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Thesis committee

Thesis supervisor
Prof. Dr. ir. Paul J. van den Brink
Professor of Chemical Stress Ecology
Wageningen University

Thesis co-supervisor
Dr. Hans M. Baveco
Research scientist, Team ecological models and monitoring, Alterra, Wageningen UR

Other members
Prof. Dr. Paul Opdam, Wageningen University
Prof. Dr. Volker Grimm, University of Potsdam, Germany
Prof. Dr. Andre M. de Roos, University of Amsterdam
Dr. Udo Hommen, Fraunhofer – IME, Schmallenberg, Germany

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Nika Galic

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For my family

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Contents

Chapter 1

Introduction

Human population is still expanding and it is expected that by 2100 it will reach 10 billion (United Nations 2011), resulting in a rising need to grow sufficient amounts of food. Agriculture is a basic human activity that is essential for sustaining the human population, but can, at the same time, be very disruptive for ecosystem health (Power 2010). Ecosystems worldwide, especially agroecosystems, provide various services that are beneficial for people, but are under increasing pressure (Millenium Ecosystem Assessment 2005). This affects the provision of essential services, such as clean water and air, erosion control, spread of disease, nutrient cycling, soil structure and fertility (Power 2010). One of the major threats agricultural activities pose on the environment is the conversion of natural habitats to agricultural lands (Matson *et al.* 1997). Currently, around 10% of the world's total area is under agricultural use (Devine & Furlong 2007), but the technological progress slowed down the expansion process by increasing overall crop yields through the intensification of land management, applications of artificial fertilizers and plant protection products, i.e. pesticides. The use of synthetic pesticides has revolutionized agricultural practices as it has massively reduced crop losses due to pests and diseases, with resulting high crop returns for their application (Pimentel 2009).

Pesticides, especially insecticides, are designed to be very toxic for their target organisms and, once spread in the environment, may have adverse effects on non-target organisms as well. Pesticides applied in the crops might end up, via drainage, aerial drift or leaching through the soil, in waterbodies adjacent to agricultural fields where they can pose risk to non-target aquatic biota. In Europe, each new compound put on the market has to go through an extensive risk assessment process to ensure no or acceptable negative effects on the environment during recommended use (Hommen *et al.* 2010). The field of ecological risk assessment (ERA) aims to assess potential adverse effects posed by various human activities, like the impact of chemical compounds on the environment. The protection goals and the description of the risk assessment are laid down in EU legislation, within different regulatory frameworks to assess the potential risks to humans and the environment (Hommen *et al.* 2010).

Pesticides were regulated within the Directive 91/414/EC which is now superseded by Regulation No 1107/2009 (EC 1991; EC 2009) where protection goals, data requirements and risk characterization are defined for the environmental compartment. Even though the protection goals are defined in general terms like that “no long-term repercussions should occur for the abundance and diversity of non-target organisms”, the legislation clearly allows for some small adverse effects if the long-term viability of the species can be ensured (EC 1991; EC 2009). This is typically interpreted as allowing for some decrease in abundances of non-target organisms if the recovery of their populations can be accomplished in a given period (SANCO 2002a). Ideally, recoveries should be accomplished within an eight week period (especially for microcosm and mesocosm studies), but these periods can be extended depending on the life-cycle and colonization potential of affected species (Hommen *et al.* 2010). Furthermore, a proper definition of recovery is lacking from the guidelines and legal documents, but is usually interpreted by academics and risk managers as a return to abundances comparable to those of control populations (Van den Brink *et al.* 2007). According to Niemi et al. (1990), recovery is defined as a return of a defined endpoint, e.g. density, structure, individual size, biomass etc., to its pre-stress levels, taking into account yearly dynamics and expected community structure. In stressed ecosystems, recovery can be accomplished from within the system, termed autogenic recovery, and is based on survivors of stress and their reproductive output. It can also originate from outside the stressed system, thus termed allogenic recovery, from individuals that colonize the stressed system from nearby, unstressed sources of habitat.

The actual potential for and speed of **recovery of populations** exposed to stress is, therefore, mainly **dependent on three sets of factors** (Gore, Kelly & Yount 1990; Niemi *et al.* 1990), those relating to **species life-history traits**, **to habitat or landscape characteristics and those relating to stressor characteristics** (Figure 1.1). Species traits such as the number of generations in the population (voltinism), fecundity, presence of insensitive stages in the population and dispersal abilities define its ecological sensitivity and post-stress colonization potential (Gardmark *et al.* 2003; Stark, Banks & Vargas 2004b; Pieters & Liess 2006; Devine & Furlong 2007; Tronstad, Tronstad & Benke 2007; Albanese, Angermeier & Peterson 2009). Toxicity of the pesticide for a certain species and its fate in the environment determine the magnitude and length of stress imposed on the populations and system as a whole (Crutchfield & Ferson 2000; Devine & Furlong 2007), and govern the recovery of the habitat that is essential for the recovery of its biotic part (Niemi *et al.* 1990). Finally, the structure of the stressed landscape, presence of refugia (at the impact site) and the vicinity of unstressed parts of the landscape that can serve as sources of colonizers (Devine & Furlong 2007; Brock *et al.* 2010b), together with prominent landscape features that can act as barriers or corridors (Reice, Wissmar & Naiman 1990), are all landscape related characteristics relevant for the recovery process.

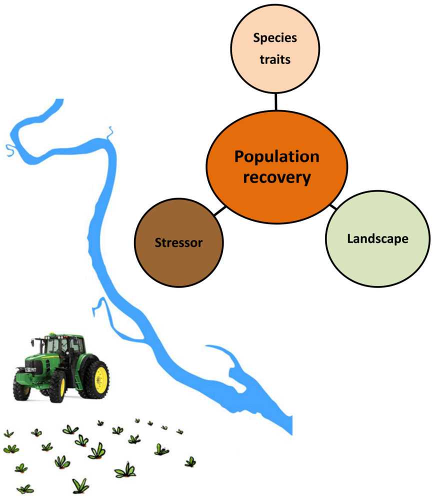

Figure 1.1. Schematic representation of the main aim of this thesis.

In the field of pesticide risk assessment, a combination of these factors will determine how much time a stressed population requires for recovery. The contribution of some of these factors can be easily estimated via empirical approaches, such as laboratory or semi-field experiments. Determining intrinsic sensitivity through standard laboratory tests to different pesticides is the central role and activity of ecotoxicology and comprises the first tiers of the risk assessment process (SANCO 2002a). In higher tiers, more ecological, but also exposure information is integrated. Species sensitivity distributions usually focus on the most sensitive group of organisms, based on the specific mode of action of the pesticide (SANCO 2002a; Hommen *et al.* 2010). Conducting semi-field and field studies integrates even more ecological information into the risk assessment process. Model ecosystems, such as, for instance, freshwater micro- and mesocosms, are able to provide information about the ecosystem and its response to different patterns of pesticide exposure, such as indirect effects within the community or the recovery process, that go beyond laboratory tests (SANCO 2002a; Hommen *et al.* 2010). However, accounting for the contribution of e.g. landscape structure or the colonization process via dispersal is beyond the abilities of most semi-field and field studies (Hommen *et al.* 2010). Ecological models have shown to be promising tools that are able to integrate different factors in a single study where outcomes from different scenarios can be compared (Bartell *et al.* 2003; Forbes *et al.* 2009). Furthermore, standard toxicity test are typically performed on the level of individuals or a handful of organisms and are, thus, unable to relate to ecologically more relevant protection endpoints, such as populations, communities or ecosystems; while these extrapolations to higher levels of biological organisation can be done with ecological models (Forbes, Calow & Sibly 2008). Hommen *et al*. (2010) defined five areas in the field of chemical risk assessment where ecological models could be especially useful, namely extrapolation of effects from the individual to the population level, extrapolation of effects between exposure profiles, assessment of recovery processes, analysis and prediction of indirect effects and prediction of bioaccumulation. Finally, the use of ecological models in ERA enables the integration of more ecological information and knowledge into the risk assessment process, a plea voiced by many researchers in the field (Van Straalen 2003; Van den Brink 2008). The latest developments in the field indicate that a more holistic and relevant definition of protection goals is being generated, using the ecosystem services framework as the major guideline (Nienstedt *et al.* 2012). This makes the use of ecological models in ERA certain and indispensable for the future of the whole field.

The **aim of this thesis** is to shed light on and quantify the contribution of species, stressor and landscape factors to the population recovery process of aquatic macroinvertebrates in the agroecosystem. In order to do this, I develop and use ecological models. I also reviewed the use of ecological models for the field of ERA.

In the **Chapter 2** of this thesis I review published modelling studies and analyse the usability of each study for the purposes of chemical risk assessment. Population models dominate the reviewed studies, but also organism-level and food web models are included in the analysis. A model database that is publicly available is an additional product of this analysis.

In Chapters 3, 4 and 5, I evaluate the contribution of different factors to population recovery of aquatic macroinvertebrates (Figure 1.1). In **Chapter 3**, I analyse the effects of timing of stress in relation to species' phenology, together with habitat connectivity, on the time to recovery. For this purpose, I describe an individual-based model (IBM) of the water louse, *Asellus aquaticus*, a freshwater isopod shown to be relatively sensitive to pesticide exposure and with limited colonization potential. In this chapter, I present an analysis of recovery times that, by comparing treated and control populations, yields a distribution of recovery times after a certain stress event. These distributions of recovery times allow for ecologically meaningful insights and are easily linked to seasonal dynamics of the species.

The same analysis of recovery was implemented in **Chapter 4**, where I investigate the relevance of toxicokinetic and toxicodynamic (TK-TD) processes for the population recovery of the freshwater amphipod, *Gammarus pulex*. By simulating exposure of individuals in the population model to different concentrations of four pesticides with different modes of action, I evaluate the effects on their survival by implementing TK-TD models, but also by using conventional dose-response models and compare the two. I first look into the impact of delayed effects, as calculated by the TK-TD model, on individual survival and subsequent population recovery. Further, I also evaluate the assessment of the magnitude of adverse effects after short-term exposures using the standardly used 96 h dose-response model and the TK-TD model. Here individual survival is assessed after exposure to 6, 12, 24 and 48 hours to 96h-LC50 concentration of the four tested pesticides. This study yields interesting results with potential implications for pesticide risk assessment for the aquatic compartment.

In **Chapter 5** I move my focus from crustaceans to aquatic insects and explore how the permeability of the landscape matrix influences population recovery and persistence across managed landscapes. For this purpose, I describe an IBM of the non-biting midge, *Chironomus riparius*, which serves as an excellent model organism due to its rather limited dispersal abilities, but also because of it significant role in energy transfer between the aquatic and terrestrial ecosystem. Besides the population model, I develop a separate model simulating dispersal across landscapes, consisting of the aquatic habitat and terrestrial matrix, accounting for different movement patterns (from the random walk family), landscape and edge permeability and distance between the aquatic habitats.

Different landscape and dispersal scenarios are evaluated with the population model and scenarios where recovery is possible are identified.

In **Chapter 6**, I discuss the possible definitions of protection goals within the ecosystem services framework and the outstanding contribution ecological models can make in that context. This chapter represents a part of the special issue on ecosystem functions, services and biodiversity in ERA and states the essential role of ecological models in making the risk assessment process ecologically more relevant. Here I provide examples of ecological models used to assess risk to services provided by agroecosystems. Furthermore, I go beyond the field of chemical ERA to include published examples of modelling studies assessing the risk of excess nutrient loads to lakes. Even though the direction of focusing on relevant ecosystem services as protection goals, especially in the context of pesticides, is a promising one, it is not without challenges that are discussed in this chapter.

Finally, in **Chapter 7**, I discuss the findings of my thesis, especially the definition of recovery, identify its shortcomings and propose improvements in the field of ERA.

Chapter 2

Potential application of population models in the European ecological risk assessment of chemicals: II review of models and their potential to address environmental protection aims

Nika Galic, Udo Hommen, Hans M. Baveco and Paul J. van den Brink

Abstract

Whereas current chemical risk assessment (RA) schemes within the European Union focus mainly on toxicity and bioaccumulation of chemicals in individual organisms, most protection goals aim at preserving populations of non-target organisms, rather than individuals. Ecological models are tools rarely recommended in official technical documents on RA of chemicals, but are widely used by researchers to assess risks to populations, communities and ecosystems. Their great advantage is the relatively straightforward integration of the sensitivity of species to chemicals, the mode of action and fate in the environment of toxicants, life-history traits of the species of concern and landscape features. In order to promote the usage of ecological models in regulatory risk assessment, this paper tries to establish whether existing, published ecological modelling studies have addressed or have the potential to address the protection aims and requirements of the chemical directives of the European Union. We reviewed 148 publications, and evaluated and analysed them in a database according to defined criteria. Published models were also classified in terms of five areas where their application would be most useful for chemical RA. All potential application areas are well represented in the published literature. Most models were developed to estimate population-level responses on the basis of individual effects, followed by recovery process assessment, both in individuals and at the level of metapopulations. We provide case studies for each of the proposed areas of ecological model application. The lack of clarity about protection goals in legislative documents made it impossible to establish a direct link between modelling studies and protection goals. Because most of the models reviewed here were not developed for regulatory risk assessment, there is great potential and a variety of ecological models in the published literature.

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Introduction

The current field of ecological risk assessment (ERA) of chemicals is characterised by a limited amount of integrated ecological theory. Lower tiers of ERA are based on the results of standard tests that assess the toxicological effects on individual organisms, while effects on higher organisational levels are not routinely taken into account. The protection aims of the various ERA schemes, however, are rarely directed towards individuals, and are more commonly assumed to focus on populations, communities or entire ecosystems (EC 2002b; Hommen *et al.* 2010). Therefore, during previous years, the international field of ERA recognized the need for more population-level oriented approaches (Barnthouse, Munns & Sorensen 2007). A full understanding of the impacts of pollutants at higher levels of biological organisation requires an understanding of fundamental ecology and the integration of more ecological data into toxicological studies. Various frameworks have been proposed to include more ecology in the decision-making process (Chapman 2002; Brock *et al.* 2006). Attempts to combine toxicology and ecology have been more numerous in recent years, both in experimental and modelling studies (Van den Brink 2008). The development of mesocosm studies (Campbell *et al.* 1998; Giddings *et al.* 2001; Van den Brink *et al.* 2006) allows the effects of substances (mostly pesticides) on semi-natural communities to be assessed. However, some important ecological processes, such as dispersal and recolonization, are not included in these experimental systems, nor are large species like predators, such as fish, which might play a central role in the community.

Our understanding of the way populations and systems function and interact with their environment, as well as the development of ecological theories, have greatly benefited from mathematical modelling (Malthus 1798; Lotka 1924; Volterra 1926). In recent decades, models are increasingly used for management purposes, especially in fisheries and wildlife management (Starfield 1997). Computational and technological progress enables researchers to model very different scales of biological and spatial organisation, ranging from very detailed processes such as the accumulation of chemicals in individuals to simulating population dynamics on a landscape scale. In the field of ERA, a major advantage of ecological models is that they are able to integrate various ecological and toxicological concepts and processes, allowing extensive scenario testing without the accompanying high costs of e.g. additional experimental setups (Forbes, Calow

& Sibly 2008). Their potential in ERA has been recognised and has resulted in an on-going development of various types of models for assessing risks of chemicals to populations, communities and ecosystems (Bartell *et al.* 2003; Pastorok *et al.* 2003).

The field of pesticide ERA is especially benefiting from these developments, as assessing and quantifying risks to non-target organisms constitute the major part of the pesticide authorisation process. Various stakeholders have acknowledged the added value that ecological models bring to ERA, resulting for instance in the LEMTOX workshop (Forbes *et al.* 2009; Thorbek *et al.* 2009) held in 2007, where representatives of academia, governmental bodies and industry identified advantages, caveats and ways forward, through a combination of presentations and discussions. The two eLINK workshops also held in 2007 focused on the problem of extrapolating effects measured for one specific exposure pattern to the variety of exposure patterns predicted by FOCUS step 3 models (Hommen *et al.* 2010; Brock *et al.* 2010a). Both workshops specifically discussed the role of ecological models in the ERA of pesticides under the 91/414/EC directive (EC 1991).

As regards legislation protecting against adverse effects of chemicals, the authorisation and registration of chemical substances in the European Union is governed by different regulatory frameworks. The directives refer to the uses of chemicals, e.g. as plant protection products, biocides, pharmaceuticals or industrial chemicals. In addition, substances are evaluated in terms of the protection of environmental compartments. Within the European Water Framework Directive (EC 2000), for example, environmental quality standards have been set up for 33 priority substances.

Hommen *et al.* (2010) compared different EU directives referring to the ecological effects of chemicals, and analysed their environmental protection goals, data requirements and risk characterisation. They also defined five application areas within RA that would benefit particularly from various models:

1. relevance of effects observed on individuals for the population level;
2. extrapolation of effects of a tested exposure pattern to other, untested, exposure patterns;

3. extrapolating recovery processes, from individual to population level recovery, including recolonization;
4. analysis and prediction of possible indirect effects in communities;
5. bioaccumulation and biomagnification within food chains or food webs.

