticulata* fecundity, 1820  $\mu\text{Gy h}^{-1}$  for *O. mykiss* hatching



**Fig 9. Effects of chronic gamma radiation on individual endpoints of three fish species *O. latipes*, *P. reticulata* and *O. mykiss***

as responses of hatching (% success), fecundity (number of offspring produced) and survival (% survival) on a range of dose rates. Datasets from tested chronic exposure (open circles) or from extrapolations (open triangles) as detailed in each graph. Dose rate-response curves fitted using the log-logistic and Brain-Cousens models (95%-confidence intervals based on a parametric bootstrap with 10,000 resampled datasets).  $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as horizontal blue dotted lines.

to 41687  $\mu\text{Gy h}^{-1}$  for *O. latipes* hatching. This observation suggested that *P. reticulata* was the most radiosensitive among the three considered fish species. However, a majority of the  $EDR_{10}$  values was derived from extrapolated dose response curves, making such conclusion highly uncertain because effects on many endpoints, were not experimentally studied under chronic gamma exposure (Table 6-2). In particular, data on fecundity which appeared to be the most sensitive endpoint in chronically exposed *P. reticulata* and *O. mykiss* was only available from acute exposure in *O. latipes*.

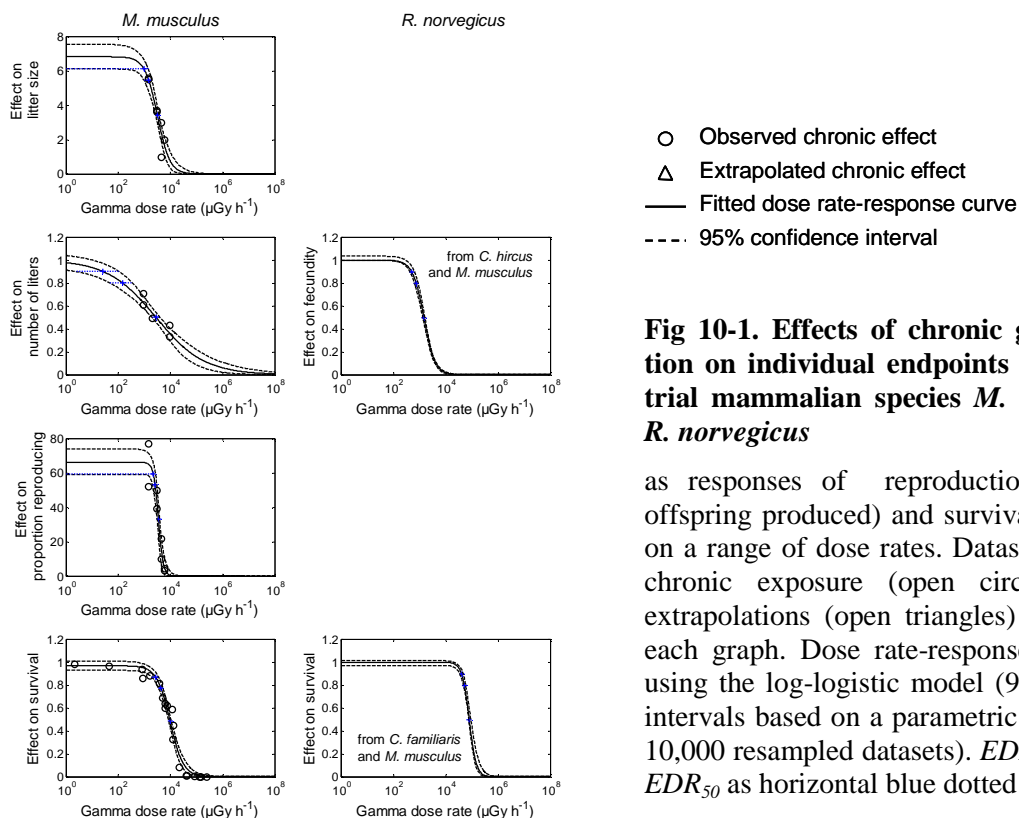
**Table 9. Effective dose rates for individual endpoints in fish species.**

$EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  inducing 10%-, 20%- and 50%-effect on hatching, fecundity and survival of each studied species as derived from log-logistic dose response curves. Confidence intervals (95%) presented into brackets built using parametric bootstrap with 10,000 resampled datasets.

Endpoint and $EDR$ ( $\mu\text{Gy/h}$ )	<i>Oryzias latipes</i>	<i>Poecilia reticulata</i>	<i>Oncorhynchus mykiss</i>
<b>Hatching</b>			
$EDR_{10}$	41686.5 [38018.5 - 45708.5]		1819.5 [0.0 - 3311.0]
$EDR_{20}$	48977.5 [45708.5 - 53703.0]	(ovoviviparous species)	2691.0 [1584.5 - 4168.5]
$EDR_{50}$	64565.0 [60255.5 - 67608.0]		5370.0 [3980.5 - 7244.0]
<b>Fecundity</b>			
$EDR_{10}$	114815.0 [109647.5 - 123026.5]	281.5 [0.0 - 794.0]	2041.5 [724.0 - 4073.5]
$EDR_{20}$	234422.5 [229086.5 - 245470.5]	630.5 [122.5 - 1258.5]	4466.5 [2570.0 - 7413.0]
$EDR_{50}$	794328.0 [776247.0 - 831763.5]	2570.0 [1513.5 - 3630.5]	16595.5 [11748.5 - 29512.0]
<b>Survival</b>			
$EDR_{10}$	89124.5 [0.0 - 107151.5]	57543.5 [48977.5 - 64565.0]	3019.5 [2884.0 - 3235.5]
$EDR_{20}$	95499.0 [63095.5 - 125892.0]	63095.5 [57543.5 - 69182.5]	3388.0 [3162.0 - 3630.5]
$EDR_{50}$	109647.5 [97723.5 - 169824.0]	75857.5 [70794.0 - 79432.5]	3980.5 [3715.0 - 4265.5]

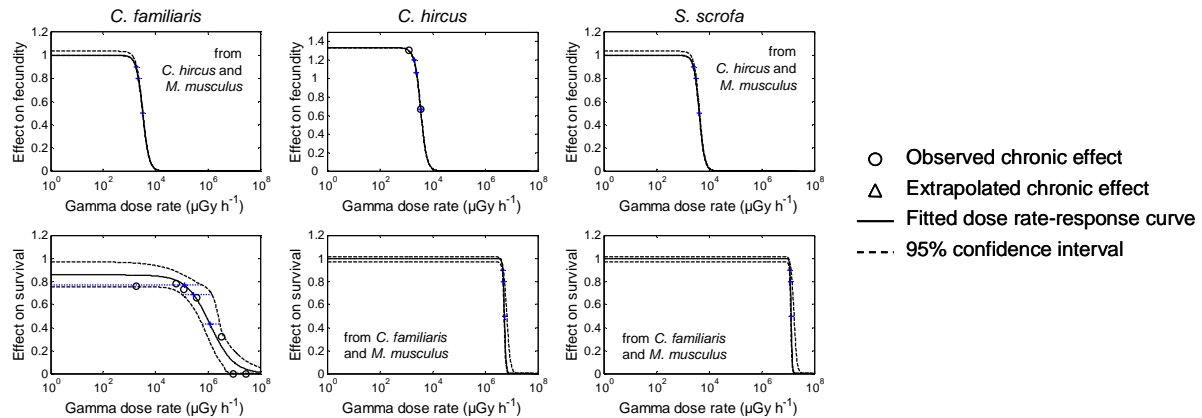
### 3.4.4. Terrestrial mammals

Although very few chronic effect data were available in mammals, this taxonomic group includes *Mus musculus* which is the most studied species under chronic gamma radiation (Figs. 10-1&2, Tables 10-1&2). The species appears as the most radiosensitive among chronically tested species (both within mammals and when all taxonomic groups are considered), with an  $EDR_{10}$  of  $26 \mu\text{Gy h}^{-1}$  for fecundity as compared to  $1995 \mu\text{Gy h}^{-1}$  in *Capra hircus*. Radiosensitivity with respect to survival is more difficult to compare. An  $EDR_{10}$  value of  $2754 \mu\text{Gy h}^{-1}$  in *M. musculus* and  $123027 \mu\text{Gy h}^{-1}$  in *C. familiaris*, indicates that the radiosensitivity differs with 2 orders of magnitude between the two species. However, this conclusion has to be mitigated, considering the difference in longevity among species. In fact, survival was normalised to a common time basis of 8 weeks, which corresponds to a



**Fig 10-1. Effects of chronic gamma radiation on individual endpoints of two terrestrial mammalian species *M. musculus* and *R. norvegicus***

as responses of reproduction (number of offspring produced) and survival (% survival) on a range of dose rates. Datasets from tested chronic exposure (open circles) or from extrapolations (open triangles) as detailed in each graph. Dose rate-response curves fitted using the log-logistic model (95%-confidence intervals based on a parametric bootstrap with 10,000 resampled datasets).  $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as horizontal blue dotted lines.



**Fig 10-2. Effects of chronic gamma radiation on individual endpoints of three terrestrial mammalian species *C. familiaris*, *C. hircus* and *S. scrofa***

as responses of reproduction (number of offspring produced) and survival (% survival) on a range of dose rates. Datasets from tested chronic exposure (open circles) or from extrapolations (open triangles) as detailed in each graph. Dose rate-response curves fitted using the log-logistic model (95%-confidence intervals based on a parametric bootstrap with 10,000 resampled datasets).  $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as horizontal blue dotted lines.

**Table 10-1. Effective dose rates for individual endpoints in terrestrial mammal species.**

$EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  inducing 10%-, 20%- and 50%-effect on reproduction (proportion reproducing, number of litters and litter size) and survival of each studied species as derived from log-logistic dose response curves. Confidence intervals (95%) presented into brackets built using parametric bootstrap with 10,000 resampled datasets.

Endpoint and $EDR$ ( $\mu\text{Gy}/\text{h}$ )	<i>Mus musculus</i>	Endpoint and $EDR$ ( $\mu\text{Gy}/\text{h}$ )	<i>Mus musculus</i>
Proportion reproducing		Litter size	
$EDR_{10}$	2238.5 [0.0 - 2753.5]	$EDR_{10}$	977.0 [0.0 - 1445.0]
$EDR_{20}$	2630.0 [2089.0 - 3090.0]	$EDR_{20}$	1513.5 [999.5 - 1995.0]
$EDR_{50}$	3548.0 [3162.0 - 3890.0]	$EDR_{50}$	3235.5 [2753.5 - 3715.0]
Number of litters		Survival	
$EDR_{10}$	26.0 [2.5 - 107.0]	$EDR_{10}$	2753.5 [1949.5 - 3548.0]
$EDR_{20}$	147.5 [48.5 - 354.5]	$EDR_{20}$	4365.0 [3548.0 - 5247.5]
$EDR_{50}$	2884.0 [2041.5 - 4073.5]	$EDR_{50}$	9772.0 [8912.0 - 10964.5]

**Table 10-2. Effective dose rates for individual endpoints in terrestrial mammal species.**

*EDR*<sub>10</sub>, *EDR*<sub>20</sub> and *EDR*<sub>50</sub> inducing 10%-, 20%- and 50%-effect on fecundity and survival of each studied species as derived from log-logistic dose response curves. Confidence intervals (95%) presented into brackets built using parametric bootstrap with 10,000 resampled datasets.

Endpoint and <i>EDR</i> (μGy/h)	<i>Canis familiaris</i>	<i>Capra hircus</i>
Fecundity		
<i>EDR</i> <sub>10</sub>	1819.5 [1778.0 - 1949.5]	1995.0 [1995.0 - 1995.0]
<i>EDR</i> <sub>20</sub>	2238.5 [2238.5 - 2344.0]	2454.5 [2454.5 - 2454.5]
<i>EDR</i> <sub>50</sub>	3311.0 [3311.0 - 3388.0]	3548.0 [3548.0 - 3548.0]
Survival		
<i>EDR</i> <sub>10</sub>	123026.5 [0.0 - 588843.0]	4786300.5 [4466835.5 - 5011872.0]
<i>EDR</i> <sub>20</sub>	281838.0 [107151.5 - 1445439.5]	5011872.0 [4897788.0 - 5623413.0]
<i>EDR</i> <sub>50</sub>	1202264.0 [602559.0 - 2884031.5]	5495408.5 [5370317.5 - 6918309.5]
Endpoint and <i>EDR</i> (μGy/h)	<i>Rattus norvegicus</i>	<i>Sus scrofa</i>
Fecundity		
<i>EDR</i> <sub>10</sub>	501.0 [426.5 - 645.0]	2570.0 [2511.5 - 2818.0]
<i>EDR</i> <sub>20</sub>	741.0 [630.5 - 870.5]	3090.0 [3019.5 - 3311.0]
<i>EDR</i> <sub>50</sub>	1479.0 [1318.0 - 1584.5]	4265.5 [4265.5 - 4466.5]
Survival		
<i>EDR</i> <sub>10</sub>	40737.5 [34673.5 - 46773.5]	11748975.5 [11220184.0 - 12882495.0]
<i>EDR</i> <sub>20</sub>	52480.5 [47862.5 - 58884.0]	12302687.5 [11748975.5 - 14454397.5]
<i>EDR</i> <sub>50</sub>	79432.5 [77624.5 - 93325.0]	13182567.0 [12589254.0 - 16982436.0]

relative age seven times older in *M. musculus* (7.1% relative to  $i_{max}$  of  $\approx 2$  years) than in *C. familiaris* (1.1% relative to  $i_{max}$  of 14 years). Expressed at an equivalent relative age (for example 1 year, 7.1% of  $i_{max}$ ), survival in *C. familiaris* would be approximately 50%, which means that the effective dose rate rather corresponds to an  $EDR_{50}$  value.

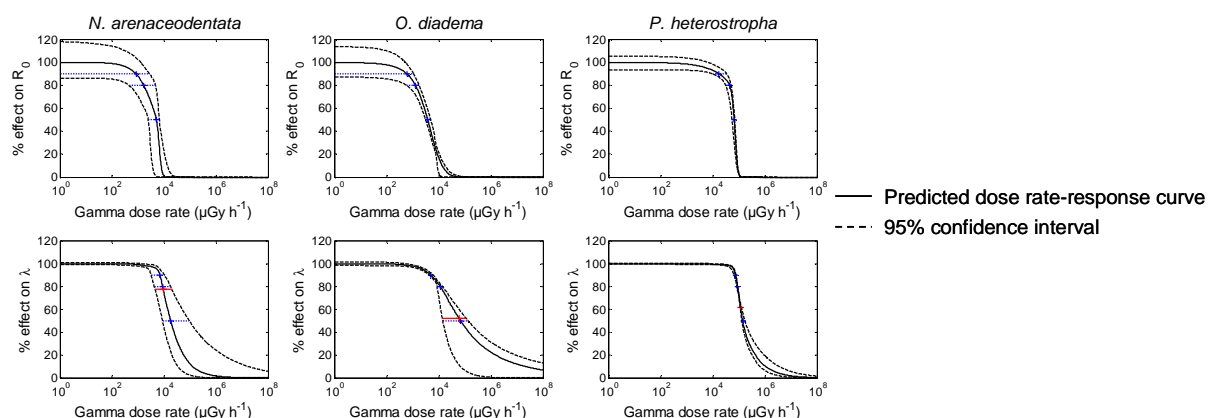
Allometric relationships lead to predictions of radioresistance with respect to survival in *C. hircus* and *S. scrofa* with  $EDR_{10}$  of 4786301 and 11748976  $\mu\text{Gy h}^{-1}$ , respectively, due to the large body mass of the two species (60 and 180 kg, respectively). These values are high compared to the  $EDR_{10}$  of 123027  $\mu\text{Gy h}^{-1}$  which was obtained experimentally for *C. familiaris* (40 kg) from chronic gamma exposure. Such inconsistent results illustrate how unsatisfactory allometric extrapolations are and strongly suggest that other extrapolations rules should be considered.