The main objective of this study was to search for existing ecological, mainly population, models that have been or can be readily used to assess risks of chemicals to non-target organisms. The aim was to understand whether they can help in addressing the protection requirements of relevant EU directives, and to establish which model types are appropriate for different application areas.

We do not attempt to present an exhaustive review of all models, as Bartell *et al.* (2003) and Pastorok *et al.* (2003) have already provided excellent reviews of ecological models and their potential use in the risk assessment of chemicals, together with their relative strengths and weaknesses. To our knowledge, however, there have not been any previous attempts to assess the role and potential position of ecological models in regulatory RA, more specifically to determine whether they can address the requirements of protection goals in various EU chemical directives. In addition, our extensive literature search allowed us to obtain and assess more recent publications than previous studies did. To illustrate our point and highlight the link with protection goals for the reader, we provide case studies for each of the above-mentioned areas of application. Lastly, the database with all models reviewed, their potential areas of application and their description using general and more technical criteria is made available as additional information with this publication (Supplemental Data, but not provided within this thesis).

Model assessment

Ecological models, or model applications, published in peer-reviewed journals were brought together in a database by means of a literature search using simple keywords relating to ecotoxicology and risk assessment (e.g. ecological models, populations, toxicants, stress, risk etc.), using all major search engines, such as Web of Science, CAB Abstracts and Scopus. The majority of references related to chemical fate or exposure models, which were excluded from further evaluation. Ecological models that included toxicological effects on organisms were preferred, but purely ecological models were also taken into account when they were considered to be potentially useful and chemical effects could be integrated in a relatively straightforward manner.

In total, we assessed 148 publications and institutional reports, grouping publications dealing with the same model (or slightly modified versions of it). This resulted in 90 evaluated entries in our model database, with additional entries that were not evaluated but were characterised as having potential value for users (Supplemental Data). These were either models relating to integrated pest management (Liu & Teng 2005; Tang *et al.* 2005; Holt & Cooper 2006) or model reviews (Koelmans *et al.* 2001; Ares 2003; Stark & Banks 2003). To evaluate the published models, we defined five groups of descriptors: model identification, model focus, model characterisation, potential areas of application and model evaluation.

'Model identification' lists the name of the publication and/or model and the main reference. When multiple publications deal with the same model, the whole list is given in a separate sheet in the database.

'Model focus' presents general information on the focal group of organisms modelled, the habitat type considered and the level of organisation, i.e. whether it is an individual-, population-, community- or ecosystem-level model.

'Model characterisation' provides information on the formalism of each model, discriminating between different levels of spatial and biological organisation by using four different model types: scalar or unstructured, matrix, physiologically structured and individual-based models. Furthermore, it notes whether the model includes any type of toxicological effects, how exposure is considered and which chemical (or type of chemical) is evaluated. The classification of the exposure–effects link is based on eLINK documents (Brock *et al.* 2010b) and includes direct link models, toxicokinetic–toxicodynamic (TK-TD) models, simple population models, complex population models and food web/ecosystem models. Finally, this category indicates the spatial and temporal scales used and whether stochastic events are included.

'Potential areas of application' indicates which areas can be addressed by the model. These areas are summarised in the introduction and will be explained further in the Case Studies part of this paper.

'Model evaluation' summarises more technical details of a model, such as the ease with which parameters can be estimated, whether and how validation, calibration, uncertainty and sensitivity analyses have been carried out, model flexibility and availability of the program or code. Finally, the type of output is provided, as well as, in the case of a purely ecological model, its potential for use in the ERA of chemicals.

Model database analysis

In total, we evaluated 63 models that included exposure to and effects of toxicants and can or have been already directly used in chemical ERA, while 27 models included only ecological processes. Most (77%) of the 90 models assessed and described are population-level models, with the exception of a few individual- and ecosystem-level models. Model focus ranged from accurate description of specified species' life-cycles to general representations of various systems. Consequently, some models were developed to describe specific habitats and species, while others could be applied to a range of habitats and species. The majority of the models describe aquatic, mostly freshwater, habitats, while some models relate to the marine environment (Chen & Liao 2004; Raimondo & McKenney 2006). Around a quarter of the models describe terrestrial systems (e.g. Sherratt & Jepson 1993; Kjaer *et al.* 1998; Wennergren & Stark 2000).

We grouped models according, primarily, to their biological level of organisation, i.e. individual, population, metapopulation and community/ecosystem models (Tables 2.1 to 2.4). In the following sections we present some examples for each of biological levels. Additionally, we discuss a subset of individual-, population- and metapopulation-level models where spatial aspects are explicitly considered, which are also summarised in Tables 2.1 to 2.4.

Individual-Level Models

Several publications in the database addressed exclusively individual responses to toxicant exposure (Table 2.1). Apart from lethal effects, most of these individual models also address sub-lethal effects acting through impaired growth/maturation. A recent example describing the impact of exposure to a toxicant (Methyl-Hg) on behaviour was presented in Murphy *et al.* (2008). In their model, a chemically induced decrease in larval swimming speed resulted in impaired larval growth and thus increased stage duration, with increased predation risk. Klanjscek *et al.* (2007) developed an individual-level model, based on Dynamic Energy Budgets (Kooijman 2000), assessing the uptake, elimination and bioaccumulation of PCBs in a marine mammal, the right whale. Their model also serves as a potential platform for the assessment of population-level responses. The work by Ashauer *et al.* (2007a) focuses on establishing a mechanistic link between different exposure regimes of various chemicals and their effects on the survival of *Gammarus pulex*. These types of models are referred to as toxicokinetic-toxicodynamic (TK-TD) models, a class of models that mechanistically account for time-varying exposure, and, consequently, effects of chemicals to individuals (Lee, Landrum & Koh 2002; Lee & Landrum 2006; Ashauer, Boxall & Brown 2006b; Ashauer, Boxall & Brown 2007b; Ashauer, Boxall & Brown 2007c). Ashauer & Brown (2008) provide a review on this group of models, more specifically on the toxicodynamic part, linking dynamic exposure and effects, including assumptions, data requirements, advantages and constraints of these approaches. Most TK-TD models account for lethal effects, but some can model effects of toxicants on various other endpoints, such as growth or reproduction, i.e. sublethal effects (Billoir, Pery & Charles 2007). They are usually implemented on the level of individuals or groups, according to age, stage, size etc. Subsequently, these mechanistic links can be integrated into population models in order to assess effects at the population level (Péry, Mons & Garric 2004; Pery, Geffard & Garric 2006; Ducrot *et al.* 2007).

Population-Level Models

Table 2.2 provides a list of publications that describe population models. Within the table we evaluate models’ suitability to address questions in one or more of the proposed application areas.

Approximately 21% of all evaluated population models describe unstructured populations, in which all individuals are identical in terms of their life-history details, and simple processes like births and deaths determine the dynamics of the population or group. Even though they are very simple and include only the most basic processes in a population, they add more realism to ERA by assessing the effects of pollutants on cumulative demographic rates and, consequently, on projected abundance or population growth rate. Some examples in our database include Adams *et al.* (2005) where simple models, in the form of ordinary differential equations (ODEs), were fitted to data for population dynamics of aphids in broccoli fields repeatedly sprayed with pesticides. Ecosystem models (Traas & Aldenberg 1992; Hanratty & Stay 1994; Naito *et al.* 2002) are usually a combination of unstructured models for each of the functional groups.

More than a half (53%) of all population models evaluated are structured population models. These models tend towards a higher level of realism, as individuals of one species have different characteristics in different stages of their life cycle. Furthermore, effects of environmental stressors tend to be expressed differently in different life stages. Classes or groups in structured models are based on stage, age, physiological condition, size or any other demographically relevant criterion. Most common are matrix models, with distinct stage or age classes combined with a discrete time approach. Matrix models can be used to calculate the population growth rate, λ, for a given set of life cycle data (e.g. age dependent survival and fecundity). The sensitivity of the growth rate to changes in the life table data can be evaluated analytically with a so-called ‘elasticity analysis’ (for more information on matrix models, see Caswell 2000). Events and parameters are usually deterministic, which makes matrix models suitable for projecting population growth, i.e. assessing abundance or growth rate in the future based on current values. The parameters of matrix models and the impact of toxicants on these parameters are both defined directly from life-table data. Half of the matrix model applications in our database incorporated a toxicokinetic-toxicodynamic (TK-TD) model to describe mechanistically how effects depend on the body burden changing over time. Often an energy budget model simulating individual growth and reproduction, i.e. a Dynamic Energy Budget (DEB) model (Kooijman 2000) is integrated (Lopes *et al.* 2005; Liao, Chiang & Tsai 2006; Ducrot *et al.* 2007). When combined with a model for individual growth and reproduction, such matrix models can easily account for sublethal impacts (on reproduction and development).

The next class of population models regards individuals as unique, are therefore termed individual-based population models (IBMs, sometimes also called agent-based models) and make up 26% of all the population models in our review. Within IBMs, population properties are a result of keeping track of individuals’ intraspecific and interspecific interactions and the interactions of individuals with the environment. Their great advantage is their flexibility, because in principle each aspect, including complex behaviour, can be included into the model. Furthermore, inclusion of individual variability in the form of distributions from which parameter values are derived allows a direct simulation of demographic stochasticity or probabilistic behaviour. One of the disadvantages of such an approach is that in most cases, assumptions and data used in IBMs are both exhaustive and very species-specific, so their development is very data hungry, requires a lot of computing power to keep track of all individuals in a population and their analysis can become very complex and cumbersome. This puts them in the highest levels of realism and makes them suitable for use in case-specific studies in higher tiers of ERA. Early examples of IBMs are predominantly fish models, with non-ERA examples in our database including DeAngelis *et al.* (1991) and Beard & Essington (2000). Examples of non-spatial (fish) IBMs used in ecotoxicological studies are Jaworska *et al.* (1997) and Madenjian (1993). More recent examples of non-spatial IBM applications outside the field of ERA are mostly aquatic. Rinke & Petzoldt (2008) and Vanoverbeke (2008) focused on *Daphnia*, while Beaudouin *et al.* (2008) and the Piscator model (Van Nes, Lammens & Scheffer 2002) modelled fish. Recent uses of IBMs in ERA include a *Gammarus* (Schmidt 2003) and *Daphnia* model (Preuss *et al.* 2009b), mostly to refine higher tiers of the pesticide registration process. Terrestrial examples are provided in Baveco & De Roos (1996) and Davidson & Armstrong (2002), who used an IBM to assess the impact of a brodifacoum, a mouse poison, on an island population of New Zealand saddlebacks.

Ecosystem Models

A small fraction of the evaluated models address the higher level of biological organisation, such as food webfood webs, communities and ecosystems (Table 2.3). Within ERA, they have been applied mainly to freshwater ecosystems, e.g. SWACOM (O'Neill *et al.* 1982), LERAM (Hanratty & Stay 1994), CATS-4 (Traas *et al.* 1998), CASM (Naito *et al.* 2002), C-COSM (Traas *et al.* 2004) and AQUATOX (Park, Clough & Wellman 2008). An early version of the CATS model was also applied to meadow ecosystems (Traas & Aldenberg 1992), and was chosen as one of the case studies discussed below. CASM is an expanded version of SWACOM, while LERAM is a version of CASM adapted to littoral ecosystems. The definition of aquatic food web components differs slightly between these models, with phytoplankton, zooplankton, omnivorous and piscivorous fish and macro-invertebrates being among the constant factors. Dynamics of various compartments are usually represented by a set of differential equations, representing the lack of structure within a compartment, and application is usually accompanied by a sensitivity or uncertainty analysis using Monte Carlo simulation. Spatial heterogeneity, apart from heterogeneity in one dimension (depth of the water layer), is usually not taken into account.

Table 2.1. Reviewed individual-level ecological models.

				Potential application area					
#	**Model name**	**Main reference**	**Toxicity included?**	**1**	**2**	**3**	**4**	**5**	**Space considered?**
1	Threshold Damage Model	Ashauer *et al.* 2007	Y		X	X		X	N
2	Habitat and exposure modelling for ecological risk assessment: A case study for the raccoon on the Savannah River Site	Chow *et al.* 2005	Y (exposure only)					X	Y
3	A model for energetics and bioaccumulation in marine mammals with applications to the right whale	Klanjscek *et al*. 2007	Y					X	N
4	On the dynamics of chemically stressed populations - the deduction of population consequences from effects on individuals	Kooijman & Metz 1984	Y	X	X			x	N
5	Modelling larval fish behavior: Scaling the sublethal effects of methylmercury to population-relevant endpoints	Murphy *et al.* 2008	Y	X		X			N
6	A partially specified dynamic energy budget model	Nisbet *et al.* 2004	N	X		X			N
7	Use of habitat-contamination spatial correlation to determine when to perform a spatially explicit ecological risk assessment	Purucker *et al.* 2007	Y (exposure only)					X	Y
8	Modelling the influence of environmental heterogeneity on heavy metal exposure concentrations for terrestrial vertebrates in river floodplains	Schipper *et al.* 2008	Y (exposure only)					X	Y

Table 2.2. Reviewed population-level ecological models.

					Potential application area					
#	**Model name**	**Main reference**	**Model type**	**Toxicity included?**	**1**	**2**	**3**	**4**	**5**	**Space considered ?**
1	Plant-insect herbivore-pesticide interactions	Adams *et al.* 2005	Unstructured	Y	X	X				N
2	Assessing ecological risk to night heron	An, Hu & Yao 2006	Matrix	Y	X					N
3	Application of individual growth and population models of Daphnia pulex to other daphnid species	Asaeda & Acharya 2000	Stage-structured	N	X		X	X		N
4	Logistic growth model and recovery times	Barnthouse 2004	Unstructured	N			X			N
5	Impact of pesticides on lumbricids	Baveco & De Roos 1996	Structured (PDE), IBM	Y	X	X	X			N
6	Angling and life history effects on bluegill size structure	Beard & Essington 2000	IBM	N	X		X			N
7	Mosquitofish population dynamics	Beaudouin, Monod & Ginot 2008	IBM	N	X		X			N
8	Effects of toxic compounds on population dynamics of *Daphnia magna*	Billoir, Pery & Charles 2007	Matrix (DEB)	Y	X					N
9	PC-BEEPOP	Bromenshenk *et al.* 1991	Stage-structured	Y	X	X	X			N

10	Endocrine disrupting chemicals in perch populations	Brown *et al.* 2005	Stage-structured	Y	X	X	X			N
11	Synchronous versus asynchronous treatments for control of dispersing insect pests	Byers & Castle 2005	Unstructured	Y	X		X			Y
12	Mosquitofish responses to Genapol OXD-080	Cabral, Marques & Nielsen 2001	Structured	Y	X		X			N
13	Risk assessment on the basis of simplified life-history scenarios	Calow 1997	Matrix	Y	X		X			N
14	Life cycle testing and Leslie matrix	Chandler *et al.* 2004	Matrix	Y	X	X	X			N
15	Food availability and *Chironomus riparius*	Charles *et al.* 2004	Matrix (DEB)	N	X					N
16	Aggregation methods and toxicant effects in spatial systems	Chaumot *et al.* 2002	Matrix	Y	X					Y
17	Farmed abalone exposed to waterborne zinc	Chen & Liao 2004	Matrix	Y	X	X			X	N
18	Slug IBM	Choi *et al.* 2006b	IBM	N	X		X			Y
19	Effects of temperature and soil moisture on collembolan species	Choi *et al.* 2006a	Matrix	Y	X	X	X			N
20	Mark-recapture and simulation modelling of saddlebacks	Davidson & Armstrong 2002	IBM	N	X		X			N
21	Density-dependent dynamics in smallmouth bass populations	DeAngelis, Godbout & Shuter 1991	IBM	N	X		X			N
22	Demographic analysis of continuous-time life-history models	De Roos 2008	Structured (Lotka's integral eq.)	Y	X		X			N

23	DEB and population effects of zinc-spiked sediments in a gastropod	Ducrot *et al.* 2007	Matrix (DEB)	Y	X					N
24	Bayesian modelling of aphid dynamics	Fabre *et al.* 2006	Unstructured	N	X					N
25	Chlorpyrifos in aquatic environments	Giesy *et al.* 1999	Matrix	Y	X	X	X			N
26	GETLAUS01	Gosselke *et al.* 2001	Physiologically structured	N	X		X	X		N
27	Development and application of bioaccumulation models to assess persistent organic pollutant temporal trends in arctic ringed seal (*Phoca hispida*) populations	Hickie *et al.* 2005	IBM	N					X	N
28	RA of the Victorian southern rock lobster fishery	Hobday & Punt 2001	Sex and size structured	N	X		X	X		N
29	Multiple end points in life-cycle toxicity	Jager *et al.* 2004	Unstructured	Y	X					N
30	Two modes of action of cpf in the springtail *Folsomia candida*	Jager *et al.* 2007	Structured (Euler-Lotka eq.)	Y	X					N
31	PCB effects on young-of-the-year largemouth bass	Jaworska, Rose & Brenkert 1997	IBM	Y	X					N
32	Estuarine striped bass population	Kimmerer *et al.* 2001	Stage-structured	Y	X		X	X		N
33	Insecticide effects on chrysomelid beetles	Kjaer *et al.* 1998	Stage-structured	Y	X					Y
34	Integrating DEB into matrix models	Klanjscek *et al.* 2006	Matrix (DEB)	N	X					N

35	*Lumbricus rubellus* in a polluted field soil: possible consequences for the godwit	Klok, Hout & Bodt 2006	Matrix (DEB)	Y	X					N
36	DEB and Bayesian approaches for *Dendrobaena octaedra*	Klok, Holmstrup & Damgaard 2007	Matrix (DEB)	Y	X					N
37	Toxicological effects on *Lumbricus rubellus*	Klok & de Roos 1996	Matrix	Y	X	X	X			N
38	Environmental and chemical stressors on Daphnia	Koh, Hallam & Ling Lee 1997	Physiologically structured	Y	X	X				N
39	Mysid toxicity test data and population modelling techniques	Kuhn *et al.* 2000	Matrix	Y	X					N
40	Hard clam susceptibility to Hg-stressed birnavirus	Liao & Yeh 2007	Matrix with epidemiological SIM models (Des)	Y	X					N
41	Bioenergetics-based matrix population model of tilapia	Liao, Chiang & Tsai 2006	Matrix (DEB)	Y	X				X	N
42	Establishing predicted NOECs for population-level ERA	Lin 2005	Matrix	Y	X					N
43	DEBtox models in Leslie models	Lopes *et al.* 2005	Matrix (DEB)	Y	X					N
44	Accumulation of PCBs by Lake Trout	Madenjian 1993	IBM	Y	X	X	X		X	N
45	Heavy-metal pollution of fish populations	Mastala, V.-Balogh & Perenyi 1993	Structured	N (only accumulation)					X	N
46	Endocrine disruptors and fathead minnow populations	Miller & Ankley 2004	Matrix (with logistic eq.)	Y	X	X	X			N
47	Herring gull populations and DDT exposure	Nakamaru, Iwasa &	Matrix with	Y	X	X			X	N

		Nakanishi 2002	canonical extinction model							
48	WORMDYN	Pelosi *et al.* 2008	Matrix (Leslie)	N	X		X			N
49	*Chironomus riparius* in ecotoxicological risk assessment	Pery, Mons & Garric 2004	Matrix (DEB)	Y	X					N
50	*Chironomus riparius* and heavy metals	Pery, Geffard & Garric 2006	Unstructured (kinetics, DEB based) and matrix	Y	X	X				N
51	IDamP	Preuss *et al.* 2009b	IBM	Y	X	X	X		X	N
52	Modelling aquatic toxicity data	Raimondo & McKenney 2006	Matrix	Y	X	X				N
53	Diel vertical migration of Daphnia	Rinke & Petzoldt 2008	IBM	N	X		X			N
54	Temperature and food concentration effects on Daphnia	Rinke & Vijverberg 2005	Physiologically structured	N	X		X			N
55	Cadmium exposure of the freshwater gastropod, *Biomphalaria glabrata*	Salice & Miller 2003	Matrix	Y	X	X				N
56	DANIO	Schafers, Oertel & Nagel 1993	IBM	Y	X	X	X			N
57	GamMod	Schmidt 2003	IBM	Y	X		X			N
58	Population parameters for three salmon species	Spromberg & Meador 2006	Matrix	Y	X		X			N
59	MORPH	Stillman 2008	IBM	N	X		X			Y

60	Insect growth-regulating insecticides on honeybees	Thompson *et al.* 2005	Stage-structured	Y	X		X			N
61	Insecticide-contaminated dung and the abundance and distribution of dung fauna	Vale & Grant 2002	Stage-structured	Y	X	X	X			Y
62	Piscator - IBM to analyse dynamics of lake fish communities	Van Nes, Lammens & Scheffer 2002	IBM	N	X		X	X		N
63	CHARISMA	Van Nes 2003	IBM	N	X		X	X		Y
64	Sympatric populations of brown and rainbow trout	Van Winkle *et al.* 1998	IBM	N	X		X			Y
65	Behavior under food limitation and crowding and the effect on population cycling in Daphnia	Vanoverbeke 2008	IBM	N	X		X			N
66	The dynamics of pest-parasitoid-insecticide interactions	Waage, Hassell & Godfray 1985	Unstructured, matrix	Y	X		X	X		N
67	Population dynamics of thrips	Wang & Shipp 2001	Physiologically structured	Y	X	X	X			N
68	Beyond just counting dead animals	Wennergren & Stark 2000	Matrix	Y	X	X	X			N

Spatial Models

There is a small subset of individual-level models that include detailed spatial exposure patterns, combining spatial foraging models with food web or food chain accumulation models, but without the resulting effects on groups or individual organisms; e.g. Schipper *et al.* (2008) evaluated the effects of heavy metal exposure on a river floodplain. For terrestrial vertebrates, exposure is integrated over individual home ranges, assuming e.g. random walk movement and spatial heterogeneity in diet and contaminant exposure (see also Purucker *et al.* 2007) (Table 2.1).

Early analyses of the potential impact of spatial structure for population-level ERA are presented in the following papers. Maurer & Holt (1996) analysed the effect of chronic pesticide stress on populations, based on simple, demographically unstructured, spatially implicit metapopulation models. Spromberg *et al.* (1998) extended the analysis by including temporal dynamics in exposure in a simple unstructured population model incorporating diffusion between a limited number (3) of patches. Sherratt & Jepson (1993) analysed two simulation models, one stochastic model with random walk movement between 16 fields and another deterministic one including predator and prey dynamics and simple diffusion-like dispersal. These studies were mostly theoretical, providing insights and identifying potential mechanisms like ‘action at a distance’. This means that local population dynamics in unexposed patches are affected indirectly by stress, through their links (dispersal) with exposed patches. Table 2.4 lists reviewed publications where metapopulations are modelled. Vale & Grant (2002) provide another example of a simple spatial, stage-structured model, to assess the impact of insecticides on (hypothetical) species of dung fauna.

Table 2.3. Reviewed community/ecosystem-level ecological models.

					Potential application area					
#	**Model name**	**Main reference**	**Model type**	**Toxicity included ?**	**1**	**2**	**3**	**4**	**5**	**Space considered ?**
1	A food web bioaccumulation model for organic chemicals in aquatic ecosystems	Arnot & Gobas 2004	Unstructured	Y					X	N
2	Deriving water quality criteria	De Laender 2007	Unstructured	Y	X		X	X		N
3	EcoWin	Ferreira 1995	IBM	N	X					N
4	LERAM	Hanratty & Stay 1994	Unstructured	Y	X	X	X	X		N
5	CASM	Naito *et al.* 2002	Unstructured	Y	X	X	X	X		N
6	SWACOM	O'Neill *et al.* 1982	Unstructured	Y	X			X		N
7	AQUATOX	Park, Clough & Wellman 2008	Unstructured	Y	X	X		X	X	N
8	C-COSM	Traas *et al.* 2004	Unstructured	Y	X	X	X	X		N
9	CATS	Traas & Aldenberg 1992	Unstructured	Y	X	X		X	X	N
10	Recovery of macroinvertebrates in a river	Watanabe, Yoshimura & Omura 2005	Unstructured	Y	X		X	X		N

Table 2.4. Reviewed metapopulation-level ecological models; note that not all models are metapopulation models in the classical sense, but have potential to address population level issues from a metapopulation perspective.

					Potential application area					
#	**Model name**	**Main reference**	**Model type**	**Toxicity included ?**	**1**	**2**	**3**	**4**	**5**	**Space considered?**
1	Carabid metapopulation model	Sherratt & Jepson 1993	Unstructured	Y	X	X	X	X		Y
2	Metapopulation dynamics: indirect effects and multiple distinct outcomes	Spromberg, John & Landis 1998	Unstructured	Y	X		X	X		Y
3	ALMASS (potential)	Topping *et al.* 2003	IBM	N	X		X	X		Y
4	MASTEP (potential)	Van den Brink *et al.* 2007	IBM	Y	X		X			Y

Later studies have attempted to assess the risk posed to specific organisms in specific areas (spatially explicit ERA). To this end, structured population model approaches have been extended to include both a population and a spatial structure. Chaumot *et al.* (2003) used a 'multi-region' Leslie matrix approach to model the impact of cadmium on trout populations in a network of waterways. Recent examples show how spatial IBMs can be used to study population recovery in a spatial context (see Van den Brink et al. 2007, in the Case Studies section below). The ALMaSS system (Topping *et al.* 2003) is an extensive IBM at the landscape level, including landscape dynamics (management) and multispecies interactions. Topping *et al.* (2005) and Sibly *et al.* (2005) compared the results of this IBM with those obtained using a matrix approach to assess the risks posed to skylarks by an imaginary insecticide. Other examples of spatial IBMs in the database, however, do not include an ecotoxicological component, but were developed for pest and wildlife management purposes. For instance, Choi *et al.* (2006b) modelled slug population dynamics, Van Nes (2003) modelled submerged aquatic macrophyte population dynamics, while Van Winkle *et al.* (1998) modelled trout population dynamics in streams. These studies serve as examples of approaches taking into account both biological and spatial structure, which might be extended to incorporate toxicant effects.

Case studies on potential areas of application of assessed models

Models were also assessed for their potential use in the application areas (Hommen *et al.* 2010)(Figure 2.1). Some models were suitable for use in only one or two of these areas, others in up to four. None of the models had the potential to be used in all five application areas, which was to be expected as the models' main purpose is to answer questions that vary greatly between the areas. The following section elaborates on all of these application areas and provides examples of modelling approaches to address each of them. The sections start with a short introduction on the application area including a brief summary of case studies, followed by a detailed description of the case studies.

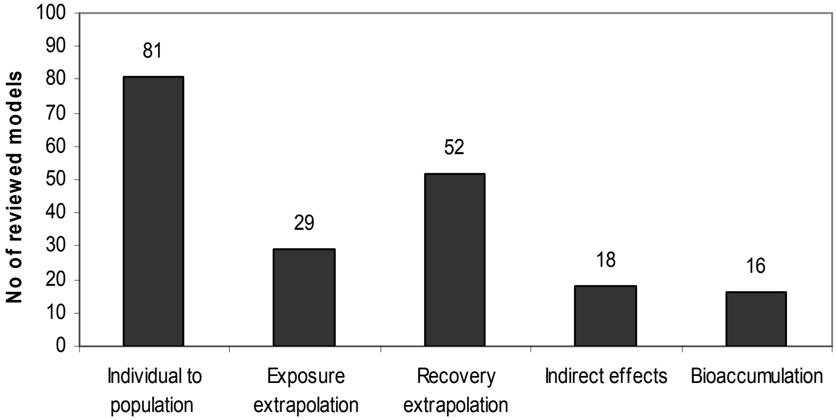

Figure 2.1. Distribution of the reviewed modelling studies across the proposed application areas.

1. Population-level Relevance of Individual-level Effects

The first application area relates to assessing population-level responses to individual-level effects, since most directives aim to protect local populations, rather than individuals (with the exception of vertebrates). It is clear that species-specific life-history traits are highly relevant when assessing risks of chemicals to non-target species. For example, some chemical effects are expressed differently in juveniles and adults and in order to account for these differences, at least some of life-history needs to be included for the population-level risk assessment (Sibly *et al.* 2005). Our review showed that of the 90 model entries in the database, 81 (90%) could be used for extrapolating effects from the individual to the population level (Figure 2.1). The most commonly used method to estimate effects of chemicals on populations and their growth rate uses data on vital rates from life table response experiments or toxicity tests (Kuhn *et al.* 2000; Chandler *et al.* 2004). Vital parameters derived from stressed individuals as well as from the control group are then projected using a population model and compared with an unstressed situation (Klok & de Roos 1996; Salice & Miller 2003). The type of model most commonly used for this form of extrapolation is that of matrix models. There are also models that link toxicant effects in a more mechanistic manner (Naito *et al.* 2002; Van den Brink *et al.* 2007), and models based on DEB theory (Jager *et al.* 2004; Billoir, Pery & Charles 2007; Ducrot *et al.* 2007).

The following case studies have been chosen to cover the range of approaches, focal organisms and output that can be used for ERA. The first publication, on susceptibility of biological agents to pesticide stress (Stark, Banks & Acheampong 2004a), is a clear and simple example of how integrating basic life-history traits in a matrix model results in different outcomes for the species considered. It emphasises that it is not only the species-specific susceptibility to toxicants that is important in risk assessment, but also the ecology of the species itself. In this sense it is the exemplar of the integration of ecology into toxicology and risk assessment. The model clearly shows that the pest predator, the lady beetle, is more susceptible due to its higher number of pre-adult stages, i.e. needs a longer development time before reaching a reproductive stage that ensures population persistence. The second publication, on population-level effects of individual growth of earthworms in copper-polluted soil (Klok & de Roos 1996), was chosen to demonstrate a somewhat more complex matrix model, one that takes into account individual processes such as growth and some basic calculations of energetics, and projects them to population level responses using a matrix model. Toxicant effects are not explicitly modelled but are implicit in the data sets from polluted soils. Rather than explaining the mechanisms, it concentrates on more specific processes in an organism, considering the distribution of acquired energy among various individual-level processes, and the effects of toxicants on this distribution. Although the model shows that individual earthworms do grow even after the concentration of copper in the soil exceeds the safe concentrations, one must be careful in accepting it as harmless, as the trapping of individuals in a subadult stage has obvious consequences for the total population, and even for the food chain or ecosystem.

Finally, the individual-based model of a largemouth bass population and the effects of PCBs on young-of-year clearly demonstrates the amount of data and ecological functions needed for such a modelling approach (Jaworska, Rose & Brenkert 1997). Constructing an individual-based fish population model requires many variables to be considered, from life-history traits and metabolic processes to lethal and sublethal effects of a specific toxicant. This is often very disadvantageous, as much of this kind of data is still not available, while many processes or aspects of species behaviour might not be known either. However, even with the clear difficulties faced when constructing an IBM, the advantages of investigating emergent processes and results that reflect natural behaviour may outweigh the problems. The largemouth bass population, for instance, shows an increased juvenile mortality by the presence of PCB. This results in less competition within the cohort for zooplankton, leading to increased weight and length of the surviving individuals. Nevertheless, in order to understand individual-based models and interpret the results correctly, their processes and assumptions need to be properly understood, as well as the temporal and spatial scales. This is also emphasised by the authors themselves.

Susceptibility of Biological Control Agents to Pesticides

Stark *et al.* (2004) investigated the role that life-history differences play in population responses to pesticides. It focused on mortality and reduction of fecundity (as the sublethal effect), and the influence of population structure on the dynamics of three species with different life-history traits: a predatory lady beetle, *Coccinella septempunctata*, its prey, the pea aphid, *Acyrthosiphon pisum*, and a common aphid parasitoid, *Diaeretiella rapae*. This combination of species represents an important predator-prey complex in biological control. Entries for the age-structured Leslie projection matrix model (Leslie 1945) are life-history parameters, such as survivorship in different stages and fecundity of the population.

Although the toxicant used in this study was only hypothetical and its effects were mimicked by decreasing fecundity and survival, it was shown that differences between species in even a small number of life-history parameters greatly impacts the population susceptibility to pesticides. Equal levels of mortality or reduction of fecundity have different impacts on different species. The predatory lady beetle shows the greatest response, due to its higher number of life stages which implies a longer development time before reaching reproductive age, and a lower reproductive output than the other two species modelled.

Toxicological Effects of Copper on Individual Growth and Reproduction in Earthworm Populations

Klok & de Roos (1996) developed a model to assess the impact of copper-polluted soil on earthworm (*Lumbricus rubellus*) populations. The model consists of two levels, an individual level describing growth and fecundity of earthworms, and a stage-structured matrix model that projects population-level effects of individual growth and reproductive output in copper-stressed conditions.

The *individual-level model* follows the dynamic energy budgets theory Kooijman (2000), the central assumption being that maintenance and growth compete more directly with each other than with reproduction. Energy requirements for maintenance always take priority over growth and reproduction. Food intake is proportional to the surface area, while growth and maintenance are proportional to the wet weight (*W*) of the individual organism. The surface area is assumed to be proportional to $W^{2/3}$ and reproduction is assumed to start after a certain threshold size (adult size) has been reached. Under constant food conditions, individuals are assumed to grow according to the von Bertalanffy growth curve.

The *population-level model* is a matrix projection model, based on 4 stages, namely the cocoon, juvenile, subadult and adult stages. Entries in the matrix represent the following transitional probabilities: the probability of remaining in the same stage, the probability of developing into the next stage and reproductive output, which is a property only of the adult stage. Values of all these entries are determined by the model for individual growth and reproduction.

This study investigated 3 possible toxicity scenarios: decrease in energy assimilation, increased maintenance costs for detoxification and a best-fit scenario (increased maintenance costs and extra energy for cocoon production). The results show that, in all scenarios, individuals get trapped in the subadult stage and are thus incapable of reproduction. The authors suggest that data on the duration of juvenile stages, rather than only on hampered reproduction, might be a better estimate of toxic effects at a population level.