### 3.5. Combined effects of ionising radiation on individual $R_0$ and population $\lambda$

#### 3.5.1. Aquatic invertebrates

Compared to results on individual endpoints identifying *N. arenaceodentata* as the most radiosensitive species, consequences of combined effects for individual  $R_0$  and population  $\lambda$  led to a different order of radiosensitivity among species (Fig. 11, Table 11). In fact, *O. diadema* exhibited the lowest  $EDR_{10}$  for both  $R_0$  (616  $\mu\text{Gy h}^{-1}$ ) and  $\lambda$  (5012  $\mu\text{Gy h}^{-1}$ ). *P. heterostropha* remained the least sensitive species with  $EDR_{10}$  values of 17378 and 74131  $\mu\text{Gy h}^{-1}$  for  $R_0$  and  $\lambda$  respectively.

Due to their respective sensitivity to changes in individual life history traits, 10% reduction was observed at lower dose rates for net reproductive rate  $R_0$  than for asymptotic population growth rate  $\lambda$ , with a 4 to 8-fold factor in  $EDR_{10}$  values between  $R_0$  and  $\lambda$  in every



**Fig 11. Effects of chronic gamma radiation on net reproductive rate  $R_0$  (offspring produced per individual over a lifetime) and asymptotic population growth rate  $\lambda$  in three aquatic invertebrate species *N. arenaceodentata*, *O. diadema* and *P. heterostropha***

as a response to combined reductions in hatching, fecundity and survival on a range of dose rates (95%-confidence intervals as dotted lines based on a parametric bootstrap with 10,000 resampled datasets).  $R_0$ - and  $\lambda$ -EDR<sub>10</sub>, EDR<sub>20</sub> and EDR<sub>50</sub> as blue dotted lines;  $R_0$ - and  $\lambda$ -EDR causing population extinction as red continuous lines.

species (Table 11). Thus, 10%-reduction in  $\lambda$  was predicted only when several individual endpoints were strongly affected: >50% in hatching and survival in *N. arenaceodentata*; >20% in hatching, fecundity and survival in *O. diadema*; >10% in hatching and survival and >50% in fecundity in *P. heterostropha*. Population extinction ( $\lambda \leq 1$ ) was predicted at dose rates above the  $\lambda$ -EDR<sub>10</sub> in every species, for reductions in  $\lambda$  ranging from 22.3% (*N. arenaceodentata*) to 48.0% (*O. diadema*). These observations suggested that 10% reduction in  $\lambda$  or population extinction was too severe an effect to be used as a “safe” target level for protection of species at the population level.

In two species, lowest significant changes in  $R_0$  and  $\lambda$  were predicted at dose rates ( $R_0$ -loEDR and  $\lambda$ -loEDR) of 760 and 716  $\mu\text{Gy h}^{-1}$  in *O. diadema* and of 12767 and 13759  $\mu\text{Gy h}^{-1}$  in *P. heterostropha*, below the lowest EDR<sub>10</sub> reported for individual endpoints (1288  $\mu\text{Gy h}^{-1}$  in *O. diadema* and 54954  $\mu\text{Gy h}^{-1}$  in *P. heterostropha*). This suggested that some significant change in  $R_0$  and  $\lambda$  might occur, as a result of slight concomitant changes on several

**Table 11. Effective dose rates for individual  $R_0$  and population  $\lambda$  in aquatic invertebrates species.**

Dose rates inducing  $x = 10, 20$  and  $50\%$ -effect on net reproductive rate  $R_0$  and asymptotic population growth rate  $\lambda$  (respectively  $R_0$ -EDR $_x$  and  $\lambda$ -EDR $_x$ ), predicted population extinction ( $\lambda \leq 1$ ) ( $Ex$ -EDR) and lowest significant change ( $f = 0.05$ ) in  $R_0$  and  $\lambda$  (respectively  $R_0$ -loEDR and  $\lambda$ -loEDR). Confidence intervals (95%) presented into brackets built using a parametric bootstrap with 10,000 resampled datasets.

Endpoint and EDR ( $\mu\text{Gy/h}$ )	<i>Neanthes arenaceodentata</i>	<i>Ophryotrocha diadema</i>	<i>Physa heterostropha</i>
Net reproductive rate $R_0$			
$R_0$ -EDR $_{10}$	832 [0 - 2818]	616 [0 - 1096]	17378 [9550 - 33884]
$R_0$ -EDR $_{20}$	1660 [447 - 4577]	1288 [602 - 1820]	43651 [31623 - 50119]
$R_0$ -EDR $_{50}$	5128 [2512 - 6607]	3802 [3162 - 5012]	66069 [54954 - 69183]
Asymptotic population growth rate $\lambda$			
$\lambda$ -EDR $_{10}$	6918 [3236 - 10471]	5012 [4266 - 6166]	74131 [64565 - 77625]
$\lambda$ -EDR $_{20}$	8709 [4266 - 17783]	11482 [8709 - 13804]	89125 [83176 - 91201]
$\lambda$ -EDR $_{50}$	17783 [8709 - 91201]	70794 [14454 - 134896]	141254 [131826 - 169824]
Population extinction ( $\lambda \leq 1$ )			
Effect on $\lambda$ $Ex$ -EDR	22.3% 9332 [4467 - 19498]	48.0% 61659 [13804 - 114815]	38.7% 114815 [112202 - 125892]
Lowest significant change			
$R_0$ -loEDR	n = 5000 1412 [1346 - 1478]	n = 5000 760 [736 - 789]	n = 5000 12767 [12259 - 13307]
$\lambda$ -loEDR	1412 [1346 - 1478]	716 [689 - 742]	13759 [13221 - 14341]

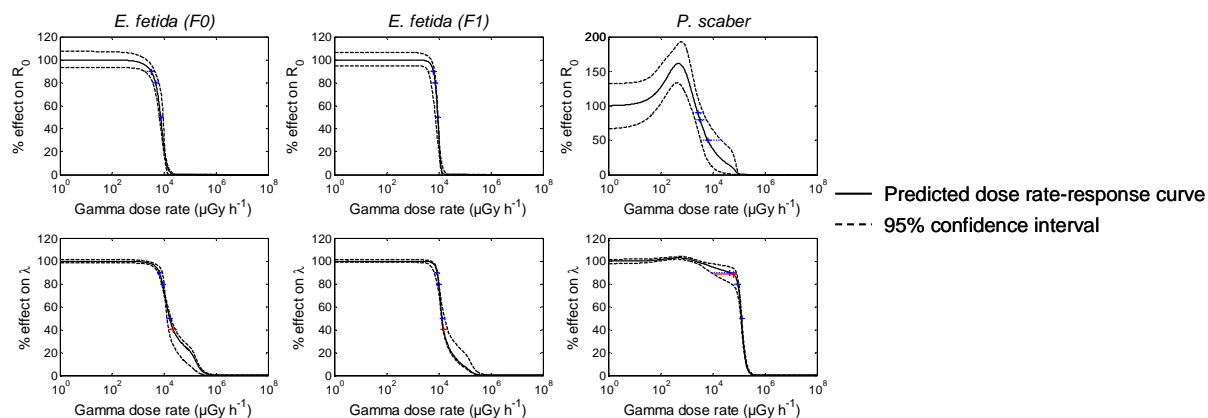
individual endpoints. In *N. arenaceodentata*, the calculated  $R_0$ - and  $\lambda$ -loEDR ( $1412 \mu\text{Gy h}^{-1}$ ) were above the lowest EDR $_{10}$  ( $832 \mu\text{Gy h}^{-1}$  for hatching). In this species, effects on several end points could not combine as fecundity and survival were affected at comparatively higher



dose rates. Finally in all species, reported *loEDR* differed only slightly between  $R_0$  and  $\lambda$ , with no difference in *N. arenaceodentata* and overlapping 95%-confidence intervals in *O. diadema* and *P. heterostropha*. Predicted values also varied significantly with the considered target frequency  $f$ , with for example  $\lambda$ -*loEDR* ranging from 2326 to 4819  $\mu\text{Gy h}^{-1}$  in *N. arenaceodentata*, from 1038 to 1413  $\mu\text{Gy h}^{-1}$  in *O. diadema* and from 20857 to 29204  $\mu\text{Gy h}^{-1}$  in *P. heterostropha*, respectively for  $f=0.01$  and  $f=0.001$ .

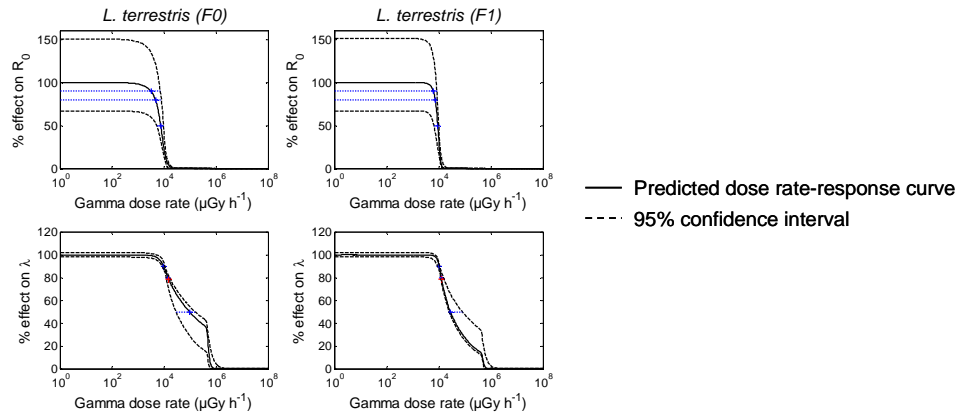
### 3.5.2. Soil invertebrates

The influence of different life history strategies on  $R_0$  and  $\lambda$  was explored in the earthworms *Eisenia fetida* and *Lumbricus terrestris* (Figs. 12-1&2, Tables 12-1&2). Responses of  $R_0$  and  $\lambda$  to gamma irradiation were calculated based on the same dose response curves for hatching and fecundity (*i.e.* those established for *E. fetida*) and distinct dose responses curves for survival (*i.e.* those specifically established for *E. fetida* and *L. terrestris*).



**Fig 12-1. Effects of chronic gamma radiation on net reproductive rate  $R_0$  (offspring produced per individual over a lifetime) and asymptotic population growth rate  $\lambda$  in two soil invertebrate species *E. fetida* and *P. scaber***

as a response to combined reductions in hatching, fecundity and survival on a range of dose rates (95%-confidence intervals as dotted lines based on a parametric bootstrap with 10,000 resampled datasets).  $R_0$ - and  $\lambda$ - $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as blue dotted lines;  $R_0$ - and  $\lambda$ -  $EDR$  causing population extinction as red continuous lines.



**Fig 12-2. Effects of chronic gamma radiation on net reproductive rate  $R_0$  (offspring produced per individual over a lifetime) and asymptotic population growth rate  $\lambda$  in a soil invertebrate species *L. terrestris***

as a response to combined reductions in hatching, fecundity and survival on a range of dose rates (95%-confidence intervals as dotted lines based on a parametric bootstrap with 10,000 resampled datasets).  $R_0$ - and  $\lambda$ - $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as blue dotted lines;  $R_0$ - and  $\lambda$ -  $EDR$  causing population extinction as red continuous lines.

In earthworms however, survival started to decline at dose rates where fecundity and hatching were strongly impaired (Figs. 8-1&2). Thus,  $R_0$  and  $\lambda$  responses to gamma irradiation were driven by changes in fecundity and hatching. Changes in  $R_0$  were predicted at a same  $R_0$ - $EDR_{10}$  in the two species, with values of 3236 and 6306  $\mu\text{Gy h}^{-1}$  respectively in generations F0 and F1. This was because  $R_0$  was equally sensitive to changes in individual endpoints between *E. fetida* and *L. terrestris* (Fig. 4-A&B). One might conclude that in earthworms, life history had no influence on  $R_0$ . However, due to different uncertainty in control  $R_0$  values between the two species, lowest significant changes in  $R_0$  were detected at higher  $R_0$ - $loEDR$  in *L. terrestris* (7059 and 8246  $\mu\text{Gy h}^{-1}$  in F0 and F1 respectively) than in *E. fetida* (2610 and 5200  $\mu\text{Gy h}^{-1}$  in F0 and F1 respectively). Conversely, changes in  $\lambda$  were predicted at different  $\lambda$ - $EDR_{10}$  between the two species, with F0 and F1 values of 6607 and 8709  $\mu\text{Gy h}^{-1}$  in *E. fetida* and of 9550 and 10471  $\mu\text{Gy h}^{-1}$  in *L. terrestris*, depending on the generation. This was because  $\lambda$  was more sensitive to changes in individual endpoints in *E. fetida* than *L. terrestris* (Fig. 4-A&B). As in aquatic invertebrates,  $\lambda$ - $loEDR$  followed the same trend as  $R_0$ - $loEDR$

(Fig. 4-A&B). As in aquatic invertebrates,  $\lambda$ -loEDR followed the same trend as  $R_0$ -loEDR (Tables 12-1&2). Finally, with a two-fold factor in control values of  $\lambda$  between the fast growing *E. fetida* and the slow growing *L. terrestris*, population extinction was predicted for

**Table 12.1. Effective dose rates for individual  $R_0$  and population  $\lambda$  in soil invertebrate species.**

Dose rates inducing  $x = 10, 20$  and  $50\%$ -effect on net reproductive rate  $R_0$  and asymptotic population growth rate  $\lambda$  (respectively  $R_0$ -EDR $_x$  and  $\lambda$ -EDR $_x$ ), predicted population extinction ( $\lambda \leq 1$ ) ( $Ex$ -EDR) and lowest significant change ( $f = 0.05$ ) in  $R_0$  and  $\lambda$  (respectively  $R_0$ -loEDR and  $\lambda$ -loEDR). Confidence intervals (95%) presented into brackets built using a parametric bootstrap with 10,000 resampled datasets.

Endpoint and EDR ( $\mu\text{Gy/h}$ )	<i>Eisenia fetida</i> F0	<i>Eisenia fetida</i> F1	<i>Porcellio scaber</i>
Net reproductive rate $R_0$			
$R_0$ -EDR $_{10}$	3235.5 [1778.0 - 4466.5]	6309.5 [3890.0 - 6918.0]	2630.0 [1737.5 - 4265.5]
$R_0$ -EDR $_{20}$	4677.0 [3715.0 - 6309.5]	7413.0 [5128.0 - 7762.0]	3162.0 [2089.0 - 5888.0]
$R_0$ -EDR $_{50}$	7413.0 [6760.5 - 9332.0]	9332.0 [7585.5 - 9549.5]	6606.5 [3388.0 - 21877.0]
Asymptotic population growth rate $\lambda$			
$\lambda$ -EDR $_{10}$	6606.5 [5754.0 - 8709.0]	8709.0 [6760.5 - 8912.0]	44668.0 [8709.0 - 79432.5]
$\lambda$ -EDR $_{20}$	8709.0 [8128.0 - 9999.5]	9999.5 [8709.0 - 10232.5]	91201.0 [52480.5 - 97723.5]
$\lambda$ -EDR $_{50}$	16217.5 [12882.0 - 18196.5]	13489.5 [12882.0 - 16982.0]	125892.0 [117489.5 - 128824.5]
Population extinction ( $\lambda \leq 1$ )			
Effect on $\lambda$	59.7%	59.7%	11.5%
$Ex$ -EDR	22386.5 [14791.0 - 26915.0]	15135.5 [14454.0 - 22386.5]	61659.0 [11219.5 - 83176.0]
Lowest significant change			
$R_0$ -loEDR	n = 2500 2610.0 [2549.0 - 2670.0]	n = 2500 5199.9 [5135.0 - 5263.0]	n = 2500 5062.8 [4268.0 - 7413.0]
$\lambda$ -loEDR	2606.2 [2548.0 - 2666.0]	5198.0 [5129.0 - 5261.0]	5102.4 [4266.0 - 7763.0]

much smaller effects and at lower dose rates in *L. terrestris* (*Ex*-EDR of 12882-15136  $\mu\text{Gy h}^{-1}$ ) than in *E. fetida* (*Ex*-EDR of 15136-22387  $\mu\text{Gy h}^{-1}$ ). This illustrated the fact that equal radiosensitivity at the individual level might mean different risks for populations.