Individual-Based Modelling of PCB Effects on Largemouth Bass

Since individual-based models generally demand a lot of data and ecological functions, we limit ourselves to describing only the most relevant processes in the model.

Jaworska *et al.* (1997) developed an individual-based model that simulates the daily development, growth and survival of largemouth bass, *Micropterus salmoides,* from the egg stage, set at 1 April, to the end of their first growing season, set at 15 October. Nest creation, growth (through consumption) and egg mortality are temperature-dependent. The modelled environment represents a strip of shoreline where bass construct their nests and young-of-the-year (YOY) life stages are usually found. Reproduction starts with nest construction by male spawners, whose numbers and length distribution are specified by the user/modeller. Number of eggs is a function of male length, as it is assumed that larger males attract larger females and fecundity depends on female size. The timing of nest creation and the development rate from the egg to the swim-up larval stage is temperature-dependent. After hatching, yolk-sac larvae are assumed to have a constant growth rate until they reach the initiation size of the swim-up larval stage. Daily consumption depends on an individual's random encounters with zooplankton, benthos and shad prey types, the first two of which are represented by multiple size classes, while shad prey is represented by 18 week cohorts. Mortality of YOY stages is a combination of constant rates, size-dependent rate, nest desertion and starvation. PCB exposure levels are expressed as TCDD (tetrachlorodibenzo-*p*-dioxin) concentrations in muscle tissue, ranging from 6 to 20 ppm, and no uptake or depuration of PCBs is simulated. Toxic effects of accumulated PCBs include increased mortality of post-egg life stages and reduced growth of swim-up larvae and juveniles. PCB-induced mortality of fish decreases with their age. Growth reduction is a function of toxicant concentration that starts from zero level at NEC and reaches one at the concentration causing 100% growth inhibition, which is modelled by a hyperbolic function, and arises from the increased metabolic costs due to processing PCBs and reduced feeding.

The results showed that density-dependent survival was operating, as density and biomass density levelled-off with increasing spawner density. The mean length visibly decreased with spawner density due to higher consumption of zooplankton and shad prey by the bass population. Lower growth resulted in lower survival as smaller fish experience a higher mortality rate. PCB effects were apparent but rather small relative to the natural variation in the model predictions. Density, biomass density, mean condition factor and survivorship all decreased, while the mean length increased slightly with increasing PCB levels. Interestingly, at the lower spawner densities at the 6 and 10 ppm PCB levels, predicted density and biomass density were higher for the chronically stressed population. The most important input affecting densities and survivorship of the bass population was zooplankton carrying capacity. However, the study did not include other possible density-dependent mechanisms that might potentially have a large influence on system behaviour.

2. Extrapolation of Effects Across Exposure Patterns

One of the biggest challenges in pesticide ERA is how to deal with exposure regimes that vary in time and extrapolate effects observed after one peak exposure in the laboratory to multiple exposures in the field that occur due to spray drift, run-off or drainage. For non-pesticides, e.g. industrial chemicals or pharmaceuticals, usually a more constant, chronic exposure can be assumed. Techniques that can account for effects of variable temporal exposure include ecological modelling. Focusing on pesticides, the eLINK workshop provided some recommendations on this issue (Brock *et al.* 2010a). In our database, 29 (32%) models include the extrapolation of effects across different exposure patterns. Due to their straightforward construction, matrix models can easily incorporate data on vital parameters from different constant concentrations (Miller & Ankley 2004). However, they only include dose-response functions relating the survival of organisms based on external concentrations, which is a simple form of linking exposure with effects. For a more mechanistic coupling of exposure and effects using internal concentrations TK-TD models can be used. As these models require extensive laboratory studies for model parameterisation, they are still scarce and focus mostly on individuals. The following case study demonstrates how TK–TD models can be linked to population models, and how this can significantly improve the possibilities to predict population level responses at different exposure levels and regimes.

Extrapolating Population-level Effects of Daphnia magna Across Exposure Patterns

The individual-based model of *D. magna* is described in detail in Preuss *et al.* (2009b). Each daphnid in the model follows its life-cycle, including feeding on algae, aging, growing, developing and – when maturity is reached – reproducing. The modelled life-cycle is driven by the amount of ingested algae and the density of the *Daphnia* population: at low algal densities, the population dynamics is mainly driven by food supply, whereas at high algal densities, the limiting factor is 'crowding' (a density-dependent mechanism due to chemical substances released by the animals or physical contact, but independent of food competition). Thus, the parameters of the model are the coefficients of different functions describing the life-cycle traits, while individual age, developmental stage, body length, feeding rate and brood size serving as the state variables of the models. Population dynamics emerge directly from the life-cycle of individual daphnids.

The parameterisation of the model was based on several life-cycle studies with *D. magna* with different food conditions under flow-through conditions. The model was not only able to predict the total abundance of the population over time, but also predicted the size structure in good agreement with observations.

While Preuss *et al.* (2009) describe the model without considering the effects of toxicants, it has also been applied to a situation with constant exposure to 3,4-dichloroaniline and nonylphenol (Preuss *et* *al.* 2008). To be able to model acute effects of variable toxicant concentrations on *Daphnia* populations, three different submodels to link exposure and effects were tested, namely direct link, time-weighted averages (TWA) and the damage assessment model (DAM). A direct link model is a dose-response mortality curve, in this case after a 48-hour exposure. In the TWA model, effects depend on the time-weighted average of the external concentration over the individual's lifespan. Finally, the DAM model explicitly models toxicokinetics and toxicodynamics. Uptake and elimination are described by first-order kinetics (and thus by two parameters, the uptake and elimination rates [k_{in} and k_{out}]) to describe the body burden (C_B), while survival depends on the internal damage, which is also described by two rate constants (the killing rate k_k and the recovery rate k_r). Details of the DAM can be found in Lee *et al.* (2002) and Ashauer *et al.* (2006). The model was tested on the data from 12 population experiments with different exposure patterns (different numbers of pulses, different magnitudes of the pulse exposure and different intervals between pulses). In most of the cases (9 out of 12) it was the DAM that produced the best fit to the data. In three cases, the simplest model, which assumes a direct link between the actual concentration in the water and the effect, seemed to be the best sub-model.

Preuss *et al.* (2008) concluded that the direct link model can only be used for scenarios with one- or two-peaks, while more complex exposure scenarios require choosing an appropriate effect model. The TWA approach does not produce better predictions than the direct link model, and is therefore not suitable for the prediction of population dynamics in complex exposure scenarios. The DAM, however, predicts the population dynamics for complex exposure scenarios quite well. Where it does not, its predictions are protective.

3. Extrapolation of Recovery Processes

Population recovery after chemical stress has become especially interesting for the risk assessment of plant protection products since Annex VI (the Uniform Principles) offers the option of effects being acceptable if recovery within a few weeks after exposure can be demonstrated experimentally or if the likelihood of recovery under field conditions is shown to be high (EC 1991; Hommen *et al.* 2010). In fact, the extrapolation of recovery processes was the second best represented application area in our database, with 52 model entries (58%). Recovery at the individual level includes recovery by internal mechanisms (through repair and elimination processes) (Klanjscek *et al.* 2007; Ashauer, Boxall & Brown 2007c), while the population recovers through reproduction and/or recolonization of stressed habitats and reproduction (Watanabe, Yoshimura & Omura 2005; Van den Brink *et al.* 2007). Until now, the focus is on the recovery of the population, so very few models integrate toxicokinetic and/or toxicodynamic models with population modelling (Chen & Liao 2004).

The following case study was chosen as an example of a more complex approach to answering the question whether a population will recover and when. Barnthouse (2004) provides examples of simple population models, based on the logistic growth equation, used for assessing population recovery. IBMs offer the possibility to include processes which are of importance for studying population recovery and that could not be (or could with more difficulty) implemented in other modelling approaches, such as dispersal and both intra- and inter-specific interactions. This advantage also means that the number of processes and parameters increases greatly, all of which require additional data. Also, a lot of computing power is required to simulate all individuals and keep track of their status. More complex modelling approaches also require more research time and resources, and are therefore recommended for answering more specific questions in high tiers of risk assessment. An additional asset of using IBMs is that of identifying the type of data that is missing from the parameter set, thus making future research more focused and using fewer resources.

Predicting Spatial Population Dynamics of Aquatic Invertebrates After Pesticide Contamination Using a Complex Model

Van den Brink *et al.* (2007) developed an individual-based model whose main purpose was to quantify population effects and recovery of the water louse, *Asellus aquaticus*, after pesticide exposure, and especially to examine the relation between population recovery and the spatial configuration of the habitat.

The basic modelled unit is a female. The habitat is modelled using a grid representation of the water bodies in the landscape. For a fully aquatic species like the water louse, the water bodies were connected. Processes modelled included reproduction, mortality and movement or dispersal. All processes were stochastic and modelled as events; timing of these events was drawn from probability distributions. Three FOCUS (Forum for Co-Ordination of Pesticide Fate Models and Their Use 2001) scenarios are described in the publication, namely the ditch, stream and pond scenario. In the stream scenario, a movement event was sometimes turned into a drift event, involving movement to a downstream cell much further away. Mortality by insecticides was induced at a rate depending on the exposure concentration, expressed as predicted environmental concentration (PEC). The model focused on a single annual cycle of a NW European water louse, comprising two generations, the first of which consisted of individuals born in the previous year. To keep the model generic and combinable with mesocosm studies under a variety of conditions, only the bare minimum of detail on the species' life history has been incorporated. Survival at a given peak concentration in the water was defined by a dose–response curve based on data from a hypothetical mesocosm study. Some model parameters were estimated with a high degree of certainty, using published data on water louse ecology. Parameters quantifying density dependence were however highly uncertain.

Results show that, for the pond scenario, differences between the runs were small, while the ditch and stream scenarios showed a larger variation. The highest treatment level resulted in a distinctly lower summer peak than the other treatments. Initial responses for the stretch that was treated were very similar in both the stream and ditch scenarios. Empty cells in the ditch were recolonized by walking and reproducing, but both processes were quite slow, with the exception of the lowest treatment level simulated. Recovery, defined as a complete return to non-treatment densities, did not occur until autumn. The treated part of the stream exhibited a very fast recovery, showing drift to be an important factor in water louse population recovery. The difference between the stream and ditch scenarios was clearly demonstrated: very little water flow caused localised pesticide effects, while the water flow in the stream caused effects throughout the stretch. In a two-dimensional system, such as a pond, recolonization took place much faster than in a one-dimensional system such as a ditch or a stream.

4. Indirect Effects of Chemicals in Food webs

Identifying indirect effects based only on standard laboratory tests is an impossible task. Most commonly such indirect effects include effects between different trophic levels based on altered predation pressure, differing sensitivities to toxicants, effects of parasites etc. In some instances, indirect effects can result in trophic cascades (for a review of trophic cascades see Polis *et al.* 2000) and substantially change the structure and functioning of a community or ecosystem. The use of experimental multispecies systems, such as mesocosms, allows for the expression of indirect effects due to toxicant contamination. Performing these tests is, however, time and resource consuming, whereas the use of ecosystem models could be a cheaper alternative or addition. Although models describing the impact of chemicals on food webs do exist, microcosms and mesocosms are currently the only ecosystem-level tools used routinely in the risk assessment of chemicals (Van den Brink *et al.* 2006). Complete replacement of mesocosm studies by food web models seems unrealistic for the near future, as they are rather seen as tools providing additional lines of evidence. Such models can be used to interpret effects observed in cosm experiments, while insights into indirect effects could also be improved by the further development of food web/ecosystem models, using the wealth of information available from cosm experiments for hypothesis generation and validation (Traas *et al.* 2004). Our search yielded 18 models that could be used to assess indirect effects in systems (Table 2.3). Although in the following case study, the precise ecological role of individual species was largely unspecified, food web models can predict quite well the indirect effects of chemicals like pesticides. If calibrated to a specific study, interpolation/extrapolation of food web effects between exposure patterns might also be possible, although this greatly depends on the toxicokinetics and toxicodynamics, i.e. the mode of action of the compound under study.

Predicting Direct and Indirect Effects of Chemicals in Aquatic Food webs

The case study is based on the paper by Sourisseau *et al.* 2008a, describing the model development in detail, including sensitivity analysis, calibration and validation, while Sourisseau *et al.* (2008b) present the application of the model to a deltamethrin experiment in artificial streams.

The specific model of the community in the artificial streams was implemented in AQUATOX 6.21 (http://www.epa.gov/waterscience/models/aquatox/), which has been developed by the US EPA (Park & Clough 2004; Park, Clough & Wellman 2008). AQUATOX is not a single model but offers equations and standard parameter sets to build bioenergetics models that simultaneously simulate several state variables, such as the biomass of various groups of organisms (e. g. phytoplankton, zooplankton, periphyton, macrophytes, zoobenthos and fish) as well as detrital compartments, toxicants and other abiotic variables, e.g. nutrient concentrations.

Sourisseau *et al.* (2008a) modelled the food webs by first deciding on the level of aggregation of the food web: ‘The modelling efforts focused on a simplified (aggregated) food web with seven biological compartments: three for the producers (phytoplankton, periphyton and filamentous algae), two for the herbivores (zooplankton and benthic grazers), one for the benthic detritus feeders and one for the predatory invertebrates. In addition, detritus were split into two pools (suspended and sediment detritus).’ Values from a literature review were used to replace, where possible, the default AQUATOX parameters (which are mainly based on North American conditions) by parameters more appropriate for Central European conditions. Experimental data from one control artificial stream (no toxicant applications) monitored over 2 months in 2005 were used to calibrate the model. The biota were sampled four times within this period. The model parameters were modified manually, but the goodness of the fit was assessed by various quantitative measures. Of the 32 parameters that significantly affected the model outcome, the most important ones were found to be maximum photosynthetic rate and optimal temperature for periphyton and filamentous algae, and the optimal temperature, temperature response slope and maximum consumption rate for predatory invertebrates.

Deltamethrin effects were expressed as risk quotients based on the probability of e.g. a 20% decrease in a population under treatment compared with control conditions. Only short- (96 h) and medium-term (240 h) effects were considered, due to the rapid degradation of deltamethrin. The results show that direct effects were predicted according to the assumed sensitivities of different groups. The model was also able to predict an indirect effect for a dose-related probability of increased periphyton biomass.

5. Prediction of Bioaccumulation

Chemicals released into the environment are often taken up and accumulated in organisms, in the process known as bioaccumulation. Both bioconcentration and biomagnification result in accumulation of chemicals in organisms. An essential difference between bioconcentration and biomagnification is the trophic level where these processes take place: bioconcentration occurs within a trophic level and is the increase in concentration of a substance in an individual's tissues due to uptake from the surrounding environment, while biomagnification is the increase in the concentration of a substance in an organism due to food uptake. It is especially for the investigation of biomagnification that ecological models could be very useful to assess the risks posed to different trophic levels in a food web. They could be used as tools to refine experimental studies and identify the most critical compartments in an ecosystem in terms of the effects of various chemicals.

In our database of models, only 16 include bioaccumulation and/or biomagnification processes. These are either food web or ecosystem models (Traas & Aldenberg 1992; Arnot & Gobas 2004; Park, Clough & Wellman 2008), or models mainly dealing with PCBs or heavy metals in aquatic populations (Madenjian 1993; Chen & Liao 2004). In several studies (Mastala, V.-Balogh & Perenyi 1993; Klanjscek *et al.* 2007) bioaccumulation processes are examined in more detail at the individual level, including toxicant dilution through reproduction. By further developing the threshold damage model (TDM), Ashauer *et al.* (2007) examined the accumulation and depuration of various substances in *Gammarus pulex*. After a critical internal threshold has been reached, there is a certain probability that an individual will die. We also found a few terrestrial models looking into exposure and bioaccumulation, but they disregard effects of toxicants to populations and their dynamics (Chow *et al.* 2005; Schipper *et al.* 2008).

The model in the following case study was developed to study the response of a meadow ecosystem to continued loading with the persistent contaminant cadmium (Cd) (Traas & Aldenberg 1992). The probabilistic treatment of the model resulted in probability distributions of all relevant model outputs. It was therefore possible to calculate the probabilities of exceeding given environmental standards, following different Cd loadings. This type of modelling study is useful to obtain a general overview of the system and provides a rough estimate of critical compartments in a food web with regard to metal loads.

A Model for Predicting Contaminant Cadmium Accumulation in Meadows

The model belongs to the CATS group of models (Contaminants in Aquatic and Terrestrial Systems) and was developed for the ecological risk assessment of cadmium accumulation in a meadow system, on a moist, nutrient-rich peat soil in the lowland peat district in the Netherlands.