**Table 12.2. Effective dose rates for individual  $R_0$  and population  $\lambda$  in soil invertebrate species.**

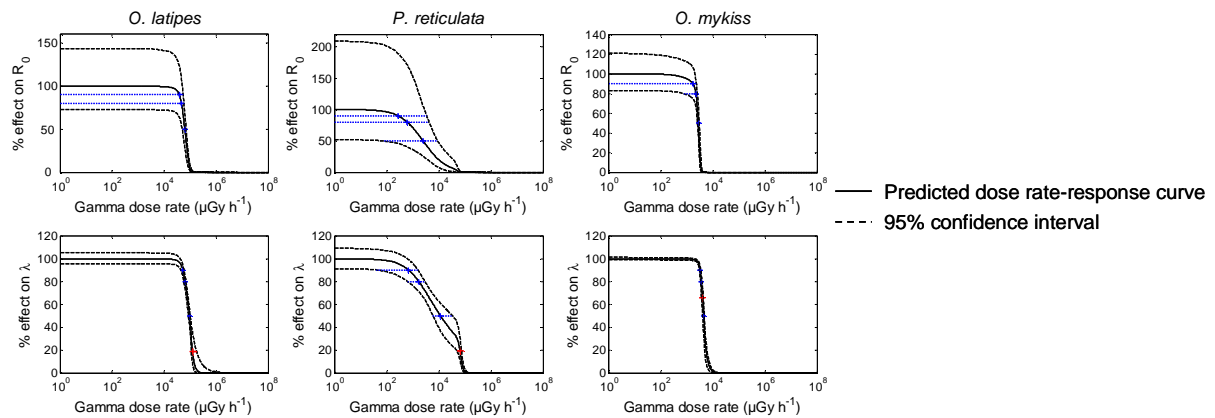
Dose rates inducing  $x = 10, 20$  and  $50\%$ -effect on net reproductive rate  $R_0$  and asymptotic population growth rate  $\lambda$  (respectively  $R_0$ -EDR $_x$  and  $\lambda$ -EDR $_x$ ), predicted population extinction ( $\lambda \leq 1$ ) (*Ex*-EDR) and lowest significant change ( $f = 0.05$ ) in  $R_0$  and  $\lambda$  (respectively  $R_0$ -loEDR and  $\lambda$ -loEDR). Confidence intervals (95%) presented into brackets built using a parametric bootstrap with 10,000 resampled datasets.

Endpoint and EDR ( $\mu\text{Gy/h}$ )	<i>Lumbricus terrestris</i> F0	<i>Lumbricus terrestris</i> F1
Net reproductive rate $R_0$		
$R_0$ -EDR $_{10}$	3235.5 [0.0 - 7244.0]	6309.5 [0.0 - 8511.0]
$R_0$ -EDR $_{20}$	4677.0 [0.0 - 7943.0]	7413.0 [0.0 - 8912.0]
$R_0$ -EDR $_{50}$	7413.0 [5247.5 - 9549.5]	9332.0 [6606.5 - 9999.5]
Asymptotic population growth rate $\lambda$		
$\lambda$ -EDR $_{10}$	9549.5 [8317.5 - 10714.5]	10471.0 [9119.5 - 10964.5]
$\lambda$ -EDR $_{20}$	14125.0 [12302.5 - 16217.5]	12589.0 [12022.5 - 15135.5]
$\lambda$ -EDR $_{50}$	95499.0 [28840.0 - 162180.5]	28840.0 [25703.5 - 83176.0]
Population extinction ( $\lambda \leq 1$ )		
Effect on $\lambda$	21.4%	21.4%
<i>Ex</i> -EDR	15135.5 [12589.0 - 17377.5]	12882.0 [12302.5 - 16217.5]
Lowest significant change		
	n = 2500	n = 2500
$R_0$ -loEDR	7059.2 [6309.0 - 8318.0]	8246.4 [7413.0 - 8913.0]
$\lambda$ -loEDR	5825.6 [5128.0 - 6918.0]	7488.3 [6607.0 - 8129.0]

In *Porcellio scaber*,  $R_0$ -EDR<sub>10</sub> was predicted at a lower dose rate (2630  $\mu\text{Gy h}^{-1}$ ) than in earthworms, as the woodlouse was the most radiosensitive soil invertebrate species at the individual level (Table 12-1, Fig. 12-1). However,  $\lambda$ -EDR<sub>10</sub> was one order of magnitude greater than in earthworms, as a result of population  $\lambda$  being moderately sensitive to changes in individual endpoints (Fig. 4C). Consequently, despite a very low value of  $\lambda$  in the control, population extinction was predicted at the greatest  $Ex$ -EDR among soil invertebrates. Thus, the lowest control  $\lambda$  and the strongest radiosensitivity in individual endpoints did not necessarily imply that the population was at risk. One critical aspect was how population growth rate responded to changes, depending on life history characteristics. Finally, *Porcellio scaber* showed similar values of  $R_0$ -loEDR and  $\lambda$ -loEDR as *E. fetida* in generation F1.

### 3.5.3. Fish

In fish, the lowest significant changes in population  $\lambda$  (for a parameter  $f$  of 0.05) are predicted at dose rates of 781  $\mu\text{Gy h}^{-1}$  in *P. reticulata*, 2170  $\mu\text{Gy h}^{-1}$  in *O. mykiss* and 43105  $\mu\text{Gy h}^{-1}$  in *O. latipes* (Table 13, Fig. 13). Thus, extrapolating radiation effects to the population level yields no change in the order of magnitude of radiosensitivity in the three considered fish species. In *P. reticulata*, radiation effects on fecundity and survival occur over distinct dose rate ranges (with EDR<sub>10</sub> of 282 and 57543  $\mu\text{Gy h}^{-1}$  respectively). In fact, their combined consequences for individual  $R_0$  and population  $\lambda$  are equivalent to those obtained from a mere effect on fecundity alone. In this species, the survival dose rate response curve result from an extrapolation from acute exposure in *Gambusia*. An experimental test of survival under chronic gamma radiation in *P. reticulata* would improve this estimation of population-level effects. In *O. mykiss*, EDR<sub>10</sub> of 1820, 2042 and 3020  $\mu\text{Gy h}^{-1}$  respectively for hatching, fecundity and survival allow a certain degree of combination among radiation



**Fig 13. Effects of chronic gamma radiation on net reproductive rate  $R_0$  (offspring produced per individual over a lifetime) and asymptotic population growth rate  $\lambda$  in three fish species *O. latipes*, *P. reticulata* and *O. mykiss***

as a response to combined reductions in hatching, fecundity and survival on a range of dose rates (95%-confidence intervals as dotted lines based on a parametric bootstrap with 10,000 resampled datasets).  $R_0$ - and  $\lambda$ -EDR<sub>10</sub>, EDR<sub>20</sub> and EDR<sub>50</sub> as blue dotted lines;  $R_0$ - and  $\lambda$ -EDR causing population extinction as red continuous lines.

effects, yielding an intermediate value for  $R_0$ - and  $\lambda$ -loEDR (2170  $\mu\text{Gy h}^{-1}$ ). Like in the aquatic invertebrate *N. arenaeodontata*, the same value is found for  $R_0$ -loEDR and  $\lambda$ -loEDR in *O. mykiss*, due to semelparity. *O. latipes* appears to be the least sensitive fish species at the population level. Like in *P. reticulata* however, chronic effects of gamma radiation are experimentally tested on fecundity only and on survival only, respectively in *O. mykiss* and *O. latipes*, while most of the modeling outcomes rely on extrapolated dose rate response curves.

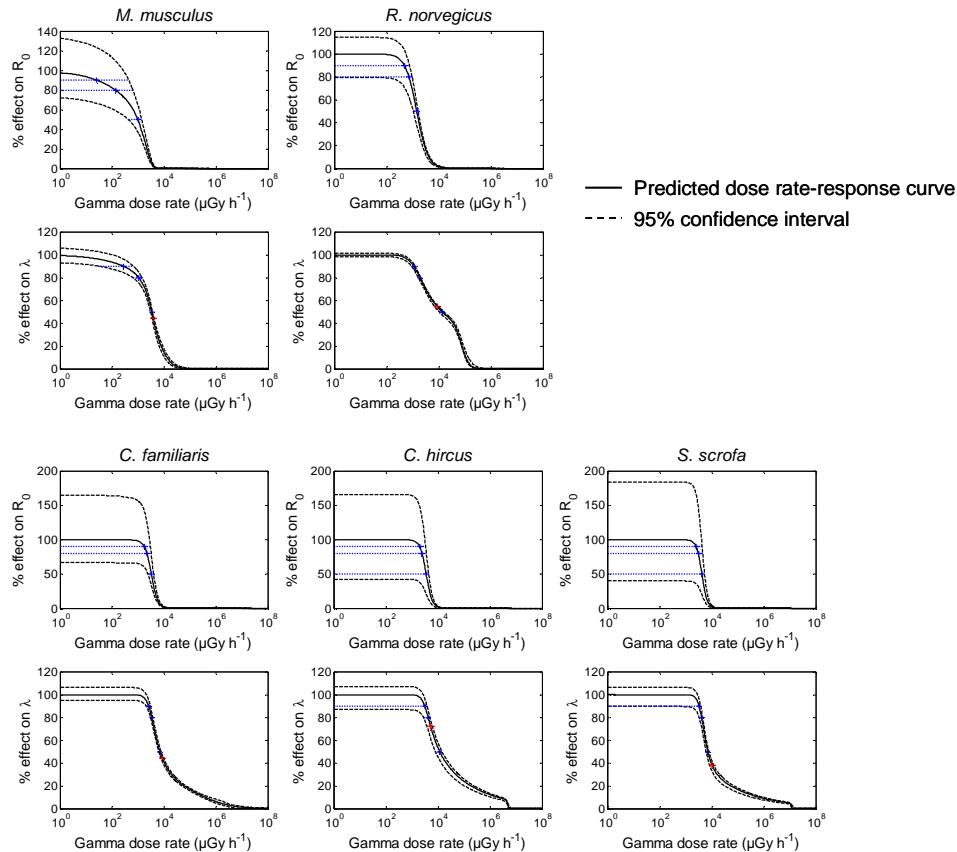
#### 3.5.4. Terrestrial mammals

*Mus musculus* offers an illustration of how interesting the approach might be when abundant chronic effect data is available. A total of four dose responses curves are combined, with effects at the individual level occurring over a same range of dose rate (with EDR<sub>50</sub> of 2884, 3236, 3548 and 9772  $\mu\text{Gy h}^{-1}$  for number of litters, litter size, proportion of reproducing adults and survival respectively), to estimate consequences for individual  $R_0$  and population  $\lambda$  (Fig. 14, Table 14-1). As a result,  $R_0$  appears more sensitive than the most sensitive

**Table 13. Effective dose rates for individual  $R_0$  and population  $\lambda$  in fish species.**

Dose rates inducing  $x = 10, 20$  and  $50\%$ -effect on net reproductive rate  $R_0$  and asymptotic population growth rate  $\lambda$  (respectively  $R_0$ -EDR $_x$  and  $\lambda$ -EDR $_x$ ), predicted population extinction ( $\lambda \leq 1$ ) ( $Ex$ -EDR) and lowest significant change ( $f = 0.05$ ) in  $R_0$  and  $\lambda$  (respectively  $R_0$ -loEDR and  $\lambda$ -loEDR). Confidence intervals (95%) presented into brackets built using a parametric bootstrap with 10,000 resampled datasets.

Endpoint and EDR ( $\mu\text{Gy/h}$ )	<i>Oryzias latipes</i>	<i>Poecilia reticulata</i>	<i>Oncorhynchus mykiss</i>
Net reproductive rate $R_0$			
$R_0$ -EDR $_{10}$	38018.5 [0.0 - 53703.0]	281.5 [0.0 - 3548.0]	1737.5 [0.0 - 2344.0]
$R_0$ -EDR $_{20}$	46773.5 [0.0 - 57543.5]	630.5 [0.0 - 4265.5]	2238.5 [758.5 - 2570.0]
$R_0$ -EDR $_{50}$	63095.5 [50118.5 - 69182.5]	2570.0 [81.0 - 9119.5]	2753.5 [2570.0 - 3019.5]
Asymptotic population growth rate $\lambda$			
$\lambda$ -EDR $_{10}$	52480.5 [43651.0 - 57543.5]	707.5 [40.5 - 1621.5]	3235.5 [3019.5 - 3467.0]
$\lambda$ -EDR $_{20}$	64565.0 [57543.5 - 69182.5]	1737.5 [660.0 - 3019.5]	3630.5 [3388.0 - 3890.0]
$\lambda$ -EDR $_{50}$	95499.0 [85113.5 - 99999.5]	11748.5 [6025.5 - 34673.5]	4466.5 [4073.5 - 4786.0]
Population extinction ( $\lambda \leq 1$ )			
Effect on $\lambda$ $Ex$ -EDR	81.6%- 125892.0 [114815.0 - 181970.0]	81.0% 67608.0 [52480.5 - 75857.5]	34.3% 3980.5 [3715.0 - 4265.5]
Lowest significant change			
$R_0$ -loEDR	n = 2500 51386.6 [50896.0 - 51875.0]	n = 2500 3269.8 [3118.0 - 3433.0]	n = 2500 2170.0 [2151.0 - 2188.0]
$\lambda$ -loEDR	43104.7 [42695.0 - 43514.0]	780.6 [749.0 - 814.0]	2170.0 [2151.0 - 2188.0]



**Fig 14. Effects of chronic gamma radiation on net reproductive rate  $R_0$  (offspring produced per individual over a lifetime) and asymptotic population growth rate  $\lambda$  in five terrestrial mammalian species *M. musculus*, *R. norvegicus*, *C. familiaris*, *C. hircus* and *S. scrofa***

as a response to combined reductions in fecundity and survival on a range of dose rates (95%-confidence intervals as dotted lines based on a parametric bootstrap with 10,000 resampled datasets).  $R_0$ - and  $\lambda$ - $EDR_{10}$ ,  $EDR_{20}$  and  $EDR_{50}$  as blue dotted lines;  $R_0$ - and  $\lambda$ -  $EDR$  causing population extinction as red continuous lines.

individual endpoint, with a  $R_0$ - $EDR_{10}$  of 26  $\mu\text{Gy h}^{-1}$  equal to that estimated for number of litters and a  $R_0$ - $EDR_{50}$  of 977  $\mu\text{Gy h}^{-1}$  below any  $EDR_{50}$  measured for individual endpoints. The value of  $\lambda$ - $EDR_{10}$  is found at 269  $\mu\text{Gy h}^{-1}$  and lowest significant changes in  $R_0$  and  $\lambda$  are respectively predicted for 144 and 344  $\mu\text{Gy h}^{-1}$ , at dose rates below the second lowest  $EDR_{10}$  estimated at the individual level for proportion of reproducing adults (977  $\mu\text{Gy h}^{-1}$ ).

In other mammalian species, effects on survival are reported or predicted at much higher dose rates (with  $EDR_{10}$  ranging from 40738  $\mu\text{Gy h}^{-1}$  to 11749  $\text{mGy h}^{-1}$ ) than effects on fecundity (with  $EDR_{10}$  ranging from 501 to 2570  $\mu\text{Gy h}^{-1}$ ). As a result, combined



consequences for individual  $R_0$  and population  $\lambda$  are equivalent to what would be obtained from a mere effect on fecundity alone (Fig. 14, Tables 14-1&2). Despite that, it is interesting to note that  $R_0$ -loEDR and  $\lambda$ -loEDR remain moderately influenced by allometry to body mass,

**Table 14.1. Effective dose rates for individual  $R_0$  and population  $\lambda$  in terrestrial mammal species.**

Dose rates inducing  $x = 10, 20$  and  $50\%$ -effect on net reproductive rate  $R_0$  and asymptotic population growth rate  $\lambda$  (respectively  $R_0$ -EDR $_x$  and  $\lambda$ -EDR $_x$ ), predicted population extinction ( $\lambda \leq 1$ ) ( $Ex$ -EDR) and lowest significant change ( $f = 0.05$ ) in  $R_0$  and  $\lambda$  (respectively  $R_0$ -loEDR and  $\lambda$ -loEDR). Confidence intervals (95%) presented into brackets built using a parametric bootstrap with 10,000 resampled datasets.

Endpoint and EDR ( $\mu\text{Gy/h}$ )	<i>Mus musculus</i>	<i>Canis familiaris</i>	<i>Capra hircus</i>
Net reproductive rate $R_0$			
$R_0$ -EDR $_{10}$	26.0 [0.0 - 436.0]	1778.0 [0.0 - 3019.5]	1995.0 [0.0 - 3388.0]
$R_0$ -EDR $_{20}$	137.5 [0.0 - 630.5]	2238.5 [0.0 - 3235.5]	2454.5 [0.0 - 3630.5]
$R_0$ -EDR $_{50}$	977.0 [426.5 - 1412.5]	3311.0 [2454.5 - 4073.5]	3548.0 [0.0 - 4466.5]
Asymptotic population growth rate $\lambda$			
$\lambda$ -EDR $_{10}$	269.0 [29.0 - 660.0]	2570.0 [2041.5 - 3019.5]	3090.0 [0.0 - 3801.5]
$\lambda$ -EDR $_{20}$	1071.0 [630.5 - 1412.5]	3388.0 [3019.5 - 3715.0]	4265.5 [2818.0 - 4897.5]
$\lambda$ -EDR $_{50}$	3388.0 [3019.5 - 3630.5]	6918.0 [6309.5 - 7762.0]	11748.5 [7943.0 - 14454.0]
Population extinction ( $\lambda \leq 1$ )			
Effect on $\lambda$	56.0%	55.7%	28.2%
$Ex$ -EDR	3801.5 [3467.0 - 4168.5]	8511.0 [7585.5 - 9549.5]	5247.5 [3801.5 - 6165.5]
Lowest significant change			
	n = 5000	n = 2500	n = 2500
$R_0$ -loEDR	344.4 [326.0 - 363.0]	2906.3 [2869.0 - 2939.0]	3719.2 [3673.0 - 3768.0]
$\lambda$ -loEDR	143.5 [133.0 - 154.0]	2187.1 [2161.0 - 2209.0]	3283.1 [3241.0 - 3323.0]

with lowest significant changes detected at dose rates ranging from 443  $\mu\text{Gy h}^{-1}$  in *R. norvegicus* to 3283  $\mu\text{Gy h}^{-1}$  in *C. hircus*. Lower values might be estimated after additional individual endpoints are experimentally tested under chronic gamma radiation.

**Table 14.2. Effective dose rates for individual  $R_0$  and population  $\lambda$  in terrestrial mammal species.**

Dose rates inducing  $x = 10, 20$  and  $50\%$ -effect on net reproductive rate  $R_0$  and asymptotic population growth rate  $\lambda$  (respectively  $R_0\text{-EDR}_x$  and  $\lambda\text{-EDR}_x$ ), predicted population extinction ( $\lambda \leq 1$ ) ( $Ex\text{-EDR}$ ) and lowest significant change ( $f = 0.05$ ) in  $R_0$  and  $\lambda$  (respectively  $R_0\text{-loEDR}$  and  $\lambda\text{-loEDR}$ ). Confidence intervals (95%) presented into brackets built using a parametric bootstrap with 10,000 resampled datasets.

Endpoint and EDR ( $\mu\text{Gy/h}$ )	<i>Rattus norvegicus</i>	<i>Sus scrofa</i>
Net reproductive rate $R_0$		
$R_0\text{-EDR}_{10}$	501.0 [0.0 - 776.0]	2570.0 [0.0 - 4365.0]
$R_0\text{-EDR}_{20}$	741.0 [0.0 - 977.0]	3090.0 [0.0 - 4570.5]
$R_0\text{-EDR}_{50}$	1479.0 [1071.0 - 1659.5]	4265.5 [81.0 - 9119.5]
Asymptotic population growth rate $\lambda$		
$\lambda\text{-EDR}_{10}$	1121.5 [911.5 - 1258.5]	3311.0 [0.0 - 3801.5]
$\lambda\text{-EDR}_{20}$	1949.5 [1698.0 - 2089.0]	4168.5 [3311.0 - 4570.5]
$\lambda\text{-EDR}_{50}$	13803.5 [10471.0 - 15848.5]	7079.0 [6165.5 - 7762.0]
Population extinction ( $\lambda \leq 1$ )		
Effect on $\lambda$	45.4%	61.7%
$Ex\text{-EDR}$	8709.0 [7079.0 - 9999.5]	10232.5 [52480.5 - 75857.5]
Lowest significant change		
	n = 2500	n = 2500
$R_0\text{-loEDR}$	725.3 [712.0 - 739.0]	4640.2 [4584.0 - 4699.0]
$\lambda\text{-loEDR}$	442.8 [435.0 - 451.0]	3272.1 [3242.0 - 3303.0]

## 4. Dual age class population model with radiation repair

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### 4.1. Model description

Most organisms can be identified over the course of their development as passing through a series of age classes. The examples derived from the literature and from life history data available on genomics databases suggest that, in most cases, the population can be subdivided in just two age classes: juvenile and adult individuals, connected by a growth rate:

$$\frac{dN_0}{dt} = M_0(t) - sN_0 - d_0N_0 + I_0(t)$$

$$\frac{dN_1}{dt} = sN_0 - d_1N_1 + I_1(t)$$

Where  $N_i$  is the abundance at time  $t$  ( $i = 0$  for juvenile and 1 for adult),  $M_0(t)$  is the number of offspring generated per unit time,  $s$  is the growth rate from juvenile to adult,  $d_i$  are the intrinsic rates of juvenile or adults loss due to mortality (intrinsic and predation) and  $I_i(t)$  represent immigration for each age group of the population. This linear model assumes ideal resources (food, shelter, temperature).

#### 4.1.1. Reproduction

As the population grows, individuals interfere with each other by competing for some critical resource, such as food or living space. This is modelled by the logistic equation

$$\frac{dN}{dt} = rF \left( 1 - \frac{N}{K} \right)$$
 where  $r$  is the multiplication rate, equal to the number of offspring produced

by a typical female multiplied by the fraction of females (usually 50%). The constant  $K$  is the ‘carrying capacity’, i.e. the maximum number of adults allowed by the resources of the ecosystem (in this study this is always assumed to be  $10^3$  organisms).

In the above logistic equation, a time-dependent fecundity function  $F$  represents the fecundity of the population, i.e. the number of individuals that are at any given time capable of reproducing. The simplest form of this function is  $F = N$ , a direct consequence of there being a limiting term  $1 - \frac{N}{K}$ . However,  $F$  is generally variable, and to represent this a more general type of model can be introduced (Kryshev et al. 2008):

$$\frac{dN}{dt} = rF \left( 1 - \frac{N}{K} \right)$$

$$\frac{dF}{dt} = -rF \left( 1 - \frac{N}{K} \right) + fF \left( 1 - \frac{F}{L} \right)$$

Here,  $f$  and  $L$  are the rates of self-recovery and the maximum fecundity of the population, respectively. It is easy to see that this system of equations still has a simple solution of the type  $F = N$  with  $K = L$ , but there are other solutions that theoretically allow for an imbalance between fecundity and population numbers, caused for example by the presence of a contaminant.

The model can be further refined by assuming that population growth is limited when population numbers are very low, due to the increased difficulty of mating:

$$\frac{dN}{dt} = rF \left( 1 - \frac{N}{K} \right) \left( 1 - \frac{W}{N} \right)$$

Where  $W$  is the minimum viable population below which the population is not sustainable ( $W \geq 2$  for sexually reproducing organisms; assumed to be 2 in our calculations).

Generalizing the previous equations to two age classes gives us the basic population model without radiation and for an isolated population:

$$\frac{dN_0}{dt} = rF \left(1 - \frac{N_0}{K_0}\right) \left(1 - \frac{W}{N_1}\right) - (s + d_0)N_0$$

$$\frac{dN_1}{dt} = sN_0 - d_1N_1$$

$$\frac{dF}{dt} = -rF \left(1 - \frac{N_1}{K_1}\right) + fF \left(1 - \frac{F}{L}\right)$$

#### 4.1.2. Equilibrium solution

A stable analytical solution for the system (beyond the trivial solution  $N_0 = N_1 = F = 0$ ) can be found by equalling the differential equations to zero and neglecting the term  $\left(1 - \frac{W}{N_1}\right)$  (a suitable approximation for non-sparse populations). The equations become further simplified in the symmetrical case  $K_1 = L$  and  $r = f$ , giving the following simple expressions for the (initial) steady-state conditions:

$$N_0^{ini} = K_c \frac{d_1}{s} \left[1 - \frac{s + d_0}{s} \frac{d_1}{r}\right]$$

$$N_1^{ini} = F = K_c \left[1 - \frac{s + d_0}{s} \frac{d_1}{r}\right]$$

Where, for convenience,  $K_c \equiv K_0 \frac{s}{d_1}$ . The maximum theoretical values that juvenile and adult populations can attain are  $K_c \frac{d_1}{s}$  and  $K_c$ , respectively; corresponding to high survival and reproduction rates and low mortalities for juvenile and adult. These values can therefore be interpreted as the carrying capacities of the ecosystem for adult and juvenile organisms.

A unique stable solution (other than trivial) for the above system exists if and only if

$$\frac{s + d_0}{s} \frac{d_1}{r} < 1.$$

### 4.1.3. Radiation effects

The effect of ionising radiation manifests itself as repairable radiation damage, reproduction effects and lethal damage (mortality). We assume that there is a pool of damaged individuals  $Y_i$  coexisting with healthy individuals  $N_i$  (Initial value of  $Y_0, Y_1 = 0$ ). A repairing pool  $R_i$  (different for each age group) represents the capacity to repair radiation damage.

The repair mechanism is a quantity symbolizing a variety of highly complex repair processes that occur at cellular and sub-cellular (genetic) level (Kryshev et al. 2008). Here, we model it in a non-mechanistic way, and therefore we do not cover explicitly the range of teratogenic, genetic, developmental and behavioural effects observed in biota. It does not account either for variations in tissue radio-sensitivity. However, this approach, which is well grounded on previous literature (Laurie and Fox, 1972), is a step forward from simpler models representing the radiation effect by relating mortality linearly to the dose rate.

By integrating the repairing pool with a population model the impact of ionising radiation can be modelled in a population context, considering repairable radiation damage, reproduction and mortality (lethal damages) as distinct modeling endpoints. For example, the fraction of adults killed by ionising radiation at any given time can be defined as  $1 - \frac{N_1 + Y_1}{N_0^{eq}}$ .

We derived the following system of seven first-order differential equations for the model:

$$\frac{dN_0}{dt} = -\alpha_0 d_r N_0 + \kappa_0 Y_0 R_0 + rF \left(1 - \frac{N_0 + Y_0}{K_0}\right) \left(1 - \frac{W}{N_1}\right) - (s + d_0) N_0$$

$$\frac{dY_0}{dt} = \alpha_0 d_r N_0 - \kappa_0 Y_0 R_0 - \varepsilon_0 Y_0 - (s + d_0) Y_0$$

$$\frac{dR_0}{dt} = r_0 R_0 \left(1 - \frac{R_0}{M_0}\right) - k_R^0 Y_0 R_0 - \alpha_R^0 d_r R_0$$

$$\frac{dN_1}{dt} = -\alpha_1 d_r N_1 + \kappa_1 Y_1 R_1 + s N_0 - d_1 N_1$$

$$\frac{dY_1}{dt} = \alpha_1 d_r N_1 - \kappa_1 Y_1 R_1 - \varepsilon_1 Y_1 + s Y_0 - d_1 Y_1$$

$$\frac{dR_1}{dt} = r_1 R_1 \left(1 - \frac{R_1}{M_1}\right) - k_R^1 Y_1 R_1 - \alpha_R^1 d_r R_1$$

$$\frac{dF}{dt} = -\alpha_f^1 d_r F - rF \left(1 - \frac{N_1}{K_1}\right) + fF \left(1 - \frac{F}{L}\right)$$

where  $\alpha_i, \alpha_R^i, \alpha_f^i, \varepsilon_i, \kappa_i, k_R^i, r_i, f$  are parameters for the radiation model, described in our previous work (Vives i Batlle et al., 2010);  $M_0$  and  $M_1$  are logistic constants for the recovery pool, made equal to  $K$  for symmetry, and  $d_r$  is the radiation dose rate.

Note that, in the above equations, the damaged individuals are not included in the fecundity saturation term  $1 - \frac{N_1}{K_1}$  or the term  $1 - \frac{W}{N_1}$  because it is assumed that damaged organisms do not participate in reproduction. However, the saturation term for juveniles  $s_T^0 = 1 - \frac{N_0 + Y_0}{K_0}$  includes the damaged population because it is assumed that healthy and damaged individuals share the same ecological space. This is very important conceptually, because it prevents mortality from becoming negative at low dose rates, an artifact that was observed in an earlier version of the model.

The model was constructed and equations solved numerically using the modeling software *ModelMaker*® version 4 (Citra 1997; Rigas 2000). For the execution of the model, Gear's method, an appropriate solver for stiff simulations where different processes happen

on very different time scales, was chosen, with daily time steps,  $10^3$  output points, a random seed of 1 and a relative error per step of  $10^{-10}$ . The accuracy of the solver was tested by comparison with the analytical solutions for the equilibrium (no effects) and lethality (acute effects) cases.