A major feature of this model is the conceptual separation of the biomass and toxicant cycles. Only bioaccumulation is modelled, without any effects on the biomass/nutrient cycle. The model considers spatial structure only in the vertical direction (i.e. soil layers, vegetation), while the area is considered to be homogeneous. Modelled species are grouped into functional groups based on their role with respect to nutrient cycling. Presence and abundance of specific vertebrates, such as raptors or carnivorous mammals, are usually considered to reflect the health of the ecosystem. Their feeding habits are quite accurately known, while ecological details of soil fauna feeding habits are much less known. Because the goal of this model was not to predict true population dynamics in the field, but to study the principal effect of emission reduction, the more phenomenological approach of logistic growth was chosen to embed mass balance principles. The major feature of the toxicant cycle is the principal role of pollutant equilibria determining the amount of Cd bound to the litter or SOM or Cd dissolved in interstitial pores. A high binding constant means that the dissolved Cd concentration is quite low and vice versa. Cd enters the system by deposition from manure brought in from outside the system and bird immigration, while it leaves the system through percolation of dissolved cadmium in excess rain water to deeper soil layers, with crop harvesting, meadow bird emigration and the deaths of cows and birds.

Biomass fluxes in the model follow similar paths for all groups: all animal functional groups consume food either from one or from several sources. Food is assimilated with a certain efficiency, and is partitioned into growth, reproduction and respiration, while non-assimilated food is egested. Toxic fluxes in animal groups include cadmium uptake from their food or from the soil solution. The non-assimilated fraction of cadmium in the food is egested with non-assimilated biomass, and is returned to litter or soil organic matter, depending on the animal's habitat. The group loses cadmium by mortality, excretion and predation, where cadmium excretion is modelled as a first-order process.

Simulations show that a steady state is reached within 3 years for all functional groups, but also for organic matter pools and all accumulation scenarios. The authors conclude that cadmium accumulation shows the same dependence on top-soil concentration for all compartments, and that steady state concentrations will be reached somewhere in year 2300. Given that this is a model with no feedback between accumulation level and the biomass cycle, an almost linear relation seems to exist between soil concentrations and concentrations in all functional groups. Results also show that environmental quality criteria for the food of birds are exceeded at the same loading scenarios, for the years 2015 and 2050. In other scenarios, where Cd load is smaller, there is no real risk to bird food. However, when it comes to food for mammals, it seems that in 2015, even with 1/8 of the current load, the standard will be exceeded by 2.4%. By 2050, the quality standards will be exceeded even if they are as high as ½ of the present load.

Do the reviewed models address the requirements for protection goals in legislative documents?

Hommen *et al.* (2010) reviewed protection goals, data requirements and risk characterisations within European chemical directives and concluded that the risk assessment approach in different directives is very similar because they are all based on a quotient of predicted or measured environmental concentrations and an ecological threshold value. Protection goals are broadly defined in both spatial and temporal terms, e.g. local vs. regional population protection and defining acceptable recovery period for affected non-target organisms. Hommen *et al.* (2010) linked the proposed areas of model application to protection principles, as defined by Brock *et al.* (2006) and European chemical directives. This linkage can be used to relate model output to protection goals, with the most common output types being population abundances, biomass (more used in ecosystem models), and population growth rates. In order to translate the output of standard laboratory tests to these higher levels of organisation, such as populations and ecosystems, which are often the level of protection, ecological models offer excellent tools.

Linking Reviewed Models to Potential Areas of Application

Some of the case studies show that more than one modelling approach can be used within one area of application, but also the potential of the evaluated models to cover more than just one application area. Since usually not one endpoint, but a combination of endpoints is of interest in chemical risk assessment, it is reasonable to expect that models will belong to more than one application area. For instance, integration of a detailed exposure–effects link, such as a TK–TD model, with a population model will produce a more realistic description of effects of time-varying exposure on field populations. Such models can also give information about effects at the individual level, due to the TK–TD component, and about population-level recovery, due to recovery-relevant vital parameters, such as survival and reproduction. Consequently, such a model can be used in three application areas.

Given the levels of biological organisation (individual, population, metapopulation and community or ecosystem) addressed by various models and the relatively narrow set of questions and interests for the risk assessment process, only some biological levels are likely to be relevant and appropriate when addressing each of the proposed application areas. Table 2.5 summarises our assessment about useful combinations between the level of biological organisation (individual, population, metapopulation and community or ecosystem), modelled entities within these levels (from internal concentrations, stages, individuals to functional groups) and potential areas of application they could address. Assumed useful combinations are denoted as grey areas, while numbers represent the findings from our review of the models and show the numbers of existing models for each of the combination. We obtained two modelling studies that focus on effects of toxicants on energy budgets in individuals that do not yet address the population levels. There is, however, a high potential in these studies to do so in the future. Not surprisingly, models at the population level generally suffice when the focus is on population-level effects. Preferably, populations in these models would be structured at least at the level of stage or age. Exposure extrapolation can be performed at either the individual or the population level. If population-level effects of time-varying or multi-peak exposure are of interest, a TK-TD type of submodel can be used to assess the effects at the individual level. On the other hand, in cases with a single peak or constant exposure, a detailed TK-TD model is not needed, and a direct link between exposure and effects can be used to model effects on individuals. Since recovery processes encompass individual- to community-based processes, all levels might be appropriate. For instance, individual recovery might be more important for vertebrates whereas for invertebrates the focus will usually be on the population level. Because indirect effects are defined as feedbacks among functional groups or trophic levels in a food web, the food web/community/ecosystem level is the relevant one for a modelling study. Finally, bioconcentration processes are best investigated at the individual level, and this was most commonly found in published studies, while at least a simple food chain is required for biomagnification. If necessary, both levels can be combined in one study. Just as with application areas, and depending on the questions asked, models relating to different biological levels of organisation can be combined.

When it comes to spatial structure, our review found a very small fraction of spatially explicit models, probably due to the high computing and data demands of such models, and because exposure is not yet commonly modelled in a spatially explicit manner. We did, however, find several modelling studies where exposure is explicitly modelled, but the effects and dynamics of exposed individuals and populations are not.

Outlook

Due to the imprecision of protection goals, researchers and risk assessors rely on different sources of guidance to bridge the gap between measurement endpoints and protection goals. These include technical documents (EC 2002; SANCO 2002) and reports from workshops where all the stakeholders (academia, regulating authorities and industry) are brought together (Campbell *et al.* 1998; Giddings *et al.* 2001; Barnthouse, Munns & Sorensen 2007; Forbes *et al.* 2009; Thorbek *et al.* 2009). So, even though the protection aims in European legislation are very broadly defined, their focus and the level of protection have been interpreted into more manageable terms. Ecological models have proven to be able to provide a strong link between measured data and foci of protection. Further development and improvement of ecological models in RA greatly depends on the needs identified by industry and regulators. During the last few years, for instance, recovery of affected species has become very important for the registration of pesticides. The fact that recovery cannot be studied for all species, even in field studies, e.g. mesocosm studies, has stimulated the development of recovery models (Van den Brink *et al.* 2007). Furthermore, with progress in computing, explicit consideration of space in exposure and effects is becoming more common, and is a vital part of a realistic ecological risk assessment process. Interestingly, almost half of the spatially explicit models in our database are also individual-based, thus representing the high ends of both biological and spatial structures, while the other half are based on biologically unstructured populations. The development of spatially explicit and spatially realistic (GIS-based) models is expected to increase for future chemical ERA purposes

Table 2.5. Proposed levels of biological organisation and modelled entities that are relevant when addressing different application areas of ecological models. Grey areas denote our suggestions, whereas the figures denote the number of modelling studies per application area found in our review. One modelling study was considered on more than 1 biological level.

Modelled level of biological organization	**Modelled entity**	**Model types (examples)**	**Model application areas**				
			Extrapolation from individual to population level effects	**Extrapolation between exposure patterns**	**Extrapolation of recovery processes**	**Analysis and prediction of indirect effects**	**Prediction of bioaccumulation**
Individual	energy budgets, internal conc.	TK/TD models, Debtox	2	2	3	0	7
Population	unstructured population	Lotka-Volterra type models	5	1	3	0	0
	age / stages	Matrix and other stage structured models	44	17	22	5	4
	individuals	IBMs	17	4	15	2	2
Metapopulation	patches (sub-populations)	spatial explicit population models	4	1	4	3	0
Community/ food web	functional or taxonomical groups	system of unstructured pop. models	9	5	5	8	3

An additional advantage of modelling studies is that they allow deficiencies in existing datasets to be identified, thus making future experimental research more focused. One of the challenges that might be faced in this field is the proper link between exposure and effects in the field. This topic was covered by the eLINK workshop (Brock *et al.* 2010) that should produce tools that correctly address the effects of extrapolation within a species, i.e. extrapolation to population-level response, as well as from the lab to field conditions. Because the emphasis is on realistic ERA, reliable data will be required on life-history traits of the species of interest, their life-cycle parameters and, in the case of spatially explicit environments, their movement and dispersal patterns. Effects of chemicals need to be looked at for all levels, including sublethal effects, so the resulting risk is not overestimated or underestimated.

This study represents one of the steps in addressing the potentials and pitfalls of ecological models published in the last two decades for the field of regulatory risk assessment. The range of modelling studies identified in our review reveals a need for more coherent modelling approaches relating to chemical risk assessment, an issue put forward by the LEMTOX workshop (Forbes *et al.* 2009). The workshop identified obstacles to a wider use of models in risk assessment of plant protection products, as well as ways forward. One of these was the development of Good Modelling Practice, an approach that would include recommendations and information on all parts of the modelling process, including design, testing, application, documentation and reporting. Model development relies heavily on the focal species or ecosystem and questions that are more or less similar in the risk assessment schemes for different types of chemicals, which clearly suggests that a more unified approach is definitely feasible. A big step forward for the field of ecological models in chemical RA is the establishment of an advisory group within SETAC, called MemoRisk, which focuses on mechanistic models in chemical risk assessment (Preuss *et al.* 2009a). Furthermore, the establishment of the CREAM EU (Grimm *et al.* 2009) project, whose main goal is to develop a suite of well-tested and validated mechanistic ecological effect models for an array of species and ecosystems relevant to chemical risk assessments, is probably the biggest leap in the right direction.

It is relatively easy to be impressed by the vast possibilities of ecological models, and we want to caution against the urge to apply them to any system, without extensive prior considerations. Ecological models are very useful, integrative tools with a high potential for extrapolation. However, it is very important to bear in mind that model output should always be regarded in a relative sense and no absolute conclusions should be drawn. The error propagation in model results arises from errors in data sampling and accumulation, false assumptions and omission of potentially relevant processes. Bartell *et al.* (2003) rightly state that the focus of risk assessors should be on the relative strengths of each modelling approach, which should be chosen based on the question at hand and protection aims.

In conclusion, the published literature offers a variety of modelling approaches that have been developed to answer various questions related to effects of chemicals. Most of them are presented as academic exercises rather than for registration purposes, although many of them have a high potential for regulatory risk assessment. Brock *et al.* (2006) mention the potential use of modelling studies in the highest tiers of RA of chemicals under the WFD and 91/414/EC directives, following standard species tests as the first, species sensitivity distributions as the second and the model ecosystem approach as the third tier. Only in the third and higher tiers, modelling studies are considered as tools for RA refinement. But even in the highest tiers of RA, some models are more generic, easier to parameterise and, thus, useful to obtain preliminary results on the effects of chemicals on populations in question. Models that include only the basic life-history of the species, e.g. unstructured or structured such as Euler-Lotka based or matrix models, could be used for an initial screening process. These modelling studies can give an overview of adverse effects and/or most sensitive life-stages, requiring a limited effort. For more specific cases and questions, more complex models including more detailed life-histories of focal species, such as IBMs, spatial structure and different exposure patterns could be more appropriate. Our review, including the database of models, represents a starting point for gaining an overview of published ecological models used to assess the effects various chemical substances have on different species. Furthermore, the case studies serve as examples of the possibilities and added value of various ecological modelling approaches for the field of chemical ERA. Finally, easily obtainable information on focal species, habitats and chemical substances, and more specific details on technical aspects of the models reviewed here, might facilitate the decision-making process for end-users.

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Chapter 3

Simulating population recovery of an aquatic isopod: effects of timing of stress and landscape structure

Nika Galic, Hans M. Baveco, Geerten M. Hengeveld, Pernille Thorbek, Eric Bruns and Paul J. van den Brink

Abstract

In agroecosystems, organisms may regularly be exposed to anthropogenic stressors, e.g. pesticides. Species' sensitivity to stress depends on toxicity, life-history, and landscape structure. We developed an individual-based model of an isopod, *Asellus aquaticus,* to explore how timing of stress events affects population dynamics in a seasonal environment. Furthermore, we tested the relevance of habitat connectivity and spatial distribution of stress for the recovery of a local and total population. The simulation results indicated that population recovery is mainly driven by reproductive periods. Furthermore, high habitat connectivity led to faster recovery both for local and total populations. However, effects of landscape structure disappeared for homogeneously stressed populations, where local survivors increased recovery rate. Finally, local populations recovered faster, implying that assessing recovery in the field needs careful consideration of spatial scale for sampling. We emphasize the need for a coherent definition of recovery for more relevant ecosystem risk assessment and management.

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Introduction

In aquatic environments, arthropod populations are often exposed to various disturbances, many of which are anthropogenic in nature, including nutrient and chemical pollution, flow modification and species invasions (Dudgeon *et al.* 2006). Agroecosystems represent one of the most human altered landscapes and may pose significant stress to its biota, due to pesticide exposure. The effects of such stress on aquatic populations and communities, and the speed of their subsequent recovery is mainly dependent on three groups of factors: 1) species specific, 2) stressor specific and 3) habitat specific (Gore, Kelly & Yount 1990; Niemi *et al.* 1990).

Species specific factors that determine a species ecological sensitivity include various life-history traits that enable certain species to recolonize empty habitats more efficiently, such as good dispersal traits (Holomuzki & Biggs 2000; Collier & Quinn 2003; Vieira *et al.* 2004; Tronstad, Tronstad & Benke 2007; Albanese, Angermeier & Peterson 2009), high fecundity and voltinism (Stark, Banks & Vargas 2004b), or presence of insensitive stages (Pieters & Liess 2006; Devine & Furlong 2007). Biotic interactions of the existing community can hamper or facilitate the recolonization process (Spanhoff & Arle 2007). Stressor specific factors such as the timing, stressor toxicity, chemical nature and persistence of the stressor can determine the speed of habitat recovery that is essential for the biotic recovery of the system (Crutchfield & Ferson 2000; Vieira *et al.* 2004; Devine & Furlong 2007). Finally, habitat specific factors include vicinity of undisturbed habitat patches that can act as sources of recolonizing individuals (Devine & Furlong 2007), presence of refugia (Robertson 2000; Lake, Bond & Reich 2007), and presence or absence of features in the landscape that can act as corridors or barriers for recolonization (Reice, Wissmar & Naiman 1990; Vieira *et al.* 2004).

Most natural populations are spatially structured and consist of a set of connected local populations which interact via dispersal and together constitute the metapopulation. Metapopulation dynamics imply that occupied habitat patches may turn vacant due to local extinctions and may be recolonized again if the habitat connectivity is adequate for the species of interest (Levins 1969; Hanski 1998). Stress may be buffered in metapopulations, as usually not all local populations are stressed at the same time or with the same intensity (Devine & Furlong 2007), however if stress events are spatially and temporally correlated they are thought to be more detrimental to metapopulation persistence (Johst & Drechsler 2003; Kallimanis *et al.* 2005; Elkin & Possingham 2008).

Insecticides currently used in Europe tend to have very short persistence (van Wijngaarden, Brock & Van den Brink 2005). This may translate into short, yet regular, exposure of aquatic environment and its biota to insecticides. Insecticides induced stress is typically correlated both spatially and temporally. For the purposes of this paper, we define homogeneous stress as an entire system exposed to the same stress severity, spatially and temporally, whereas it is heterogeneously stressed if parts of the system differ in this exposure; however, overall stress in both cases is kept the same. Resistance to, and recovery from, stress in agroecosystems are key processes that ensure the sustainability of populations and communities and maintenance of certain functions and ecosystem services (Galic *et al.* 2012b), such as decomposition and nutrient cycling (Swift, Izac & van Noordwijk 2004). One of the species that plays an important role in the decomposition of dead organic material and subsequent nutrient cycling is the waterlouse, *Asellus aquaticus*, a detritivore commonly found in European freshwater systems (Marcus, Sutcliffe & Willoughby 1978).

Population and ecosystem recovery are also important in the regulatory risk assessment of pesticides (Hommen *et al.* 2010), as it is generally considered that timely recovery can reduce the short-term negative effects of pesticides on non-target biota, current legislation allows for some adverse effects if recovery can be expected (SANCO 2002a). However, there is no clear (regulatory) consensus on the definition of recovery and what constitutes a timely recovery. If disturbance or stress is defined as a discrete removal of organisms due to an unexpected divergence from normal (expected) conditions (*sensu* Gore *et al*. 1990), then recovery can be defined as the return, in abundances or structure, of the affected biological organization (population, community or ecosystem) to its unstressed or control levels, either through reproduction of the survivors or recolonizing individuals from unstressed areas. In this paper we use a hypothetical insecticide as a stressor.

Using an individual-based model (IBM) of the waterlouse *Asellus aquaticus*, we looked into how the recovery of its populations depends on timing of stress, and on the structure of its habitat. More specifically, we addressed the following questions:

1. How does the interaction of a species' phenology and timing of stress affect recovery of its populations in a seasonal environment?
2. Given different timings of stress, what impact does habitat structure and connectivity have on the recovery of waterlouse populations? What are the consequences of spatially homogenous and heterogeneous stress exposure?
3. What is the proper spatial scale for observing the recovery process?

Materials and methods

Model species

The model organism, *Asellus aquaticus* is commonly found in European freshwater ecosystems, the number of its generations and overall population dynamics depends mainly on water temperatures and varies from univoltine in northern Europe to constant reproduction in some southern European regions (Tadini, Fano & Colangelo 1988). Here we investigate a population representative of Northwest and Central Europe, where populations are usually bivoltine (Økland 1978), with the overwintering population giving rise to the spring generation, which is usually smaller in abundance than the summer generation. *A. aquaticus* are mainly detritivores, but are also grazers on live algae. The species is not very selective in the type of waterbody it inhabits, however it is purely aquatic with relatively slow dispersal (Moon 1968). Even though it has a very small probability of dispersing over non-aquatic habitat, mainly through phoretic dispersal, i.e. via other organisms such as aquatic birds, this is an ecologically sensitive species and therefore suitable for conservative risk assessments of pesticides.

We developed an individual-based model (IBM) to explore the ecological sensitivity and recovery of waterlouse populations after a stress event. We explored the importance of landscape connectivity and movement rates by using three different landscapes (Fig. 3.1), namely two well-connected landscapes: a ditch with slow movement of the waterlouse, a stream with potentially faster movement, and, as an example of a less well connected landscape, a setting with small, scattered waterbodies, from here on termed the fragmented landscape. The latter could also represent a floodplain with many small puddles that harbour individuals who are limited in their movement abilities, but still manage to move around due to rainfall, flooding or through phoretic dispersal.

More information on the species life-history, data obtained from literature and the model itself can be found in Appendix 3.1.

Population model

We developed an IBM that was loosely based on the model described by Van den Brink *et al*. (2007). In the following sections, we provide a brief overview of the modelled life history of the water louse, following the ODD protocol (Grimm *et al.* 2006), while the full description of the model assumptions and structure are in Appendix 3.1, and the sensitivity analysis of the model is presented in Appendix 3.2.

Purpose. The purpose of the model is to assess the effects of stress on population dynamics of the water louse, *Asellus aquaticus*, especially in terms of how population recovery potential depends on the landscape structure and timing of stress, here, insecticide exposure.

Entities, state variables, and scales. Entities in the model are individual waterlouse females and square cells comprising the landscape. We distinguish between juvenile and adult stages. Individual state variables are individuals' age [days], size [length in mm], hatching date [day in the calendar year], lifespan [days] and location [continuous X and Y coordinates] in the habitat. We simulate three types of landscapes (Fig. 3.1): a) ditch - consists of a string of 100 cells of aquatic habitat, b) stream – the same as the ditch with the addition of individual drift and c) fragmented landscape – where 100 cells representing small, 1 m^2, waterbodies are randomly dispersed within the grid. All landscapes are modelled on a 50x50 square grid with periodic boundary conditions, i.e. the grid is a torus, to avoid edge effects.

The state variables of cells are the local mortality of *Asellus* induced by stress and density dependence. Each cell represents 1 m^2. The time step is one day, with 365 days in a year; simulations start on day 0 (Jan 1) and continue for six years or until there are no surviving individuals left. The output from the first year is disregarded to avoid transitional effects. All parameters and their distributions are in Table 3.1. The model is implemented in the NetLogo platform v. 4.1 (Wilensky 1999; freely downloadable from http://ccl.northwestern.edu/netlogo).

Process overview and scheduling. Processes in the model are mortality, movement, growth, and reproduction, which are scheduled for individuals in a randomized sequence. Every time step each individual ages and its mortality probability is calculated, the surviving individuals change position in the modelled habitat, followed by juvenile and adult growth. Finally, individual's mortality probability increases if exposed to stress. All individual state variables are updated immediately (asynchronous updating). Survival, growth and movement functions are constant over the whole year.

Mortality consists of background, density-dependent and stress imposed mortality. Background mortality was implemented by assigning individuals different lifespans (in days) at birth; lifespans were exponentially distributed with a mean of 90 days (Table 3.1). This resulted in 1% of individuals from the initial modelled population surviving more than 400 days, while it has been found that they can survive up to 600 days according to Vitagliano *et al.* (1991), thus making our estimate conservative. Density-dependent mortality assumes a negative effect of local densities on individual survival; whereas exposure to stress in certain times of year increases individual mortality probability. Since short-term, spatially correlated exposure to pesticides is most common in habitats adjacent to agricultural fields, we imposed stress for only one day, i.e. cell regeneration was almost instantaneous.

Individuals grow deterministically following a von Bertalanffy growth function (von Bertalanffy 1957). The maximum growth rate is affected by local density, i.e. the density in each cell. This is based on observations and measurements by Hynes & Williams (1965) who experimentally show that waterlice populations produce more offspring when housed in larger jars, even though the amount of food in their experiments was the same.

In order to mimic the observed bivoltine reproductive pattern in North-western Europe we introduced two periods in a year when individuals are able to reproduce. The reproductive periods start in the beginning of May and mid-July, and they last four and six weeks (Table 3.1), respectively. In these reproductive periods each individual female releases its offspring once, and the maximum realized fecundity is set to 100 juveniles (Arakelova 2001). Individual fecundity is positively correlated with the size (length) of the female at the time of release (Chambers 1977), resulting in bigger females releasing more juveniles.

Movement is modelled through a distribution of distances each individual can cover in one day that was obtained via a separate movement model which output was used as input for this model. In the separate movement model, simulations of correlated random walk were carried out for a large number of individuals, and it was assumed that individuals move one third of the day, i.e. one step every three minutes (based on Van den Brink *et al.* 2007). These simulations of daily number of steps with adjoining turning angle data resulted in a normal distribution of distances each individual can move to from its initial position in the modelled habitat, which was used as input for the population model (see Appendix 3.1 for details).

Table 3.1. Model parameters and distributions.

Submodel	Parameter	Distribution	Value	Unit	Reference
Habitat	System carrying capacity, K	constant	10 000	individuals	Constant K per patch (growth related)
Mortality	Lifespan	exponential	Mean 90		Adapted from Vitagliano *et al.* (1991)
	µ1	constant	0.001		Based on Van den Brink et al. (2007)
Reproduction	Onset of 1st reproductive cycle	constant	120 (April/May)	day	mimicking western European conditions
	Onset of 2nd reproductive cycle	constant	200 (July)	day	
	Maximum clutch size	constant	100	ind	Arakelova (2001)
	Length of 1st reproduction period	uniform	1 to 28	day	Adapted from Chambers (1977)
	Length of 2nd reproduction period	uniform	1 to 45	day	Adapted from Chambers (1977)
Growth	Maximum size	constant	12	mm	Okland (1978), Arakelova (2001), Marcus *et al*. (1978)
	Minimum size	distribution	mean 1, SD 0.2	mm	Adcock (1979)
	Kappa, k	constant	0.02	/ day	Determined by calibration
	Age at maturity	constant	45	day	Williams (1962)
	Density-dependent factor, *y*	constant	1		Own estimation (see sensitivity analysis)
Movement	Drift distance	exponential	mean 10	m	Based on Van den Brink et al. (2007)

	κ, variance of von Mises distribution	constant	1.73	rad	Pers. Comm. Van den Brink; used in a separate movement model
	μ, mean of von Mises distribution	constant	0.5201	rad	Pers. Comm. Van den Brink; used in a separate movement model
	Step length	lognormal	Mean – 2.83, SD 0.92	m	Pers. Comm. Van den Brink; used in a separate movement model
	Daily movement distances	normal	Mean 0.004, SD 4.444	m	Own simulation (for details, see Appendix 3.1)

Model landscapes

Landscapes representing a ditch and a stream were included to represent more realistic, connected waterlouse habitats, whereas a fragmented landscape with many small aquatic cells was added to evaluate recovery in a less connected habitat.

The modelled ditch was representative of a typical slow flowing waterbody found in Dutch agricultural fields. The stream landscape was identical to the ditch, except that here the individuals could drift, i.e. move passively over larger distances. Drift, or passive movement of macroinvertebrates in streams, is considered to be a mechanism that potentially enhances the recovery process, as it adds more individuals to stressed habitat cells than just normal daily movement (Brittain & Eikeland 1988). It is, thus, assumed that any differences in population recovery between these two landscapes arise solely due to presence of drift. Here an arbitrary 10% of population to drift on a daily basis was chosen, in addition to the movement process as in the ditch (see Table 3.1 for details on drift distance).

The position of aquatic cells in the fragmented landscape varied between simulations used for analysis; we evaluated 20 different landscapes in total. The movement procedure in the fragmented landscape was similar to the one in the ditch, with the exception that the assigned value, from the location distribution, represented a radius in which individuals detected whether there is an aquatic patch within it. If there was one, they were allocated to that cell; otherwise they remained in their original cell. Whereas in the ditch and stream individuals always changed their position, in the fragmented landscape this might not always be the case.

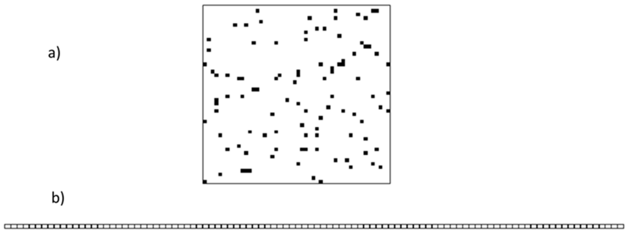

Figure 3.1. Landscapes modelled in this study: (a) the fragmented landscape where black cells represent aquatic habitat and (b) the ditch/stream landscape; all cells represent 1 m^2.

Simulation experiments

In the following section we briefly describe control and treatment scenario series.

Control scenario. Population in the control scenario were not exposed to any stress; they were, otherwise, identical to treatment scenarios.

Timing scenario. To study the influence of the timing of stress on the recovery of waterlouse populations the following days were chosen: 1) just before and 2) just after the first generation, 3) just before the second generation peak and 4) after the reproductive season (Fig. 3.2). Stress events were scheduled for mid-April (Julian day 110), beginning of June (day 160), beginning of August (day 210) and mid-September (day 260). This is consistent with insecticide applications in NW Europe, where the first applications of insecticides typically start between March and April, and while applications in autumn are much rarer, they still occur for some crops e.g. bulbs, fruits and some vegetables are still treated in October (CBS, 2008). In the model, the toxic effect lasted for only one day, and increased the mortality probability of each individual in exposed cells in all three model landscapes. Stress related mortality probability was set either to 0.5 or to 1 (details are below).

Spatial exposure scenario. We simulated two exposure scenarios: a) all 100 aquatic cells were exposed to a mortality probability of 0.5 per individual for one day – named hereafter "homogeneous exposure scenario", and b) only 50 connected aquatic cells exposed to a mortality probability of 1.0 per individual for one day – named hereafter "heterogeneous exposure scenario".

Both of these scenarios resulted in, on average, 50% of the population dying due to inflicted stress, so the differences in recovery speed was solely due to the distribution of the stress event itself. In both the modelled ditch and stream, the downstream reach was stressed, thus leaving the unexposed, upstream population to recolonize the lower parts of the habitat.

In the fragmented landscape, stressed cells were aggregated and fully surrounded by the unstressed ones, which acted as sources of recolonizers.

Scenario analysis. The outputs from the treatment scenarios were compared to the control in the corresponding landscape. For the analysis of recovery times, we used 20 replicate simulations for each of the treatments including the control. We compared daily abundances in controls and treated populations and considered a treated population recovered if its abundance reached 95% of the abundance of the control population. Both in real aquatic systems and this model there is stochastic variation of abundances at the local scale, which may mask recovery or lack thereof, for instance, as waterlouse move from cell to cell that may lead to a very short term recovery of that cell as the abundance would go down again as soon as the waterlouse moved on. Consequently, we defined recovery as reaching the 95% or higher abundances than those of control populations for five days out of a period of ten days. Once this condition was met, day of recovery was considered to be in the middle of this period. Furthermore, we evaluated the population recovery for two different spatial scales, namely, recovery of the population in 10m^2 and 100m^2, with the larger scale hereafter termed the total population and the smaller scale hereafter termed local population. For the local population, we chose ten aggregated cells, where we observed recovery; these cells were always exposed and in the middle of the exposed area in case of the heterogeneous stress scenario. When exploring the contribution of individual drift to recovery (stream habitat), we evaluated the recovery of the population in the whole stressed part of the ditch, i.e. population on 50 m^2.

Daily population abundances of each of the 20 treated replicates were compared with each of the 20 control replicates, yielding 400 estimations of recovery times. All the resulting distributions of recovery times are presented in violin plots (Hintze & Nelson 1998). Violin plots are a combination of boxplots and kernel density plots, showing the probability density of data at different values. All the violin plots include a marker denoting a median value, and also the exact value of the median. We compare median values in different scenarios, as medians are a more robust statistic for central tendency than means in non-normally distributed datasets.

Finally, we tested the differences in recovery time distributions for different periods and habitats with a Wilcoxon rank test using the R software package (R Team 2008).

Results

Simulated populations were bivoltine, as expected, with a distinct spring and summer generation (Fig. 3.2), the latter more abundant than the former. Time to local and total population recovery in different scenarios is presented in Table 3.2.

Timing scenario

In all landscapes, time to population recovery was dependent on the timing of the stress event. Generally, time to recovery got shorter the closer the stress was to the onset of a reproductive period. In the ditch, the recovery of the total population occurred within the same season after stress imposed in April, and took longest when stress was imposed in September, i.e. after the reproductive season, with a median of 313 days to recovery (Fig. 3.3). The bimodal distribution of recovery times after stress in September indicates that part of the exposed populations recovered with the first and the other part with the second reproductive period in the following year.

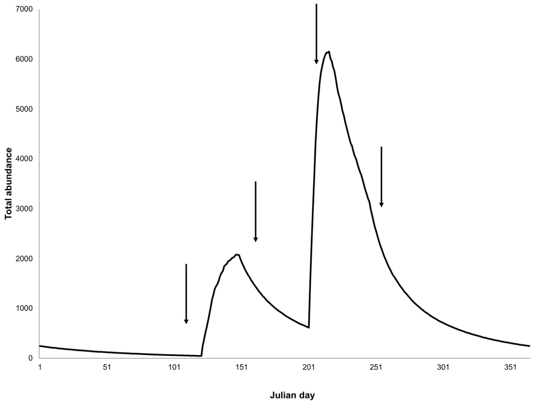

Figure 3.2. The modelled bivoltine waterlouse population. Arrows represent stress events, being Julian days 110 (April), 160 (June), 210 (August) and 260 (September).

Table 3.2. Median days to recovery in all scenarios and for both population scales. Grey boxes denote scenarios where recovery takes place in the next season.

	Ditch landscape				Fragmented landscape			
	Homogeneous		Heterogeneous		Homogeneous		Heterogeneous	
Stress event	10m	100m	10m	100m	10m	100m	10m	100m
April	**103**	**122**	**116**	**127**	**100**	**124**	**133**	**138**
June	**73**	**84**	**89**	**116**	**72.5**	**118**	**114**	**138**
August	**57**	**111**	**103**	**172**	**51**	**129**	**132**	**200**
September	**166**	**314**	**175**	**313**	**165.5**	**308**	**187**	**317**

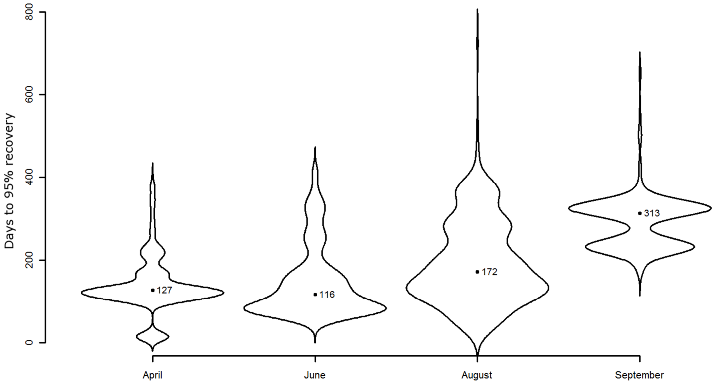

Figure 3.3. Time to population recovery (in days) of the total population in the ditch, heterogeneous exposure scenario. Each of the four violin plots (see text) represents a distribution of recovery times after stress events in April, June, August and September.

Spatial exposure scenario and effect of habitat structure

Homogeneous spatial exposure. Local populations in the homogeneously stressed ditch and fragmented landscape show almost no difference in recovery times (Table 3.2). Similarly, when the entire landscape, i.e. total population, was exposed to the same homogeneous stress event, we found little influence of the landscape connectivity on time to recovery (Fig. 3.4), as all cells retained some survivors which formed a basis for population recovery. We analysed the distributions of recovery times (Wilcoxon rank test), and found small, but significant differences between the landscapes (mostly to the $p < 0.01$ level, Fig. 3.4).