#### 4.1.4. Chronic versus acute dose effects

The equation system for our model has an important feature. At low levels of dose, the repair function acts to return damaged individuals to the healthy state (chronic effects). However, at high doses, the repair mechanism and the fecundity function are depleted,  $R_0 \sim R_1 \sim F \sim 0$  and  $N_i$  becoming  $Y_i$  (all population damaged – acute effects), hence we can approximate:

$$\begin{aligned}\frac{dN_0}{dt} &= -(\alpha_0 d_r + s + d_0)N_0 \\ \frac{dY_0}{dt} &= \alpha_0 d_r N_0 - (s + d_0 + \varepsilon_0)Y_0 \\ \frac{dN_1}{dt} &= +sN_0 - (\alpha_1 d_r + d_1)N_1 \\ \frac{dY_1}{dt} &= \alpha_1 d_r N_1 + sY_0 - (d_1 + \varepsilon_1)Y_1\end{aligned}$$

The equation for  $N_0$  can be solved as  $N_0 = N_0^{ini} e^{-(\alpha_0 d_r + s + d_0)t}$  and substituted into the other equations which, being of the type  $\frac{dy}{dx} + p(x)y = q(x)$ , can be solved as:

$$y = e^{-\int p(x)dx} \left( \int q(x)e^{\int p(x)dx} dx + c \right)$$

The solutions must verify  $Y_0 = 0$  and  $N_i = N_0^i$  for  $t=0$ ; hence:



$$N_0 = N_0^{ini} e^{-\lambda_0 t}$$

$$Y_0 = \frac{\alpha_0 d_r}{\lambda_1 - \lambda_0} N_0^{ini} (e^{-\lambda_1 t} - e^{-\lambda_0 t})$$

$$N_1 = N_1^{ini} e^{-\lambda_2 t} + \frac{s}{\lambda_2 - \lambda_0} N_0^{ini} (e^{-\lambda_2 t} - e^{-\lambda_0 t})$$

$$Y_1 = \frac{s d_r}{\lambda_0 - \lambda_3} \left( \frac{\alpha_0}{\lambda_1 - \lambda_0} + \frac{\alpha_1}{\lambda_2 - \lambda_0} \right) N_0^{ini} (e^{-\lambda_0 t} - e^{-\lambda_3 t}) - \frac{s \alpha_0 d_r}{(\lambda_1 - \lambda_0)(\lambda_1 - \lambda_3)} N_0^{ini} (e^{-\lambda_1 t} - e^{-\lambda_3 t}) - \frac{\alpha_1 d_r}{\lambda_2 - \lambda_3} \left( N_1^{ini} + \frac{s}{\lambda_2 - \lambda_0} N_0^{ini} \right) (e^{-\lambda_2 t} - e^{-\lambda_3 t})$$

where the system's eigenvalues are given by:

$$\lambda_0 = -(\alpha_0 d_r + s + d_0); \lambda_1 = -(s + d_0 + \varepsilon_0); \lambda_2 = -(\alpha_1 d_r + d_1) \text{ and } \lambda_3 = -(d_1 + \varepsilon_1)$$

It is of interest to calculate the surviving fractions for juvenile and adults with respect to the initial (equilibrium) population, or  $f_0$  and  $f_1$ . Substitution of the equilibrium values calculated in the section 'equilibrium solution' leads to:

$$f_0 = \frac{N_0 + Y_0}{N_0^{ini}} = \frac{\alpha_0 d_r}{\lambda_1 - \lambda_0} e^{-\lambda_1 t} - \varepsilon_0 e^{-\lambda_0 t}$$

$$f_1 = \frac{N_1 + Y_1}{N_1^{ini}} = e^{-\lambda_2 t} + \frac{d_1}{\lambda_2 - \lambda_0} (e^{-\lambda_2 t} - e^{-\lambda_0 t}) + \frac{d_1 d_r}{\lambda_0 - \lambda_3} \left( \frac{\alpha_0}{\lambda_1 - \lambda_0} + \frac{\alpha_1}{\lambda_2 - \lambda_0} \right) (e^{-\lambda_0 t} - e^{-\lambda_3 t}) - \frac{d_1 \alpha_0 d_r}{(\lambda_1 - \lambda_0)(\lambda_1 - \lambda_3)} (e^{-\lambda_1 t} - e^{-\lambda_3 t}) - \frac{\alpha_1 d_r}{\lambda_2 - \lambda_3} \left( 1 + \frac{d_1}{\lambda_2 - \lambda_0} \right) (e^{-\lambda_2 t} - e^{-\lambda_3 t})$$

Now, we can use the approximation that  $d_0$  and  $\varepsilon_0 = \varepsilon_1$  dominate over the remaining eigenvalue terms such that  $e^{-\lambda_0 t} < e^{-\lambda_1 t} < e^{-\lambda_2 t} \ll e^{-\lambda_3 t}$  (this was verified numerically with our model parameters for fish and mammal populations):

$$f_0 \approx \frac{\alpha_0 d_r}{\lambda_1 - \lambda_0} e^{-\lambda_1 t}$$

$$f_1 \approx d_r \left[ \frac{d_1 \alpha_0}{(\lambda_1 - \lambda_0)(\lambda_1 - \lambda_3)} + \frac{\alpha_1}{\lambda_2 - \lambda_3} \left( 1 + \frac{d_1}{\lambda_2 - \lambda_0} \right) - \frac{d_1}{\lambda_0 - \lambda_3} \left( \frac{\alpha_0}{\lambda_1 - \lambda_0} + \frac{\alpha_1}{\lambda_2 - \lambda_0} \right) \right] e^{-\lambda_3 t}$$

This indicates that at high dose rates juveniles and adults decrease exponentially. As natural death and survivorship weigh on top of radiation damage, a dose rate equal to the

LD<sub>50/30</sub> applied over 30 days reduces the population somewhat more than 50%, an inevitable result of coupled dual age-stage population modeling.

#### 4.1.5. Calibration of the model with fish data

To represent fish, the generic population model was applied to fish eggs ( $N_0$ ) coexisting with adults ( $N_1$ ). The model was calibrated using physiological parameters for the following fish species: common carp (*Cyprinus carpio*), grass carp (*Ctenopharyngodon idella*), loach (*Misgurnus fossilis*), tilapia (*Tilapia mossambica*), Siberian roach (*Rutilus rutilus lacustris*), goldfish (*Carassius auratus gibelio*), silver carp (*Hypophthalmichthys molitrix*) and pike (*Esox lucius*). The information was taken from the Animal Ageing and Longevity Database (AnAge 2012), and where not possible, from online resources such as the Centralized Digital Library of Life on Earth (ARKive 2012), the IUCN red list for threatened species (IUCN 2011) and the Global Information System on Fishes (Fishbase 2012). Additional information for carp was obtained from the Global Invasive Species Database (Radke 2005) and, elsewhere for longevity (Kolar et al. 2005).

Reproduction rate from the above sources was calculated as clutch size  $\times$  clutches per year  $\times$  female/(female + male) ratio (assumed to be  $\sim 0.5$ ). We assumed that each mature female is fertile (otherwise a corrective factor – not available here - should be included in the calculations). It must also be assumed that some of the processes e.g. reproduction are continuous and uniform. This runs counter to the fact that many species of fish spawn usually one time rather than at a continuous daily rate equal to the annual number of eggs spawned divided by 1 year. However, population as a whole may be considered to spawn over the entire season in the first approximation.

#### 4.1.6. Calculation of mortality rates

There is little information available for the adult and juvenile natural mortality rates in the environment under the effect of predation. The parameter can vary with size, sex, parasite load, density, food availability and predator numbers; however, natural mortality as a function of mass has been calculated in fish stock assessment models (Siegfried and Sansó, 1996).

For adults, defining the lifespan  $A_m$  as the age for which a fraction  $f$  of the population is still alive,  $d_1 = \ln(10)/\text{lifespan}$ , we can approximate  $d_1 = \frac{1}{A_m} \ln \frac{1}{f}$  choosing  $f = 0.01$  (only 1% of the population surviving). An improvement is to use Peterson & Wroblewski's (P-W) model (Peterson and Wroblewski 1984), an allometric approach that predicts decrease of death rate with increasing body mass. Assuming 75% water content in fish this model predicts  $d(\text{d}^{-1}) = 1.32 \times 10^{-3} m(\text{kg}; \text{fresh mass})^{-0.25}$ . Both approaches give similar result, with the allometric model an average 30% higher. For this study we adopted a P-W-calculated adult death rate of  $0.3 \text{ year}^{-1}$ , similar to the available field information (Alverson and Carney 1975; Jørgensen et al. 1991; Woodhead 2003).

For eggs with a mass of  $1.78 \times 10^{-6} \text{ kg}$ , the P-W equation gives  $d_0 = 3.6 \times 10^{-2} \text{ d}^{-1}$ . However, in the embryonic development stage, the available information indicates that the survival is very low. Not even the approximation by McGurk (1986),  $d(\text{days}^{-1}) = 2.01 \times 10^{-6} m(\text{kg}; \text{fresh mass})^{-0.85}$ , which corrects for the P-W model tendency to underestimate slightly for small organisms, predicting  $d_0 \sim 10^{-1} \text{ d}^{-1}$  suffices to reduce the egg production rate of  $\sim 10^3 \text{ d}^{-1}$  to levels compatible with the low survival probabilities observed. This is because, in the natural environment, very high fish fecundities are balanced by very low hatching success and high egg and larval mortalities (Dahlberg 1979). To solve this

problem, we based our estimate on the survivorship for fish eggs calculated previously in another model (Kryshev et al. 2008), or  $5.0 \times 10^{-2} \text{ d}^{-1}$ .

#### 4.1.7. Calculation of the death rate as a function of the survivorship

Starting from the previously calculated model solutions for a state of equilibrium, it is possible to calculate the net production rate for adults at steady-state as:

$$sN_0 = K_c d_1 \left[ 1 - \frac{(s + d_0) d_1}{s r} \right]$$

This can be compared with a single life stage model having the equations:

$$\frac{dN}{dt} = rF \left( 1 - \frac{N}{K} \right) - d_1 N; \quad \frac{dF}{dt} = -rF \left( 1 - \frac{N}{K} \right) + fF \left( 1 - \frac{F}{L} \right)$$

with  $K_c = N_{max} = L = F_{max}$ , assuming that the adult has the same death rate  $d_1$  and carrying capacity  $K_c$  for both models. In this case, the equilibrium solution would be

$$\frac{dN}{dt} = r'N \left( 1 - \frac{N}{K_c} \right) - d_1 N = 0, \quad \text{from where } N = K_c \left( 1 - \frac{d_1}{r'} \right), \quad \text{with a net production rate}$$

$$d_1 N = K_c d_1 \left( 1 - \frac{d_1}{r'} \right). \quad \text{For both types of model to have the same net production rate a certain}$$

relationship must exist between the "effective" (rate of formation of mature individuals) reproduction rate  $r'$  of the single life stage model and the constants  $r$ ,  $s$ ,  $d_0$  and  $d_1$  of the dual

life stage model:  $1 - \frac{(s + d_0) d_1}{s r} = 1 - \frac{d_1}{r'}$ . Henceforth,  $r' = \left( \frac{s}{s + d_0} \right) r$  or  $d_0 = s \left( \frac{r}{r'} - 1 \right)$ . Using  $r$

$= 7.53 \times 10^2 \text{ d}^{-1}$  (the mean reproduction rate for the species in this study, see below) and  $r' = 5 \times 10^{-2} \text{ d}^{-1}$  gives  $d_0 = 2.6 \text{ d}^{-1}$ .

The use of a formation rate  $r'$  of  $0.05 \text{ d}^{-1}$  is not only consistent with Kryshev's single-age class model but also with the predicted mean survivorship to metamorphosis of a cohort of freshwater fish larvae being 5.3% per day (Houde 1994) (5% of the population still alive at

maximum age giving a generation rate of  $5.3 \times 10^{-2} \text{ d}^{-1}$ ). This value gains credence by indirect evidence from other freshwater fish species:  $13 \times 10^{-2} \text{ d}^{-1}$  survivorship (Forney 1976) (yolk-sac larvae alone, hence an upper estimate for the full growth process from egg to adult), and lost eggs/larvae owing to the predation reaching 92.4% per clutch in smallmouth bass (Iguchi et al. 2004). Indeed, if we assume the predation occurs within 24 h after laying the clutch (according to (Dahlberg 1979) the majority of the loss for river fish eggs occurs within a timescale of a few days and carp eggs hatch within 2 to 4 days), this is equivalent to a death rate of  $-\ln(1-0.924)/(2 - 4 \text{ d}) = 0.6 - 1.3 \text{ d}^{-1}$  – compatible with our value.

#### 4.1.8. Organism masses and growth rate

A simple scaling approach can be used to calculate the mass of the juvenile organism where direct data was not available but organism length was obtainable:

$$m_0 = \left( \frac{L_0}{L_1} \right)^3 m_1$$

For example, grass carp length (juvenile) = 20 – 45 cm and length (adult) = 1.2 m so mass (juvenile) =  $24.8 \text{ kg} \times (0.2 / 1.2)^3 = 0.115 \text{ kg}$ . As the common carp can also grow to 1.2 m, we adopted the ratio  $(0.2 / 1.2)^3$  for all carp species.

The mass of the egg, necessary if the population model considers the lower life stage to be the eggs themselves, was derived as follows. For Tilapia mean egg diameter is  $d = 1.5 \text{ mm}$  (Coward and Bromage 1999) so the mass is  $m = \rho V_{\text{egg}} = \frac{1}{6} \pi \rho d^3 = 1.8 \times 10^{-6} \text{ kg}$ . For pike and goldfish  $d = 2.68$  and  $1.29 \text{ mm}$ , respectively (Bonisławska et al. 2001) so the mass is  $1.0 \times 10^{-5}$  and  $1.1 \times 10^{-6} \text{ kg}$ , respectively. For roach and carp species an egg diameter between 1.25 and 1.5 mm, equivalent to an average of  $1.36 \times 10^{-6} \text{ kg}$ , was obtained ([http://www.fishing.visitwales.com/en/content/cms/coarse/general\\_coarse\\_fish/species/](http://www.fishing.visitwales.com/en/content/cms/coarse/general_coarse_fish/species/)). For the catfish (loach) the size is between 1.3 and 1.5 mm, equivalent to an average of  $1.44 \times 10^{-6}$

kg. An allometric relationship between body mass and volume of egg has been found (Blueweiss et al. 1978), but this is too unreliable for use here, having a  $r^2$  of only 0.26.

The growth rate  $s$ , determining the speed at which  $N_0$  becomes  $N_1$ , was obtained from a simple approximation assuming that for the mean age at maturity  $A_m$  a large fraction  $f$  of the eggs becomes adult. Therefore:

$$(1-f)N_0 = N_0 e^{-sA_m} \text{ or } s = \frac{1}{A_m} \ln\left(\frac{1}{1-f}\right).$$

The dataset derived from the above approximations lead to population model parameters for a "generic" fish (Table 15). With these parameters, the generic model gives a stable population of 987 adults and 7,665 eggs, with a survivorship of 5%. The adult/egg ratio of a stable population can be calculated as follows. Starting with an initial amount of eggs  $N_0^{ini}$  and neglecting reproduction and the adult death rate  $d_1$ ,  $\frac{dN_0}{dt} = -(s + d_0)N_0$  and  $\frac{dN_1}{dt} = sN_0 - d_1N_1$ .

Thus:

$$N_0 = N_0^{ini} e^{-(s+d_0)t}$$

$$N_1 = sN_0^{ini} e^{-d_1 t} \int_0^t e^{-(s+d_0-d_1)t} dt = \frac{sN_0^{ini} e^{-d_1 t}}{s+d_0-d_1} (1 - e^{-(s+d_0-d_1)t})$$

The first derivative of the above equation can be used to calculate the maximum value of  $N_1$ :

$$N_1^{\max} = sN_0^{ini} e^{-d_1 t} \int_0^t e^{-(s+d_0-d_1)t} dt = \frac{sN_0^{ini}}{s+d_0} \left(\frac{d_1}{s+d_0}\right)^{\frac{d_1}{s+d_0-d_1}}$$

When  $d_1$  tends to zero,  $\xi \equiv \frac{N_1^{\max}}{N_0^{ini}} = \frac{s}{s+d_0}$ . For our input data this gives  $\xi \sim 10^{-4}$ . This value

gains credibility by the indirect evidence that the early period of carp (*Cyprinus carpio*) has the highest mortality rate with less than one in  $10^3$  fish surviving the first few weeks, indicating an upper limit for  $\xi$  of  $10^{-3}$  (AnglingTimes 2010). For pike, one study of 1.25

million eggs produced 39 pike living to 3 years (the mean age of maturity) corresponding to an overall survival probability of  $3.12 \times 10^{-5}$  (Broughton 2000).

**Table 15. Model parameters for fish (calculated for this report), mouse and other mammals (calculated for EMRAS II)**

Data in italics are calculated using allometric relationships.