Heterogeneous spatial exposure. In this stress scenario, local populations went extinct, as mortality was 100%, and the 10 stressed cells were in between other stressed cells. Stress in fragmented landscapes led to longer recovery times for the local populations than in the ditch, where connectivity was better (Fig. 3.5). As a consequence of movement of individuals to stressed cells, abundances in unstressed parts of both landscapes declined (results not shown). The effects of habitat fragmentation on recovery times were significant for the first three stress events, but not for the last, because recovery in both habitats occurred only with the first generation in the next year.

For the total population, recovery after heterogeneous stress was also slower in the fragmented landscape than in the ditch (Fig. 3.6), and even more so since recovery times after all stress events significantly differed between the two landscapes (Wilcoxon rank test, p < 0.001) (effects of individual drift in the stream landscape are described below). The greatest difference was noticeable after stress in August, when populations in the fragmented landscape took 28 days longer to recover than those in the ditch. In both landscapes, distributions of recovery times after the last stress event were bimodal (Fig. 3.6), thus some populations recovered with the first generation of the next season, but most did not recover until the second generation.

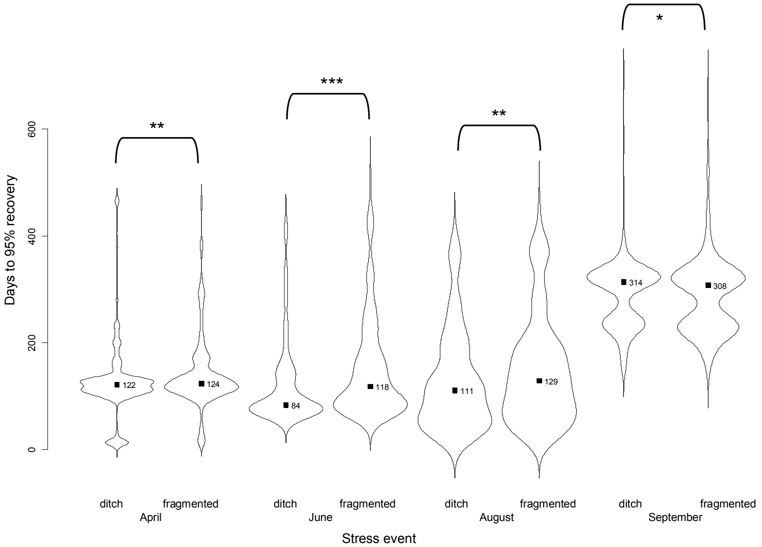

Figure 3.4. Time for the total population to recover (in days) in the ditch and fragmented landscape, homogeneous stress scenario. Within each stress event (April, June, August and September), recovery time in both landscapes was compared with Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

For all landscapes, exposure to homogeneous stress led to shorter recovery times for the total population than exposure to heterogeneous stress (Fig. 3.4 and 3.6, Table 3.2). These differences were more prominent after stress in August, and to a lesser extent after stress in June. The spatial pattern of exposure had impact on time to recovery, thus, for ditches the recovery took 61 days longer (after stress in August) in the heterogeneous exposure scenario than in the homogenous exposure scenario. In the fragmented landscape, the difference between exposure patterns was even more pronounced with recovery taking 71 days longer in the heterogeneous exposure scenario. Overall, these differences were largest after stress in August and the results indicated that as most of the reproduction had been completed at time of stress, too few reproducing individuals were left to ensure recovery within the same year. Finally, stress after the reproductive season (September) resulted in similar recovery times for all scenarios (landscape and exposure), as populations in both landscapes and scenarios recovered only with the next season's generations.

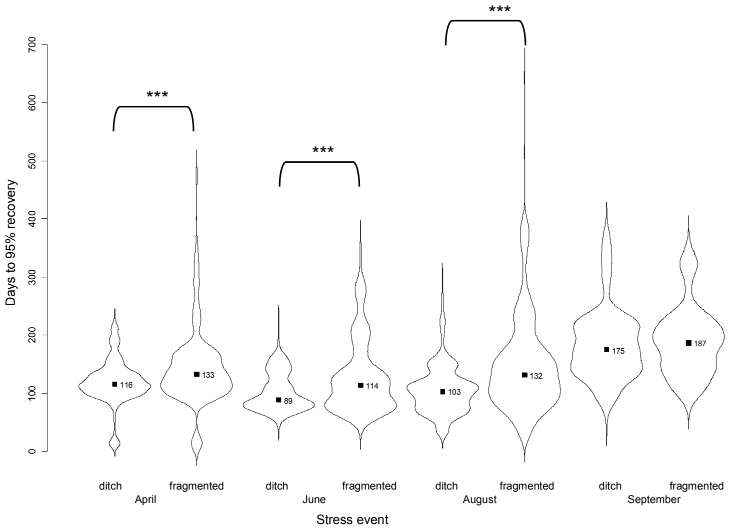

Figure 3.5. Time for the local population to recover (in days) in the ditch and fragmented landscape, heterogeneous stress scenario. Within each stress event (April, June, August and September), recovery time in both landscapes was compared with Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

Effects of individual drift

The effect of drift on recovery was explored by comparing streams and ditches, which differ only in the waterlouse drift. In homogeneously stressed streams, the results indicated that drift had no effect on time to recovery irrespective of whether recovery was measured at the scale of total or local populations (results not shown).

In heterogeneously stressed streams, drift speeded up the recovery process after the first three stress events, but these differences were not consistent after the last stress event (Fig. 3.7). In all cases, there was a small but significant difference in time to recovery (Wilcoxon rank test, $p < 0.01$ and $p < 0.001$).

Effects of spatial scale in evaluating recovery

The recovery times of the total population were consistently longer than those of the local populations (Table 3.2), across all scenarios and landscapes. Thus, time to recovery depended on the spatial scale at which it was measured.

Sensitivity analysis

We performed an analysis of the effects of alternative parameter values and functions on the model output. Due to a lack of information on certain species' traits, we especially tested the effects of density dependent mortality and growth, as well as movement distances, on recovery times in different scenarios. A detailed analysis is presented in the Appendix 3.2. We found that the model output is relatively robust to changes in parameter values and that the most marked difference in output is obtained when the daily movement is greatly reduced, resulting in longer recovery times.

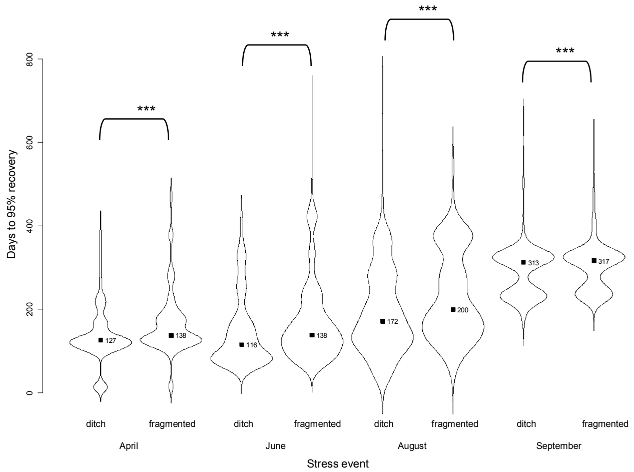

Figure 3.6. Time for the total population to recover (in days) in the ditch and fragmented landscape, heterogeneous stress scenario. Within each stress event (April, June, August and September), recovery time in both landscapes was compared with Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

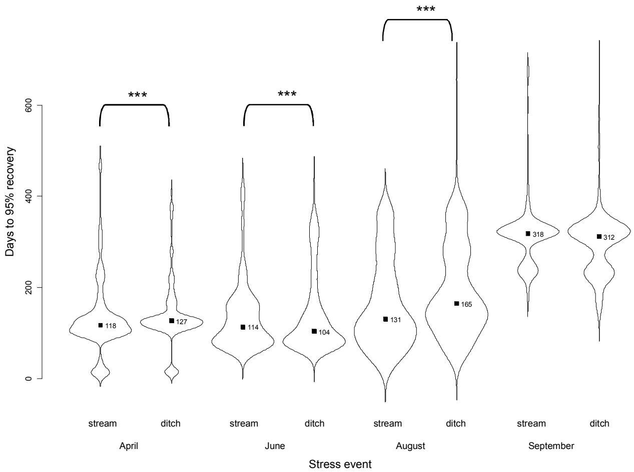

Figure 3.7. Effects of drift on the recovery of the population in the exposed stretch, i.e. 50 m^2 population in a stream. Here, 10% of the population is allowed to drift in addition to short distance movement. Within each stress event (April, June, August and September), recovery time in both landscapes was compared with Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

Discussion

Recovery of populations after stress has been shown to depend on ecological processes (Gardmark *et al.* 2003), landscape structure and connectivity (Niemi *et al.* 1990) and stressor related factors (Crutchfield & Ferson 2000; Johst & Drechsler 2003). Here we first focused on how the recovery of waterlouse populations is driven by its phenology in a seasonal environment. By exposing the population to short-term stress, in different parts of the year, we showed that the recovery of waterlouse populations was mainly governed by the timing of its two reproductive cycles, i.e. the closer the stress event was to a reproductive period, the faster the population recovered. Multivoltine and species with high intrinsic growth rate (Stark, Banks & Vargas 2004b) tend to recover faster and their recovery is not as determined by the timing of stress events, whereas recovery of species with fewer yearly generation cycles was shown to be highly dependent on the timing of stress in relation to their reproductive periods (Niemi *et al.* 1990; Whiles & Wallace 1995). Even though it has been found that, in disturbed streams, taxa with short life-cycles recovered faster (Whiles & Wallace 1995), the exact time to recovery in relation to a species' phenology has not been quantified. Recovery after exposure to stress late in the season (median is 313 days for populations in the ditch) is in accordance with Niemi *et al*. (1990) who show that isopods in disturbed streams could take more than one year after disturbance to recover.

Next we explored the significance of landscape structure on the recovery potential. For fully aquatic species, without any aerially dispersing life stages, the vicinity and landscape connectivity to unstressed areas plays an essential role in the recolonization and recovery process (Yount & Niemi 1990; Whiles & Wallace 1992; Whiles & Wallace 1995). In our model, both local and total waterlouse populations recovered quicker in the ditch than in the fragmented landscape (Table 3.2). These differences were much more prominent in heterogeneous stress scenario than in the homogenous one. Understandably, in a homogenously, i.e. fully, exposed system, the benefit of individuals redistributing in the landscape will not significantly add to the recovery process; the recovery of populations in such systems will be solely dependent on the reproduction. Both the local and total population recovered quicker in homogenously stressed landscapes as the presence of survivors accelerated the recovery process, whereas in heterogeneously stressed landscapes the process was lagged, depending on dispersal abilities and speed of stressed species (Vieira *et al.* 2004).

Including drift in the stream increased the connectivity of the landscape even more, and modelled populations after the first three stress events showed quicker recovery in comparison to the ditch (Fig. 3.7.). Drift is typically considered to be a very strong recolonizing mechanism as it brings more individuals from upstream reaches of streams to stressed patches (Brittain & Eikeland 1988; Yount & Niemi 1990). However, it comes with a price of relatively depleting the abundance of individuals from unstressed parts, i.e. from sources of individuals, as was also shown in the modelled unstressed cells in the heterogeneous scenario. Such “action at distance” was also found in experimental systems (Brock *et al.* 2010b). Furthermore, drift of certain size groups can leave a changed population size structure in the unstressed parts of the system (Greathouse, March & Pringle 2005). Moreover, Matthaei *et al.* (1996) suggest that in their system, a Swiss prealpine river, drift was not the major contributing mechanism in macroinvertebrate community recovery. Therefore, the actual contribution, but also potential population consequences of drift as a recolonization mechanism need more thorough quantification. This is of even more importance for agroecosystems, where frequent stress is expected, thus implying that effects on the system from outside of pesticide-exposed areas must also be considered.

Whereas most modelled populations recovered during the first or second following reproductive period, populations stressed in August, and to a lesser extent those stressed in July, recovered after the reproductive season, during simulated late autumn and winter months, mainly due to the stochastic nature of modelled dynamics. This recovery outside the reproductive period was especially noted for local populations that showed faster recovery due to redistribution of individuals and local colonization events (Sheldon 1984). Redistribution at the local level increases the probability that local abundances of stressed populations reach those in control, thus noted as recovery in our analysis. Consequently, local abundances increased faster than total abundances in all tested scenarios. This observation has important implications for assessment of population recovery in the field, and emphasizes the importance of selecting an appropriate spatial scale of measurement or sampling, indicating the need to look for effects and recovery further than only in exposed areas. It has also been shown that community recovery after major disturbance works on different timescales where different parts of the community recover at different rates (Peck *et al.* 1999).

Overall, we found very long recovery times in all scenarios. Whether absence or decreased abundances of this species would affect ecosystem service delivery is hard to determine, as it is a community of macroinvertebrates, rather than single species, that contribute to decomposition and nutrient cycling in freshwater systems (EFSA PPR 2010), allowing, thus, for compensatory dynamics to occur (Gonzalez & Loreau 2009). Quantifying the impact of long recovery periods of single species within a community on ecosystem services remains an interesting and important research direction. In our study, the simulated exposure scenarios were purposefully exaggerated, as the aim of this study was not to simulate the effects of realistic pesticide exposure conditions, but to explore different factors governing the recovery process. In a different study, waterlouse populations were exposed to more realistic exposure regimes yielding recovery within the same season for most scenarios (Van den Brink *et al.* 2007). However, whether more frequent exposure to pesticides in real application scenarios would affect the long-term population viability of this species is a relevant research question, but beyond the scope of this paper.

The discussion on the importance of properly defined ecological, spatial and temporal scales for stress and recovery in lotic systems is not recent (see Gore *et al.* 1990 and references therein). Whether our definition of recovery is sufficiently robust to assess population recovery in the field, or another definition, such as reaching the abundance of control populations with the first next reproductive period or focusing on the population size or stage structure, would be more relevant, is still an open question. Placing the contribution of tested species into a wider, ecologically more relevant context, such as ecosystem service provision or food web relevance, might facilitate the proper definition of what acceptable recovery times for a certain population are; we do expect that these definitions will be very context specific. Still, our analysis of recovery times allowed not only the calculation of statistics such as median time to recovery, but also obtaining ecologically meaningful insights from the distribution of recovery times, such as the link to seasonal dynamics (especially clear after exposure in September).

In the field of ecological risk assessment, transparent communication between regulatory and academic authorities will aid the decision-making process on acceptable recovery periods. This is especially relevant for biota in agroecosystems that may frequently be exposed to multiple stressors, as accurately defining when and at which spatial scale population, but also community, recovery should be expected, will ensure better risk assessment and agroecosystem management.

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Chapter 4

The relevance of toxicokinetic and toxicodynamic processes for the population recovery of Gammarus pulex after exposure to pesticides

Nika Galic, Roman Ashauer, Hans M. Baveco, Anna-Maija Nyman, Alpar Barsi, Pernille Thorbek, Eric Bruns and Paul J. van den Brink

Abstract

As aquatic arthropods may be regularly exposed to pesticides in edge of the field waterbodies, a correct assessment of potential adverse effects and subsequent population recovery potential is essential to ensure the sustainability of their populations. We evaluated adverse effects of four pesticides with different modes of action on the survival of *Gammarus pulex* after exposure in different scenarios. Effects on survival were calculated using dose-response relationships and the threshold damage model (TDM), which accounts for detailed processes of toxicokinetics and toxicodynamics. We developed an individual-based model of *Gammarus pulex* in order to assess the potential for population recovery after exposure to pesticides. Our results demonstrate that delayed effects calculated by the TDM have a significant impact on both individual survival as well as subsequent population recovery times. We also evaluated the assessment of effects after short-term exposures using the standardly used 96 h dose-response relationship and the TDM. Our results indicate that such practice is sufficiently protective for three of the four chemicals when exposure is shorter than 24 hours and for all when exposure is shorter than 12 hours. This study emphasizes the need to reconsider standard tests, especially for pesticides with specific modes of action, to allow for quantification of possible delayed effects.

Introduction

Populations of aquatic non-target arthropods may be exposed to pesticides in edge of the field waterbodies in agroecosystems. Exposure to pesticides may lead to adverse effects on their survival, the magnitude of which depends on intrinsic sensitivity of exposed organisms and pesticide concentration and its fate in aquatic environments. Standard toxicity tests provide information about the magnitude of lethal and/or sublethal effects across different exposure concentrations (Brock *et al.* 2010a). The results of these tests are analysed using dose-response models in order to obtain dose-response relationships that describes the occurrence of a certain response (mortality, immobility, etc.) over a range of exposure concentrations. From these dose-response relationships, statistics such as EC50 and LC50, i.e. concentration that affects or kills 50% of tested organisms, are used in first tiers of prospective risk assessment for deriving conservative “safe concentrations” and in the retrospective risk assessment to assess the toxicity of existing concentrations (SANCO 2002b). Such tests are performed at constant concentrations maintained for fixed periods of time, and are regulated within legal documents (EC 2009). The risk characterization is carried out by comparing EC or LC values with predicted environmental concentration (PEC) of the pesticide, typically expressed in a “toxicity-exposure ratio” or “risk quotient”. Even though dose-response relationships are widely used for risk assessment and comparison of potential effects across different exposure regimes and different pesticides, they are based on effects visible only within defined durations of standard toxicity studies. Consequently, they might underestimate risks since possible effects occurring after the testing period, i.e. delayed effects, are not taken into account (Reinert, Giddings & Judd 2002). Furthermore, dose-response relationships are unable to handle time-variable exposure patterns (Brock *et al.* 2010a) which can be very complex due to multiple pathways of pesticide entry into the waterbodies, making their use very limited for a more realistic ecological risk assessment.