<b>Parameter</b>	<b>Generic fish</b>	<b>Tilapia</b>	<b>Carp</b>	<b>Pike</b>
Death rate( $d^{-1}$ )				
for juvenile	1.23E+00	<i>1.23E+00</i>	1.84E+00	1.44E+00
for adult	8.85E-04	<i>1.49E-03</i>	7.57E-04	6.64E-04
Mass (kg)				
for juvenile	1.78E-06	<i>1.78E-06</i>	1.30E-06	1.01E-05
for adult	4.94E+00	<i>6.22E-01</i>	9.26E+00	1.56E+01
Growth rate ( $d^{-1}$ )	1.14E-04	<i>4.54E-04</i>	8.20E-05	1.05E-04
Recovery rate for fecundity ( $d^{-1}$ )	7.53E+02	<i>7.53E+02</i>	1.37E+03	6.85E+02
Reproduction rate ( $d^{-1}$ )	7.53E+02	<i>7.53E+02</i>	1.37E+03	6.85E+02
Carrying capacity of fecundity (-)	1.00E+03	<i>1.00E+03</i>	1.00E+03	1.00E+03
Carrying capacity of ecosystem (-)	1.00E+03	<i>1.00E+03</i>	1.00E+03	1.00E+03

<b>Parameter</b>	<b>Mouse</b>	<b>Hare/rabbit</b>	<b>Wolf/dog</b>	<b>Deer</b>
Death rate ( $d^{-1}$ )				
for juvenile	2.74E-05	<i>1.34E-05</i>	<i>9.68E-06</i>	<i>5.80E-06</i>
for adult	1.42E-03	6.40E-04	3.15E-04	2.93E-04
Mass (kg)				
for juvenile	1.90E-03	8.25E-02	4.50E-01	6.71E+00
for adult	2.32E-02	3.00E+00	3.33E+01	1.49E+02
Growth rate ( $d^{-1}$ )	4.12E-02	2.10E-02	2.11E-02	4.87E-03
Recovery rate for fecundity ( $d^{-1}$ )	2.98E-02	1.99E-02	7.39E-03	1.60E-03
Reproduction rate ( $d^{-1}$ )	2.98E-02	1.99E-02	7.39E-03	1.60E-03
Carrying capacity of fecundity (-)	1.00E+03	1.00E+03	1.00E+03	1.00E+03
Carrying capacity of ecosystem (-)	1.00E+03	1.00E+03	1.00E+03	1.00E+03

## 4.2. Calibration of the model

### 4.2.1. Life history parameters

The characteristic physiological parameters for the species chosen in the (intercomparison) benchmark scenario for generic mice, hare/rabbit, wolf/wild dog and deer populations were taken from the online AnAge database (AnAge 2012). There was no information available in the database for the adult and juvenile mortality rate in the natural environment under the effect of predation. Hence, for the adult we used the definition of lifespan as the age of the 10% oldest survivors, and an average mortality rate of  $\ln(10)/\text{lifespan}$  was thus derived. For juveniles, only the mice have initial mortality rate (IMR) data in the database. The following approach was used: observing that the adult death rate follows an allometric law,  $d_I = 7.11 \times 10^{-4} \times m_I^{-0.19}$ ;  $R^2 = 0.977$ , we adapt this law to fit the IMR of the juvenile mouse with the same exponent:  $2.74 \times 10^{-5} = \alpha \times (1.90 \times 10^{-3})^{-0.19}$  so  $\alpha = 8.32 \times 10^{-6}$  and  $d_0 = 8.32 \times 10^{-6} \times m_0^{-0.19}$ . The full set of model parameters thus derived for mammals is also shown in Table 15.

### 4.2.2. Parameterisation of the radiation model

The point of departure for parameterizing the radiation model is the following set of equations for a single population model by Kryshev et al (Kryshev et al. 2008):

$$\frac{dx}{dt} = -\alpha p x + \kappa y R + \mu F(x_{\max} - x); \quad \frac{dy}{dt} = \alpha p x - \varepsilon y - \kappa y R$$
$$\frac{dR}{dt} = \mu_R R(R_{\max} - R) - k_R y R - \alpha_R p R; \quad \frac{dF}{dt} = -\alpha_f p F - \mu F(x_{\max} - x) + \mu_f F(F_{\max} - F)$$

Where  $x$  and  $y$  represent healthy and damaged individuals,  $p$  is the dose rate ( $\text{Gy d}^{-1}$ ),  $\alpha$  is the repairable radiation damage rate constant ( $\text{Gy}^{-1}$ ),  $\varepsilon$  is the lethality rate constant ( $\text{d}^{-1}$ ) and  $\alpha_R$ ,  $\alpha_f$  are repairing pool and reproduction function rate constants (all in  $\text{Gy}^{-1}$ ). Additionally,  $k$  and  $k_R$



are repair rate constants for the damaged population and the repairing pool itself ( $d^{-1}$ ), respectively. Also,  $\mu$  and  $\mu_r$  are the normalized reproduction rates.

#### 4.2.3. Determination of the radiation model rate constants

Following previous work (Vives i Batlle et al., 2010) we took  $\alpha_f = 10 \times \alpha$  and  $\alpha_R = 2 \times \alpha_f = 20 \times \alpha$ , with  $\alpha = \frac{\ln(2)}{LD_{50/30}}$ . We further took  $\varepsilon = \frac{\ln(2)}{30} = 0.023 \text{ d}^{-1}$ , designed so that in the limit

case of high exposure, when  $R$  and  $N$  are 0 and all the organisms are damaged, application of a dose equal to the  $LD_{50/30}$  gives 50% reduction of the population in 30 days. Since  $\varepsilon$  is a constant, this model is therefore linked to the  $LD_{50/30}$  at high doses, extrapolating to low doses by means of the repair mechanism.

Next, we calculated  $\kappa_R \approx 1.5\kappa = \frac{1.5}{R_{\max}}$  as done previously (Vives i Batlle et al., 2010) and consistent with Kryshev's fish model (Kryshev et al. 2008). We also used the relation  $x_{\max} = R_{\max} = F_{\max} = K$ ,  $L$  and  $M$  (symmetry of fecundity, repair and population saturation), as well as  $r = f$ . The latter derives logically from the fact that, if  $f < r$ , the population cannot recover and collapses following a start from low population numbers. Conversely, if  $f > r$  the number of individuals capable of reproducing would be generated at a higher rate than the total number of individuals. Hence,  $r$  must be equal to  $f$ .

The rate constants for the recovery function  $r_i$  were deduced from the fact that, in the single age group model by Kryshev et al. (2008),  $\mu_R$  (equivalent to  $r_I$  in our model) is set to 1.5 times the reproduction rate  $r$ . Our dual life stage model should tend to Kryshev's formalism when  $s$  tends to  $\infty$ . For this to happen, a certain relationship must exist between the "effective" rate of formation of mature individuals  $r'$  and the reproduction rate  $r$  of the single

life stage model, involving  $d_0$  and  $d_1$ :  $1 - \frac{s+d_0}{s} \frac{d_1}{r} = 1 - \frac{d_1}{r'}$ . Therefore,  $r' = \left( \frac{s}{s+d_0} \right) r$  and

$$r_0 = r_1 = 1.5 \left( \frac{s}{s+d_0} \right) r.$$

#### 4.2.4. Estimation of the LD<sub>50/30</sub> for fish and mammals

It has been reported that, for fish,  $\alpha = 1.2 \times 10^{-4} \text{mGy}^{-1}$  so LD<sub>50/30</sub> = 5.78 Gy (Kryshev et al. 2008). Using Bytwerk's allometric formula for the LD<sub>50/30</sub> (Bytwerk 2006; Higley and Bytwerk 2007) with an egg mass of  $1.78 \times 10^{-6}$  and an adult mass of 4.94 kg would give LD<sub>50/30</sub>'s of 40.1 and 5.86 Gy, respectively. For adults this is similar to Kryshev's constant, thus validating it. In another study, it is reported that the embryos of carp (*Cyprinus carpio*) have a similar LD<sub>50/30</sub> of 6.01 Gy for low-LET  $\gamma$ -radiation (Blaylock and Griffith 1971). It is therefore reasonable to use an LD<sub>50/30</sub> of 5.78 for adult fish.

For fish eggs the allometric relationship gives an LD<sub>50/30</sub> of 40.1 Gy which is obviously too high, because embryos are more radiosensitive than the adults despite their smaller size. Bytwerk's formula is only valid for adults. We therefore adopt a LD<sub>50/30</sub> of 3 Gy for fish eggs, again following previous work (Kryshev et al. 2006) who applied an LD<sub>50/30</sub> of 3 Gy for salmon eggs exposed to  $\gamma$ -radiation at the initial period of development (Gorodilov 1971).

For mammals, the species-dependent (free) parameters relating to radiation: LD<sub>50/30</sub>'s for juvenile and adult of each species, were re-calculated as follows. The allometrically calculated LD<sub>50/30</sub>'s for mouse, hare/rabbit, wolf/wild dog and deer are 11.7, 6.3, 4.6 and 3.8 Gy, respectively. However, direct data exists for the first three species: 11.1 (Golley et al. 1965; Gambino et al. 1968), 10.2 (Pryor et al. 1967) and 2.6 Gy (Norris et al. 1968) for mouse, rabbit and dog, respectively. For deer no information was found, though an average of

2.3 Gy (Sasser et al. 1971; Von Zallinger and Tempel 1998) for organisms of similar mass (donkey and cattle) can perhaps be taken as a reasonable approximation.

The same values were assumed for the juvenile as for the adult of each organism, given the paucity of data. As stated previously, it would be incorrect to apply Bytwerk's allometric relationship to the juvenile of each species. Taken together, the LD<sub>50/30</sub> data selected are consistent with acute lethal doses (LD<sub>50/30</sub>) of typically 6-10 Gy for small mammals and 1.2–3.9 Gy for larger animals and domesticated livestock, indicating the higher radiation sensitivity of large mammals compared with small mammals (ICRP 2008).

### 4.3. Results

#### 4.3.1. Validation of the model for fish

When modeling effects on fish eggs, and particularly for mortality on short time periods (tens of days), it is necessary to perform some model alterations to mimic the experiments in which these effects were measured. The egg production rate is so high that it would mask any radiation-induced lethality effects. There would have been no adult fish actually reproducing in the tanks used for the egg experiments, so reproduction is disallowed in the model. Likewise, the large death rates for fish eggs must be set to zero, since we are interested in modeling the radiation effects in excess of a control population.

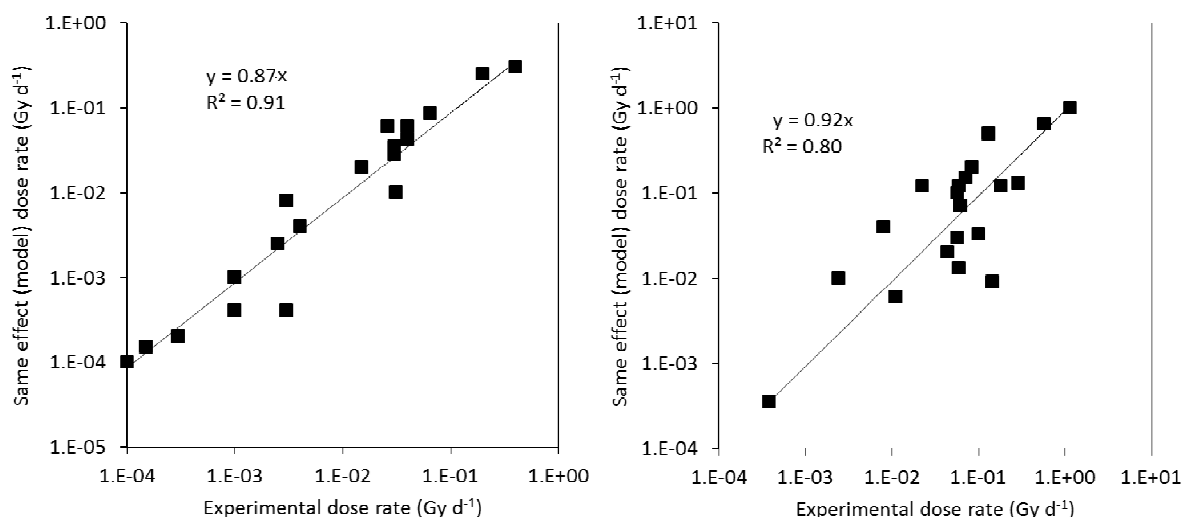
In general, the dual-age class model was found to predict successfully most of the experimental observations for loss of fecundity/survival/repair (mean of absolute differences = 13%, 77% of the data within  $\pm 20\%$ ) and tends to be reasonably compatible with previous fish modeling results for eggs and adults (Kryshev et al. 2006;. 2008) (mean of absolute differences = 10%, 88% of the data within  $\pm 20\%$ ). The calibration for acute effects using the

experimentally observed LD<sub>50/30</sub> values for egg and adult appears indeed to work well for chronic doses.

There are some limitations. For fish eggs there was a single anomaly in that practically total mortality of eggs is predicted for a dose rate of 39.200  $\mu\text{Gy h}^{-1}$  applied over 14 days. With a LD<sub>50/30</sub> of 3 Gy d<sup>-1</sup> the model cannot reproduce this result because it implies a higher LD<sub>50/30</sub> for acute doses. The above notwithstanding, our model can clearly predict tipping points around which significant onset of the effect calculated occurs, namely: (a) mortality for fast-developing eggs in the dose rate range 125000-208300  $\mu\text{Gy h}^{-1}$ ; (b) mortality for slowly-developing eggs in the dose rate range 1250-1667  $\mu\text{Gy h}^{-1}$ ; (c) mortality for adult in the dose rate range 833-1250  $\mu\text{Gy h}^{-1}$ ; (d) significant depletion of repair pool for eggs in the dose rate range 417-833  $\mu\text{Gy h}^{-1}$ ; (e) significant depletion of repair pool for adult in the dose rate range 417-1250  $\mu\text{Gy h}^{-1}$  and (f) fecundity in the dose rate range 1250-2500  $\mu\text{Gy h}^{-1}$ . Around the tipping point, model predictions can vary significantly compared with experimental values, but in reality the dose rates triggering significant effects are very close to dose rate values for which the model predicts the same effects.

To illustrate the above point, we compared the mean experimental dose rates for fish at which the various effects are observed with the model-predicted dose rate to achieve same effect. Figure 15 (left) shows that the two sets of data are strongly correlated, with a coefficient of determination R<sup>2</sup> of 0.91 on a wide range of dose (chronic as well as acute) from 10<sup>-4</sup> to 1 Gy d<sup>-1</sup>, and for a wide variety of different effects in both fish and fish eggs (mortality, morbidity – interpreted as depletion of the repair pool – and fecundity).

We verified mathematically that the tipping points for loss of repairing pool, fecundity and survival result from a predicted quasi-sigmoidal dose-response relationship with a shallow no-effect region at low doses followed by large variation over a narrow interval



**Fig. 15. Comparison of experimental results and model predictions**

Comparison of experimental dose rates for different effects with model-predicted dose rate needed to obtain the same observed effect in fish (data from the EPIC study; left) and mice (data from the FREDERICA database).

around the tipping value, whereupon the dose-response curve stabilizes to near-100% effect. This is typical of deterministic effects, in which many cells are killed by radiation resulting in a significant loss of organ function above the threshold dose value, resulting in significant effects at population level.

As an additional exercise, the model was tested against further data from the radiation dose effects database FREDERICA (Brown et al. 2008; Copplestone et al. 2008). We extracted from the database fish data for (low-LET)  $\gamma$ -radiation, eliminating all  $\alpha$ -,  $\beta$ - and mixed exposure data (the latter, because we could not be sure if it was low-LET radiation or not). This comparison excluded information that cannot be calculated by our model such as hormetic effects, specific effects such as changes in blood composition or changes in size or lifespan. We also excluded qualitative information of the type 'effect observed but no value given', or effects for which exposure time cannot be calculated because the cumulative dose was not reported.

As seen in Figure 15, this comparison too appears successful in that (a) similar effects are reasonably reproduced at similar doses, (b) observed no-effect doses tend to coincide with doses for which modelled effects are < a few percent and (c) experimental doses at which effects were observed and those for which the model predicts the same effect are well correlated ( $y = 1.04x$ ;  $R^2 = 0.89$ ), lending further credence to the model.

#### 4.3.2. Validation of the model for mammals

We compared the predictions for small mammals (mouse/voles) with effects data based on whole body external gamma irradiation studies from the FREDERICA database (Coppstone et al. 2008). The reason for limiting the comparison to small mammals is that some 50% of the 106 FREDERICA effects data for mammals are for mice and voles, whilst only 5% of the information is for dogs and no data are available for rabbits or deer.

Again, the logistic dual-age class model was found to approximate most of the experimental observations (mean difference of loss of fecundity/survival/repair between modelled and experimental prediction = 22%, 75% of the predictions to  $\pm 30\%$ ). As can be seen in Figure 15, these results are somewhat less accurate than for fish, due to differences in radiation sensitivity between mice species.

Results of this comparison were quantified in terms of dose rate for the model to reproduce an observed effect over the given time of dose application, versus the experimental dose rate at which the actual effect was reported. With the exception of a single effect corresponding to an acute dose of 7.7 Gy applied over a 20-minute period, which could not be modelled, a linear relationship exists between the model-predicted doses for a given effect and the experimental data (Figure 15). This relationship has a satisfactory coefficient of determination ( $y = 0.92x$ ,  $R^2 = 0.81$ ), lending additional credence to this model.

#### 4.3.3. Predictions for a 'benchmark scenario'

We used the benchmark scenario developed by the IAEA Biota Dose Modeling Group<sup>1</sup> of the EMRAS II Programme for generic populations of mice, hare/rabbit, wolf/wild dog, and deer. Each population, initially consisting of  $10^3$  animals equivalent to the carrying capacity of the ecosystem, were chronically exposed on a range of dose rates from 417 to 2083  $\mu\text{Gy h}^{-1}$  for 1 to 5 years. Two additional years after the cessation of exposure were considered to test for recovery of the population. Model predictions for mice (Table 16) indicated that at dose rates  $< 1250 \mu\text{Gy h}^{-1}$ , the population reaches a new stable level with losses after 5 years ranging 2.5 - 9% of the initial population, depending on dose.

#### 4.3.4. Further observations

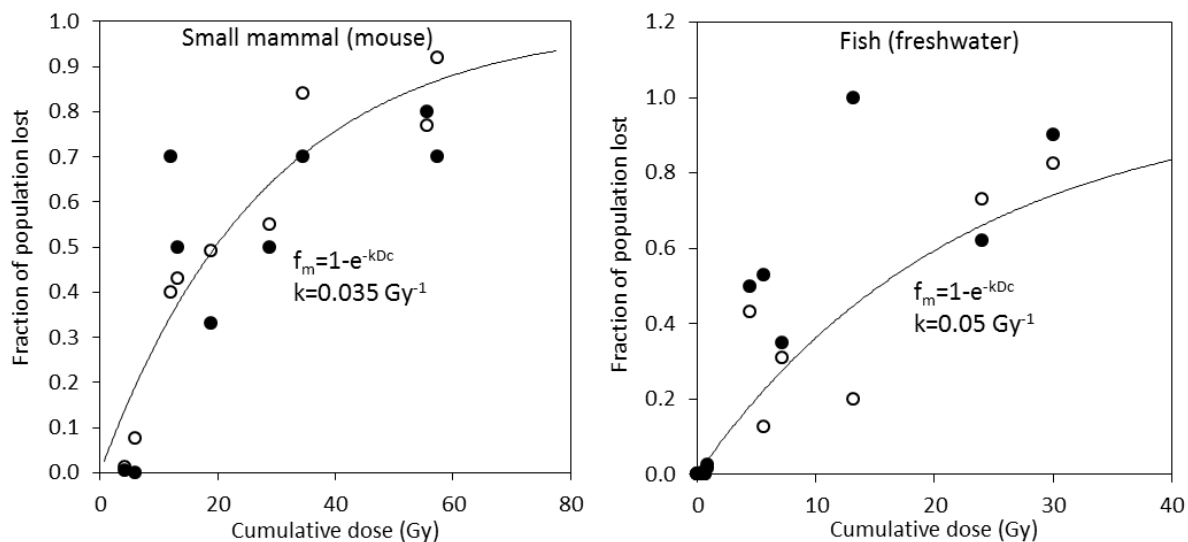
The present study suggests that population behaviour and radiological effects can be successfully integrated, providing indicative data for natural wildlife populations where an exhaustive experimental study is not yet available.

An example of the potential of the model is its ability to interpret data for different dose rates and lengths of exposure. For instance, the experimental data for fish and small mammals show that the mortality (or  $f_m$ ) follows a trend with the cumulative dose  $D_c$  which can be loosely approximated as  $f_m = 1 - e^{-kD_c}$ . The modelled data also follows the same pattern. For

**Table 16. Predicted surviving fraction from initial population at different dose rates ( $\mu\text{Gy h}^{-1}$ )  $d_r$  for mice populations**

Organism	Time (y)	$d_r = 417$	$d_r = 833$	$d_r = 1250$	$d_r = 1667$	$d_r = 2083$
Mouse/vole	1	99.0	96.8	75.0	54.3	38.6
	2	98.3	94.2	40.4	15.2	7.5
	3	97.8	92.6	14.6	3.6	1.4
	4	97.5	91.6	4.4	0.9	0.3
	5	97.4	91.0	1.3	0.2	0.1

<sup>1</sup><http://www-ns.iaea.org/projects/emras/emras2/working-groups/working-group-six.asp?s=8>



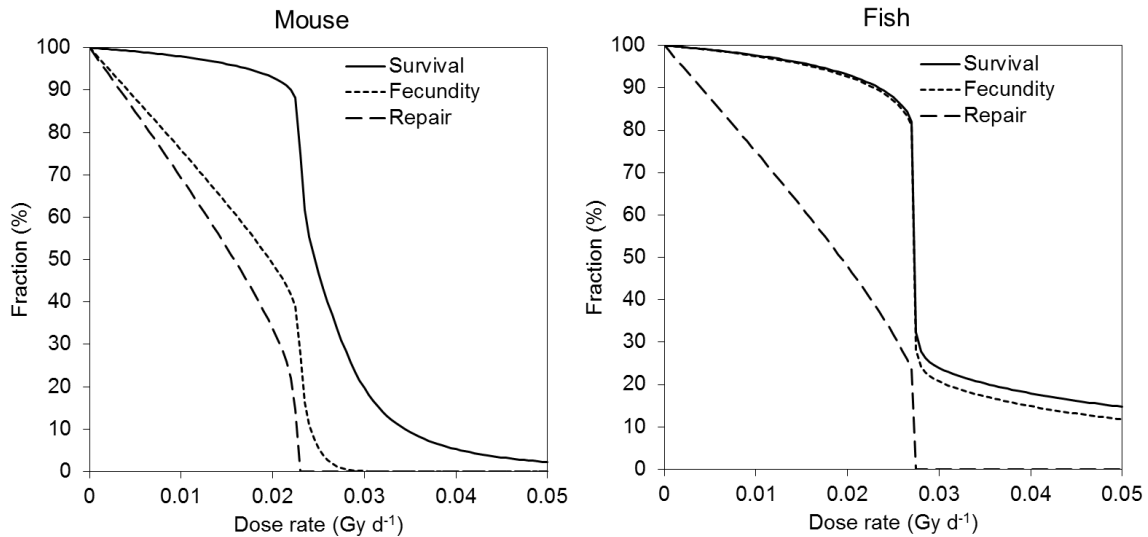
**Fig. 16. Observed and model-predicted reduction in survival at different cumulated dose (Gy) in mice and fish**

Observed data (●) and model predictions (○) of loss of survival at different values of cumulative dose for adult mice (left) and fish (right); solid line: fit through modeled data.

mammals,  $k = 0.035 \text{ Gy}^{-1}$  for modelled data vs.  $0.031 \text{ Gy}^{-1}$  for FREDERICA effects data represented in this way (Figure 16). For fish,  $k = 0.05 \text{ Gy}^{-1}$  for modelled data vs.  $0.11 \text{ Gy}^{-1}$  for EPIC effects data (eggs and adults).

In another example of the model's potential, we studied the relative difference in effect of adopting a “lethal damages / total damages” ratio of 0.02 ( $\gamma$ -radiation) or 0.90 ( $\alpha$ -radiation). Whilst for small mammals (mice) a low-LET radiation dose rate of  $417 \mu\text{Gy h}^{-1}$  induces a 2.1% loss of survival (mortality) after  $10^3$  days, an equivalent  $\alpha$ -radiation dose rate of  $292 \mu\text{Gy h}^{-1}$  is required to generate the same effect in the model. This suggests a radiation quality factor of 14 for high-LET  $\alpha$ -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 a ratio of 0.25 (the intermediate  $< 10 \text{ keV}$   $\beta$ -radiation case) the equivalent dose rate was  $92 \mu\text{Gy h}^{-1}$  which gives a radiation quality factor of 4.5, resembling the factor of 3 for low-energy  $\beta$ -radiation adopted in non-human biota dose assessments by analogy to  $^3\text{H}$  dosimetry. For fish,





**Fig. 17. Relative survival, fecundity and repair pool in mice and fish as a function of dose rate**

Survival, fecundity and repair pool (fraction of initial population) of the adult mouse (left) and fish (right) as a function of dose rate (from 417 to 2083  $\mu\text{Gy h}^{-1}$ ).

the model-predicted radiation quality factors are 25 for  $\alpha$  - similar to the value of 30 calculated in our previous work (Vives i Batlle et al., 2010) - and 7.5 for  $< 10$  keV  $\beta$ -radiation. These higher values result from the asymmetric population effect on species that have a very high fecundity but a very low survival from egg to adult (Figure 17).

The FREDERICA database contains only 5 references of quantifiable effects (mainly fecundity) of chronic exposure to  $< 10$  keV  $\beta$ -radiation (Tritium) to small mammals which can be interpreted on the basis of our model. Some of the records are for rat rather than mice species; hence model runs for those data were adapted for the different  $\text{LD}_{50/30}$  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  $< 208 \mu\text{Gy h}^{-1}$  and significant effects at doses in the order of  $833 \mu\text{Gy h}^{-1}$ , a factor of  $\sim 3$  below the doses at which low-energy  $\beta$ -radiation produces significant effect on reproduction. Without adjusting the  $\text{LD}_{50/30}$ , a single acute effect in mice fecundity at  $708 \mu\text{Gy h}^{-1}$ , 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  $\beta$  radiation on mammals and other species becomes available.

## **5. General discussion, lessons learnt, limitations and perspectives for improvements**

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### **5.1. Propagating radiosensitivity from individual to population levels**

In our studies based on Leslie matrices or dual age-class continuous time population models, we explored population response to chronic ionising radiation in aquatic and soil invertebrates, fish and mammalian species based on 1) a review of radiation effects on their main life history traits and 2) a modeling exercise examining how population growth or carrying capacity declined as a result of combined changes in several life history traits. These approaches were in agreement with the hypothesis that population-level effects depended both on how key biological functions are affected by toxicity at the organism level and how population dynamics respond to such effects. In this context, previous studies concluded that the same level of effect could have different consequences for the population depending on the impaired individual endpoint and on life history strategies (Forbes and Calow, 1999; 2002; Heppel et al., 2000; Stark et al., 2004; Raimondo et al. 2006; Alonzo et al., 2008a). Using Leslie matrices, sensitivity analyses confirmed earlier findings that effects of ionising radiation cannot be directly compared between the individual and the population level. Our results pointed that net reproductive rate  $R_0$  and population  $\lambda$  were respectively most

influenced by changes in fecundity and delay in reproduction, e.g. that critical end points differed between the individual and population levels. Furthermore, predicted levels of change depended on life history characteristics of the tested species. Our simulations supported, independent of the modeling approach considered, the earlier assumption that the most influential individual endpoint for population dynamics was not necessarily the most sensitive to radiological (or chemical) toxicity (Kammenga et al., 1996). The dual age-class population model verified mathematically that survival, fecundity and repairing pool have quasi-sigmoidal dose-response relationships with dose rate (Figure 17). The most sensitive endpoint seems to be repairing pool, followed by fecundity and effect on survival.

With the Leslie matrix approach, no direct correlation was observed between life history strategy and radiosensitivity that might have allowed some degree of simplification. In fact in aquatic invertebrates, the slow growing *N. arenaceodentata* and fast growing *O. diadema* (with respective  $\lambda$  values of 1.29 and 1.92 in control conditions) were equally sensitive to ionising radiation at the individual level whereas *P. heterostropha* with an intermediate  $\lambda$  of 1.63 was the most radioresistant among the three species. In soil invertebrates, fecundity showed comparable sensitivity to ionising radiation between *Eisenia fetida* and *Porcellio scaber*, although respective values of 2.48 and 1.13 were estimated for  $\lambda$  in each species. A similar comparison was more difficult to address in other taxonomic groups due to the scarcity of effect data giving no basis for comparing radiosensitivity.

Results from the dual age-class continuous time population model reinforce the fact that propagating radiosensitivity from individual to population levels results in different patterns than expected for an individual organism. For example, a population of mice appears more radiosensitive than fish despite the lower LD<sub>50/30</sub> 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. The model also suggests that adverse radiation effects to fish embryos have stronger consequences for populations in slow growing species (*i.e.* those with low fecundity or a long juvenile stage) than in fast growing ones (*i.e.* those with high fecundity or a short juvenile stage). In mammalian species, population survival under radiation exposure was higher in species with high reproduction capacity (Vives et al., in press).

## 5.2. Compared population-level predictions

### 5.2.1. Comparison with literature benchmarks

With the Leslie matrix approach, combining available effects observed in each species on distinct life stages and individual endpoints yielded significant changes in both individual  $R_0$  and/or population  $\lambda$  at minimum dose rates of 716 and 2,606  $\mu\text{Gy h}^{-1}$  respectively in aquatic (*O. diadema*) and soil (*E. fetida*) invertebrates and of 781 and 144  $\mu\text{Gy h}^{-1}$  respectively in fish (*P. reticulata*) and terrestrial mammals (*M. musculus*). Such results suggest that the generic provisional benchmark values of 200  $\mu\text{Gy h}^{-1}$  and 2  $\mu\text{Gy h}^{-1}$  (incremental dose rates) proposed by PROTECT respectively for invertebrates and vertebrates (Garnier-Laplace et al., 2008; 2010) might be protective of theoretical population simulated in each considered species.

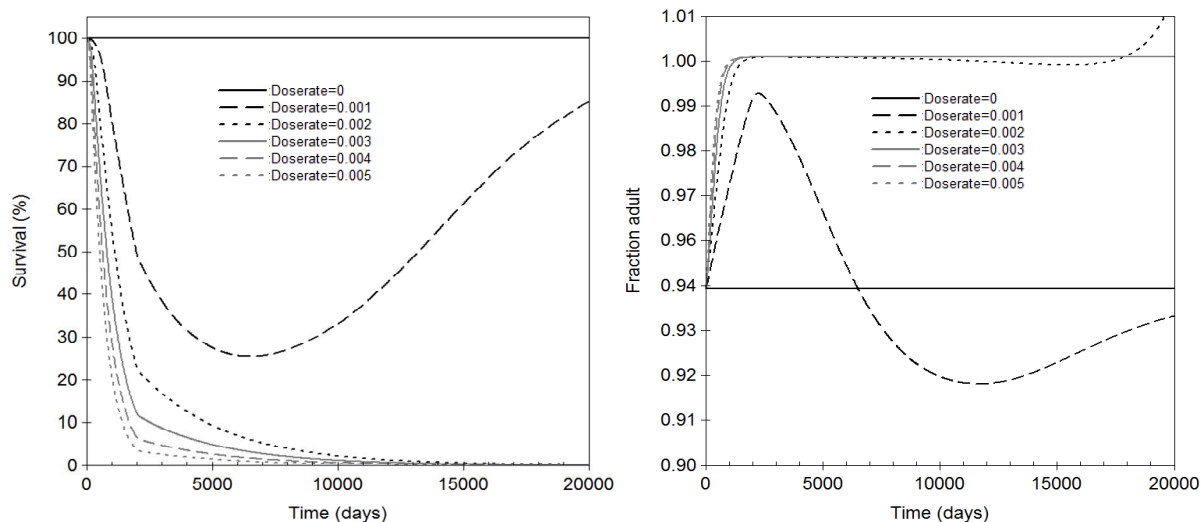
In the PROTECT project, derivation of generic benchmark values was based on the set of lowest individual  $EDR_{10}$  estimated among tested endpoints for each selected species (Garnier-Laplace et al., 2010). This approach was based on the assumption that a population was protected from ionising radiation when the most sensitive individual endpoint was protected. Our simulations suggested that this assumption was not verified, as shown in the aquatic invertebrates *O. diadema* and *P. heterostropha* and in the earthworm *E. fetida*. In fact, significant reduction in individual  $R_0$  or population  $\lambda$  resulting from a combination of slight

effects (<10% reduction) on several life history traits, was predicted at dose rates below any  $EDR_{10}$  derived for the species at the individual level (lowest  $EDR_{10}$  of 1288, 54954 and 2606  $\mu\text{Gy h}^{-1}$  respectively in *O. diadema*, *P. heterostropha* and *E. fetida*). This observation supported the idea that a species might not be protected (against an effect of 10% or lower) below the  $EDR_{10}$  derived for the most sensitive individual endpoint, if several life history traits are simultaneously affected. Although values estimated at the population level remained at the same order of magnitude as the lowest  $EDR_{10}$  at the individual level, benchmark values might be slightly but significantly reduced if derived from a set of population-level  $EDR$ . This issue underlined the need for population modeling to integrate all observed effects, including those most sensitive on molecular and cellular endpoints. This challenge must be solved before outcomes of population dynamics are used for establishing population-level radioprotection criteria for the different taxonomic groups. When all observed effects are taken into account, population response might be more sensitive than individual endpoints such as survival, fecundity and hatching.

The results from the logistic, dual-age class population model tend to confirm the ERICA benchmark value of 10  $\mu\text{Gy h}^{-1}$  for all biota as a dose rate below which adverse effects are not expected, with expectations that measurable effects begin to appear about an order of magnitude above this value, and also support the similar USDoE benchmark of 40  $\mu\text{Gy h}^{-1}$  for terrestrial animals, with the expectation that observable effects on mammals may occur at about one order of magnitude higher.

#### 5.2.2. Comparison between modeling approaches

For taxonomic groups which were considered with both modeling approaches, namely fish and mammals, it is interesting to compare simulation outcomes between the dual age class model and the Leslie matrices.



**Fig. 18. Example of effect gamma radiation on population structure and population self-recovery for deer at low dose rates**

Self-recovery of the population of deer at low dose rates (left) and effect gamma radiation on population structure (right) for deer – dose rates of 0 – 42  $\mu\text{Gy h}^{-1}$  (0 – 0.005  $\text{Gy d}^{-1}$ ) administered over 2,000 days. The fraction > 100% adults in the population structure graph at high dose rates is a numerical artifact that only appears at extremely low population numbers.

In a previous study (Vives et al., in press), the dual age-class population model was applied to generic populations of mice, hare/rabbit, wolf/wild dog, and deer exposed for 5 years to a chronic dose rate range from 417 to 2083  $\mu\text{Gy h}^{-1}$  followed by 2 year-recovery (EMRAS II benchmark scenario). Simulations of changes in population size predicted that populations reached a new stable size >90% of the initial size at dose rates of 833  $\mu\text{Gy h}^{-1}$  in mice and 417  $\mu\text{Gy h}^{-1}$  in rabbit. Extinction (or a severe decrease in population size) was predicted at higher dose rate in the two species. A dose rate of 417  $\mu\text{Gy h}^{-1}$  caused extinction in wolf and deer populations. An additional simulation in the most radiosensitive species (deer) suggests that a dose rate of 42  $\mu\text{Gy h}^{-1}$  is the highest that will not drive the population to extinction (Figure 18). In fish, a decline in population was predicted at dose rates of ~1100  $\mu\text{Gy h}^{-1}$ .

These results contrasted with those obtained with the Leslie matrix approach. Combining chronic dose rate response curves suggested that population extinction was induced at dose

rates ranging from 3802  $\mu\text{Gy h}^{-1}$  in the mouse to 8511  $\mu\text{Gy h}^{-1}$  in the dog and at 3981  $\mu\text{Gy h}^{-1}$  in the most radiosensitive fish (*O. mykiss*). Thus, dose rates causing extinction differed by one order of magnitude, in agreement with the statement that allometrically-derived  $\text{LD}_{50/30}$  resulted in conservative estimations of chronic dose rates threshold causing mortality (Bytwerk 2006). With the Leslie matrix, variations in radiosensitivity among species suggested that large mammals might be more resistant than small mammals. Due to data scarcity however, both approaches rely to a large extent on extrapolations with the result that robust conclusions could not be drawn under the circumstance.

### 5.3. Relevance of effect data for population modeling

Ecological risk assessment focused on the population level gains 1) in robustness by considering consequences of combined effects on several individual endpoints and integrating life history properties of the different species, and 2) in ecological relevancy compared to approaches based on the organism level (Forbes and Calow, 2002; Stark et al., 2004; De Mott et al., 2005; Raimondo et al., 2006). Matrix population models have previously been recognized as valuable tools to predict toxic effects on population dynamics (Forbes et al., 2009; Salice and Miller, 2003; Chandler et al., 2004; Bin-Le and Yaobin, 2009; Charles et al., 2009). The method is promising under the condition that detailed descriptions of life histories and robust datasets on biological effects of ionising radiation are available for reliability of model predictions (Klok and de Roos, 1996). However, predictions may be questionable when such knowledge is scarce, limited to few individual endpoints– as is often the case in the literature – or even absent for some critical life history trait or life stage. In our study, this was particularly true of delay in reproduction, for which radiation effects were examined in few species although this life history trait was identified as critical for population  $\lambda$  in all

tested species. In this context, one can wonder whether the set of radiation effects considered in this study was relevant for population modeling.

The experimental range of dose rates on which our modeling was based should be discussed as the lowest tested dose rate varied widely among species, from 2  $\mu\text{Gy h}^{-1}$  for *M. musculus* (an acceptable value considering the calculated  $\lambda$ -loEDR of 144  $\mu\text{Gy h}^{-1}$ ) to 10.0  $\text{mGy h}^{-1}$  for *P. heterostropha*. In cases such as *P. heterostropha* where the lowest tested dose rate was high, fitted dose rate response curves implicitly assumed that the level of effects continuously decreased to the control. This assumption is not supported by a number of studies describing a biphasic response curve in cell damages with larger effects at low doses (ECRR, 2010).

The fact that our modeling approach did not include effects at lowest levels of biological organisation had strong implications for the predicted radiosensitivity at the population level. Our working assumption was justified considering that links between molecular or cellular responses and population dynamics remain difficult to establish (Fedorenkova et al., 2010; Van Straalen et al., 2010). Many examples of genetic, molecular and cellular damages were reported in the considered species. In *N. arenaceodentata* for example, such effects occur at much lower doses compared to those at the individual level (Dallas et al., 2012). In this context, one can hypothesise that damages at the genetic, molecular and cellular levels could serve as early warning indicators for environmental effects at doses where fitness-related effects are not visible, at least over short-term laboratory experiments.

The previous assumption cannot be tested for long-term exposure situations because radiation effects have mainly been explored for exposures limited to one life stage or one generation, whereas populations might be exposed for durations largely exceeding organism lifespans. Several studies have showed that toxic effects of radionuclides, such as  $^{241}\text{Am}$  or



depleted U, on survival and reproduction could increase in severity over successively exposed generations (Alonzo et al., 2008b; Massarin et al., 2010). One might question the relevance for population dynamics of effect data reported for one generation if results are not representative of effects in the subsequent generations.

External gamma radiation employed in our approach might not be representative of environmental exposure, at least for alpha and beta radiation. In fact, several studies have reported larger effects of internal exposure to waterborne tritiated water at comparable dose rates (Jha et al., 2006; Dallas et al., 2012). In those cases, the nature of the radiation source (water) and the type of emitted radiation (low energy beta-particles) might also contribute to the difference in toxicity, compared to external gamma irradiation. The consequences of chronic internal alpha and beta exposure remain to be investigated under laboratory conditions as the majority of gamma radiation effects reported in the literature to date concern external exposures.

The dual age class population approach faces additional issues regarding the relevance of effects data. A specific problem is raised by how morbidity data are interpreted to adjust the percentage depletion of the recovery pool. In particular, the limitation concerns the use of a generic variable which covers a wide range of effects, from peripheral blood changes, to reduced growth or organ mass loss, cancer induction, etc.). Because the approach is not mechanistic, the radiation repair mechanism cannot cover the whole range of teratogenic, genetic, developmental and behavioural effects reported in FREDERICA and cannot predict stochastic effects such as chromosomal aberrations and cancers.

## 5.4. Need for robust mechanistic models instead of extrapolations

In any population modeling exercise, the validity of predictions depends on the availability of detailed descriptions of life-histories and robust datasets on biological effects (Klok and De Roos, 1996). However, predictions may be put under question when such knowledge is scarce or limited. The fact that our models strongly relied on extrapolations in order to overcome the scarcity of useable effect data represented one of the main limits of our approaches.

- **Extrapolations from acute to chronic effects** remain highly debatable as they represent both an extrapolation from high to low doses and from pulsed to continuous exposures. Organisms are very unlikely to respond linearly to these two situations. On the one hand, chronically cumulated doses at a low dose rate leave more time for organisms to develop compensatory responses such as repair mechanisms. Repair processes might reduce damages and effect severity up to a dose threshold above which reparation capacity becomes overloaded and/or damaged. Such a threshold has a higher chance of being exceeded after short-term acute doses than under chronic low dose rates. On the other hand, continuous long term exposures increase the chance that a radiosensitive life stage or process gets exposed and observed ionising radiation effects increase in severity.
- **Extrapolations using allometry**, especially under chronic exposure, appeared poorly consistent with the fact that organisms are unlikely to respond in the long-term depending on an index of their body volume only, but rather have strong specific (metabolic, physiological, cytological etc.) features which modulate their response to ionising radiation.
- Basing modeling on **dose rate response curves** established at fixed time exposures reduced the number of effect data points and implied effect **extrapolations among age classes**. The fact that effects were not considered as dynamic processes ranked a significant fraction of

effect data as not useable in a preliminary screening analysis because a sufficient effect range for establishing a dose rate response curve is not reported for every exposure time. This screening step, as well as unnecessary extrapolations among age classes, can be avoided if models are able to describe effect variations over time with increasing organism age.

Alternative mechanistic approaches such DEBtox and GUTS (Kooijman and Bedaux, 1996; Jager et al., 2011; Jager and Zimmer, 2012) offer a conceptual framework to integrate toxic sublethal and lethal effects as dynamic processes over time. By describing how toxic contaminants cumulated in organisms or induce cumulative pools of damages over time, these approaches have a strong potential for integrating effect data which are collected at various exposure times, instead of considering endpoint responses at single exposure times, and under different (constant or time-varying) exposure time patterns (Billoir et al., 2012). Based on threshold toxicity functions, these approaches allow exploration of various hypotheses on an exposure range from low sublethal doses to high lethal doses and might fill a gap between acute and chronic exposure situations. Mechanistic approaches offer insight in underlying modes of action, which have strong potential for linking effects among different levels of biological organisation, for conceptual extrapolations of common underlying mechanisms among species of a same taxonomic group and for modeling of their consequences for life history depending on specific, physiological and morphological characteristics (Swain et al., 2010; Wren et al. 2011). Recently, the DEBtox approach has been successfully applied to radionuclides in the case of *Daphnia magna* exposed to depleted uranium (Massarin et al., 2011) and has demonstrated that effects on growth and reproduction could be jointly explained by a reduction in assimilation, a toxic mode of action which was confirmed in daphnids through complementary physiological analyses and observations of histological damages on the gut epithelium. Such damages were also observed in *Eisenia fetida* exposed

to natural and depleted uranium (Giovanetti et al., 2010) suggesting a common mode of action among daphnids and earthworms.

## 5.5. Ecological realism in population models

Extrapolating model predictions to natural populations is further complicated because population dynamics depend on many additional environmental factors such as fluctuating trophic conditions and temperature, predation pressure, density-dependence, exposure to mixtures of toxicants, etc. as well as interactions among species in a community-level context (Forbes and Calow, 2002; Pennington, 2003). In this context, applying a logistic function to survival and the fertility rates, as proposed in the dual age class population model, is an interesting approach to simulate density-dependence in a theoretical population. However, parameterising such functions requires that the combined effect of radiotoxicity and crowding is explored under laboratory controlled conditions. Other ecological constraints, such as food conditions, are also of interest. For example, Gilbin et al. (2008) showed that resistance to starvation declined in early larval stages of *Daphnia magna* exposed to ionising radiation. Their result illustrated how responses of irradiated populations might differ under constant or depleted food conditions. Modeling approaches in this study assumed that populations were growing in a theoretical spatially unlimited habitat and under optimal environmental conditions (as that provided in laboratory tests) or that density dependence theoretically did not modulate the capacity of organisms to cope with ionising radiation (i.e. that effect data observed under favourable laboratory conditions were representative of crowded, limiting environmental conditions), as a simplified approach for modeling population effects of ionising radiation.

Extrapolating effects from organisms to populations raises the critical question of defining an acceptable level of radiological protection which guarantees the persistence of a population (Wilson et al 2009). The Leslie matrix approach showed that 10%-reduction in population  $\lambda$  was a result of concomitant strong effects on several individual endpoints in every species. From this point of view, such a criterion may not appear sufficiently “safe” for organisms. Authors recently used population extinction (population  $\lambda < 1$ ) as an endpoint for population-level risk assessment of zinc on a range of wildlife species (Kamo and Naito, 2008; Tsushima et al., 2010). On this basis, the “environmentally safe” concentrations for populations were one order of magnitude greater than corresponding no-observed-effect concentrations for individual endpoints. In agreement with these results, population extinction was predicted in our study at dose rates which largely exceeded  $EDR_{10}$  calculated for every endpoint (except fecundity in *N. arenaceodentata*). A target dose rate (or toxicant concentration) which reduces  $\lambda$  to 1 and theoretically brings populations to the edge of extinction in controlled laboratory conditions seems much likely to cause their extinction in a realistic ecological context characterized by changing – and temporarily unfavourable – environmental conditions. From this point of view, the lowest dose rate inducing a statistically significant change in individual  $R_0$  or population  $\lambda$  seemed a more acceptable criterion for radiological protection of wildlife species. Which level of statistical significance is ecologically significant is an issue which remains to be examined.

## 5.6. Conclusions / Research perspectives

Population models constructed in this study from demographic data of the literature also allowed integration of all available radiation effect data measured at the individual level in order to derive dose rates above which theoretical population growth was significantly

affected compared to unexposed control. This method may be limited by the lack of data on chronic effect of ionising radiation on life history traits in non-human species. However, it is helpful to identify critical endpoints for population growth in various species with different life history strategies and to focus future laboratory investigations. One big challenge for the approach consists in experimentally testing and conceptually building the link between effects observed at molecular levels with those which are relevant for population dynamics, by conducting exposure experiments on relevant time scales for the population (including those susceptible to give rise to adaptive response) and testing trans-generational effects of radiation. Population-level evaluation of radiation effects should also be extended include more species that cover the diversity in physiological and life history characteristics and extended radiation effect models to deal both with acute and chronic exposure situations.

Both Leslie matrix and modeling results cannot be interpreted as final model validation because long-term experimental studies of population dynamics in the wild under the effect of radiation are very scarce and not well documented, though some limited evidence exists that might at least provide a yardstick for future model predictions (Mihok 2004). Moreover, the effects data used here are dominated by acute exposure studies with relatively few experiments conducted over long-term exposures to low radiation doses. However, the modeling studies given in this report provide evidence that population behaviour and radiological effects can be successfully integrated, giving indicative information for natural wildlife populations where an exhaustive experimental study is not yet possible.

Future research directions can concern the study of radiation effects at the community level, with the ability to link the transfer and effect models (Wilson et al. 2010) and analyse radiation-induced perturbations in predator-prey relationships in simple trophic webs. To improve the predictive ability of different population dose effects models would involve, for

example, studying the influence of natural immigration on population recovery after exposure to ionising radiation, and analysing synergistic effects of radioactive substances with other toxic contaminants.

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