To counter this, a modelling approach for linking exposure to lethal effects that takes into account detailed processes of toxicokinetics and toxicodynamics (Brock *et al.* 2010a) has been proposed for more frequent usage in pesticide risk assessment. Toxicokinetic-toxicodynamic (TKTD) models are dynamic models for toxic processes and simulate endpoints such as survival at the level of individual organisms or their averages in a uniform population (see Ashauer & Escher 2010 for an introduction). Toxicokinetic processes consider uptake of the pesticide from the environment into the exposed organism and elimination back to the environment, whereas toxicodynamics account for the internal processes of damage and organism recovery. More refined toxicokinetic models may also include the process of biotransformation or internal distribution of the compound. The threshold damage model (TDM) (Ashauer, Boxall & Brown 2007a) considers both toxicokinetic and toxicodynamic processes in simulating survival of aquatic invertebrates during and after exposure to pesticides and therefore, it is able to calculate pesticide toxicity that goes beyond the exposure period. The impact on survival is calculated via the hazard rate that grows above zero if the threshold for damage is exceeded (Box 1). Furthermore, it can calculate organism recovery times, it is able to account for effects of carry-over toxicity (Ashauer *et al.* 2010a) and is flexible enough to extrapolate effects across various exposure patterns (Ashauer, Boxall & Brown 2007a; Ashauer, Boxall & Brown 2007a).

Recovery of populations from exposure to pesticides is considered to mitigate the short-term negative effects of exposure, and is, thus, used as a proxy for acceptability of some adverse effects on non-target populations (SANCO 2002b), making it an important endpoint in pesticide risk assessment (Hommen *et al.* 2010). In closed or isolated systems, which lack nearby sources for colonization or refugia, population recovery is solely dependent on species reproductive life-history traits and intrinsic sensitivity of exposed individuals. In such systems, traits such as high fecundity and voltinism typically ensure quick recovery (Gardmark *et al.* 2003; Stark, Banks & Vargas 2004b; EC 2009), as they heavily influence population growth. Determining intrinsic sensitivity of a myriad of species to as many kinds of pesticides has been the central activity of ecotoxicology and pesticide risk assessment. However, the joint impact of intrinsic sensitivity and pesticide specific factors on population recovery has still not been thoroughly investigated.

Furthermore, modern pesticides typically have short half-lives (Wijngaarden, Brock & Brink 2005) and the exposure duration is often in the range of hours (e.g. in case of some pyrethroids, see Laskowski 2002), especially in flowing waterbodies such as streams. Standard risk assessment applies 96h dose-response relationships to evaluate effects of such short-term exposure on aquatic invertebrates. However, the consequences of the impact of the use of a toxicity endpoint which is based on a longer exposure period than the one that is evaluated in the risk assessment on population recovery have yet to be properly evaluated.

This study, therefore, had two aims. The first aim was to evaluate the magnitude of the delayed effects on survival of a freshwater amphipod beyond certain exposure duration, i.e. when exposure has ended, and to assess the consequences of such effects for population recovery. We addressed this aim by evaluating the effects on individual survival after exposure to concentrations equivalent to LC50 values, calculated by the threshold-damage model (TDM) (Ashauer, Boxall & Brown 2007a), in different exposure scenarios and compared to mortality calculated with a log-logistic dose-response model (see Box 1 for details on the TDM and dose-response model, and the methods section for details on deriving LC50 values). By doing so, the delayed mortality occurring after the time period for which the dose-response relationship was calculated, was assessed by the TDM. All the TDM parameters are species and pesticide specific, and the model is currently parameterized for simulating effects on survival of *Gammarus pulex* after exposure to four pesticides with different modes of action, namely diazinon, chlorpyrifos, carbaryl and pentachlorophenol (Ashauer, Boxall & Brown 2006a; Ashauer, Boxall & Brown 2007b; Ashauer *et al.* 2010a) (Table 4.2).

Box 4.1. Brief description of the threshold damage and dose-response model used in this study.

The threshold-damage model (TDM)

The TDM accounts for the processes of toxicokinetics and toxicodynamics. Toxicokinetics is described as one-compartment first-order kinetics and simulates the dynamics of internal concentration in relation to environmental concentrations,

$$\frac{dC_{\text{int}}(t)}{dt} = k_{in} \cdot C(t) - k_{out} \cdot C_{\text{int}}(t) \qquad \text{eq. 1}$$

where C_{int} is the internal concentration [amount×mass^{-1}], C is the environmental concentration [amount×volume^{-1}], k_{in} is the uptake constant [volume×mass^{-1}×time^{-1}] and k_{out} is the elimination rate constant [time^{-1}].

Toxicodynamics consists of damage accrual and organism recovery or repair of damage

$$\frac{dD(t)}{dt} = k_k \cdot C_{\text{int}} - k_r \cdot D(t) \qquad \text{eq. 2}$$

where D is damage [-], k_{k} is the killing rate constant [mass×amount^{-1}×time^{-1}] and k_{r} is the recovery or damage repair rate constant [time^{-1}].

The amount of damage will determine the hazard rate, which is the probability of the organisms dying at a given time

$$\frac{dH(t)}{dt} = \theta \cdot \max[D(t) - threshold\ ,0] \qquad \text{eq. 3}$$

where *threshold* is a threshold parameter [-] and ϑ is a proportionality constant [time^{-1}] set to one as it cannot be estimated independently of k_{k}.

If the level of damage exceeds the threshold, the hazard rate increases and impacts the survival probability, *S*(t)

$$S(t) = e^{-H(t)} \qquad \text{eq. 4}$$

Finally, individual mortalities are calculated as

$$M(t) = 1 - S(t) \qquad \text{eq. 5}$$

Dose-response model

Here we used a sigmoidal, log-logistic dose-response model to calculate individual mortality probability based on the exposure dose, i.e. concentration

$$Mortality(conc) = \frac{1}{1 + e^{b \cdot (\ln(conc) - \ln(LC50))}} \qquad \text{eq. 6}$$

where *b* is the slope of the sigmoidal function [-].

The insecticides diazinon, chlorpyrifos and carbaryl are acetylcholinesterase (AChE) inhibitors, while pentachlorophenol is a general use pesticide mostly used for wood preservation. Diazinon and chlorpyrifos are organophosphorus compounds whose oxon analogues bind irreversibly to AChE, so that recovery of AChE is only possible via de novo synthesis of AChE. Carbaryl binds reversibly to AChE and thus allows faster recovery of AChE levels. Pentachlorophenol is an uncoupler of oxidative phosphorylation, an action that is quickly stopped as soon as the compound is removed from the target site.

The second aim was to compare the effects of the use of the two models on individual survival and consequences for recovery at the population level using short exposure times. We, therefore, compared the effects on survival of *Gammarus pulex* calculated by the TDM and a, standardly used, 96h dose-response relationship in different short-term exposure scenarios.

This freshwater amphipod is an important contributor to organic material decomposition in freshwater ecosystems. Due to its relatively low resistance to hypoxia (Maltby 1995), it is extensively used as an indicator species for ecosystem health and in biomonitoring studies (Gerhardt *et al.* 1994; Maltby *et al.* 2002). Since it is relatively sensitive to various insecticides (Rubach, Baird & Van Den Brink 2010), it represents a good model organism for ecotoxicological research (see also Kunz *et al.* 2010).

Materials and methods

We developed an individual-based model, IBM, of *Gammarus pulex*, a freshwater shrimp commonly found in Eurasian freshwater ecosystems (Meijering 1971). Here we provide just a brief overview of the population model, following the ODD protocol (Grimm *et al.* 2006), while the full description of the model assumptions, structure and parameter set can be found in Appendix 4.1, and the sensitivity analysis in Appendix 4.2.

Purpose. The purpose of the IBM was to quantify the effects on survival after exposure to four different pesticides and the consequences of this reduced survival for population recovery of *Gammarus pulex*. Both the TDM and the dose-response models were implemented as different submodels to translate pesticide exposure to effects on individual survival.

Entities, variables and scales. Entities in the model were individual females and square cells representing an isolated ditch. We distinguished between a juvenile and an adult stage. Individual state variables were age [days], size [length in mm] and location [continuous X and Y coordinates] in the ditch. In addition, adult females, i.e. individuals bigger than 6.5 mm, had a counter that counted the number of realized broods.

The ditch consisted of a string of 200 cells of aquatic habitat. The state variables of cells were the mortality probability induced by the density of individuals in the cell and by exposure concentrations in different scenarios. Each cell represented 1 m^2.

The basic time step in the model was one day, whereas the TDM was modelled in five minute time steps. Simulations started on day 0 (January 1) and continued for nine years or until there were no surviving individuals left; each year had 360 days. To avoid transitional effects, populations were exposed to pesticides in the third year of the simulation, which left six simulation years for analysis.

All species- and pesticide-relevant parameters and their distributions are listed in Table 4.1 and Table 4.2, respectively. This model was implemented in the NetLogo platform v. 4.1 (Wilensky 1999), and the code will be shared upon request. The implementation of the TDM in NetLogo was verified by comparing simulations in NetLogo with a TDM implemented in ModelMaker (v4.0, Cherwell Scientific Ltd, Oxford, UK), a software platform designed for numerical simulations of dynamic systems.

Process overview and scheduling. Processes in the population model included mortality, movement, reproduction and individual growth and were scheduled in a randomized sequence. In every time step, each individual had a constant background mortality probability, but also a probability of dying due to densities of conspecifics in a local cell. Surviving individuals moved and changed positions in the simulated ditch, followed by reproduction, i.e. release of offspring from gravid females. The females were assumed to be reproducing between mid-March and end of October (see Appendix 4.1 and 4.2 for assumptions on water temperatures and reproductive activity). Those females that released their young were assumed to be fertilized again immediately. All individuals grew until they attained their maximum assigned size. Finally, individuals in treated populations had a probability of dying based on exposure to four different pesticides. This probability was calculated using a dose-response model or a TDM. All life-history parameters were constant throughout the year.

Here we described only the mortality submodel in detail, while detailed description of all other processes can be found in Appendix 4.1.

Mortality consisted of a constant background, density-dependent and pesticide induced mortality. We implemented a constant background mortality probability of 0.01 for all individuals, which translated into 1% of initial population surviving up to 540 days, as observed by (Sutcliffe, Carrick & Willoughby 1981). Density-dependent mortality assumed a negative effect on individual survival through realized densities in the local cell. Background and density-dependent mortality probability were added and their sum determined the probability of an individual dying in each time step.

Pesticide mortality

Modelled individuals were exposed to LC50 concentrations of four pesticides, in two different scenarios. Effects on survival were calculated via a log-logistic dose-response model and the TDM (Box 1). Based on the dose-response model, survival probability was calculated for each day of exposure. Because the TDM accounts for processes of uptake, elimination, damage and recovery of individual organisms, the survival probability was calculated as long as there was internal damage. Consequently, pesticide induced mortality was considered even after the exposure period. We evaluated only adverse effects on survival.

To ensure consistency between the dose-response models and the TDM, the LC50 data was generated using the TDM. If experimental LC50 data was used, there might have been a chance of introducing additional sources of variation to the model comparison. Inter-experimental variation, between the LC50 experiments and the experiments used to calibrate the TDM, would obscure the model comparison. Further, we can generate LC50 data for any desired test duration using the TDM, which was calibrated in previous studies for the four pesticides investigated here (Ashauer, Boxall & Brown 2007b; Ashauer *et al.* 2010a). The simulated survival data was then used to fit a conventional, sigmoidal (log-logistic) dose-response model for 24h, 96h and 16d (Box 1, eq. 6). From these dose-response models we derived LC50 values and slope parameters.

Thus we generated LC50 concentrations for diazinon, chlorpyrifos, carbaryl and pentachlorophenol in *Gammarus pulex* that were based on the same experiments as used to parameterise the TDM. Note that only the TDM derived LC50 concentrations were used in all our comparisons and throughout this study and will be, from here on, termed predicted LC50 concentrations.

Simulation scenarios

To address the proposed aims, we made the following scenarios:

1. Assessment of the cumulative survival probability after exposure of 24h to the predicted 24h-LC50 as calculated by the dose-response 24h-LC50 relationship. These analyses were also performed using exposure patterns of 96 h to the predicted 96h-LC50 and 16 d to the predicted 16d-LC50, which were evaluated using the 96h-LC50 and 16d-LC50 dose-response relationships, respectively. These calculations were then compared with an assessment of survival as calculated by the TDM using the same exposure regimes.

2. Assessment of the cumulative survival probability after exposure of 96h to the predicted 96h-LC50 as evaluated by the 96h-LC50 dose-response relationship. This calculation was then compared with an assessment of survival by the TDM using durations of 6 h, 12 h, 24 h and 48 h of exposure to the predicted 96h-LC50.

All these calculations were performed for all four compounds; exposure started on day 150, representing June 1st. Deriving LC50 concentrations with the TDM was carried out in ModelMaker (v4.0, Cherwell Scientific Ltd, Oxford, UK) and dose-response models were fit using GraphPad Prism (v. 4.03, GraphPad Software Inc., USA).

For practicality, from here on populations where exposure and effects were linked via a dose-response model and TDM were termed DR- and TDM-populations, respectively.

Table 4.1. Species specific life-history parameters used in the individual-based model.

	Parameter	**Distribution**	**Value**	**Unit**	**Reference**
Mortality	Background mortality probability	Constant	0.01		Estimated from Sutcliffe, Carrick & Willoughby (1981)
	μ_1, density-dependent scaling factor	Constant	0.0005	/ind	Based on Van den Brink *et al.* (2007)
Reproduction	Number of broods per female	Constant	5 or 6	broods	Hynes (1955), Welton & Clarke (1980)
Growth	Mature size threshold	Constant	6.5	mm	Adapted from Hynes (1955), Welton (1979)
	Maximum length, l_{max}	Constant	13	mm	Hynes (1955), Welton (1979), Welton&Clarke (1980)
	Individual growth rate, *r*	Constant	0.016	/day	Adapted from Sutcliffe *et al.* (1981)
	Reaching maturity, *i*	Uniform	120 - 133	days	Hynes (1955), Welton&Clarke (1980), McCahon & Pascoe (1988a)
Movement	Distance distribution	Normal	0 ± 6	m	Own estimations, based on (Elliott 2002a; Elliott 2003)

Table 4.2. Pesticide parameters, both for the TDM as for the dose-response model used to evaluate the different exposure profiles. Parameters specific only for the biotransformation of diazinon are denoted with *. All TDM parameters are obtained from Ashauer *et al.* (2007) and Ashauer *et al.* (2010). The dose-response model parameters were calculated using the TDM for respective pesticides (see text for more detail).

Parameter	Unit	Diazinon	Chlorpyrifos	Carbaryl	Pentachlorophenol
uptake rate, k_{in}	L/(kg*d)	118.9	747	23.4	89
elimination rate, k_{out}	1/d	8.464	0.45	0.27	1.76
diazoxon activation rate*	1/d	0.896	/	/	/
diazoxon elimination rate*	1/d	3.278	/	/	/
killing rate, k_k	g/(pmol*d)	0.000897	0.000047	8.5E-05	0.0000162
recovery rate, k_r	1/d	0.11	0.169	0.97	66
threshold	-	0.197	0.022	0.067	0.037
proportionality constant, θ	1/d	1	1	1	1
24 h LC50	nmol/L	1237	130.7	2882	105989
24 h slope	/	-1.852	-1.509	-1.635	-1.568
96 h LC50	nmol/L	75.13	3.449	120.1	19306
96 h slope	/	-2.784	-1.67	-2.027	-1.895
16 day LC50	nmol/L	14.25	0.2558	19.65	6880
16 day slope	/	-5.674	-2.235	-3.535	-3

Analysis of population recovery times

The model outputs from treated populations were compared with those from control populations. For the analysis of recovery times after each of simulated exposures, we used 20 replicate simulations of each of the treatments and controls. Daily abundances of 20 treated populations were compared to 20 replicates of control populations, yielding 400 recovery times. Recovery times were measured from the first day after exposure. A treated population was considered to be potentially recovered once its abundance reached or was higher than 95% of abundance of the control population. If this condition was met for five days within a ten day period, we deemed the population recovered (Galic *et al.* 2012a). The day of recovery was then noted to be in the middle of this 10 day period. All recovery time distributions are presented in boxplots, with depicted median and interquartile ranges.

Results and discussion

Modelled populations of *Gammarus pulex* exhibited eight distinct generations in the given reproductive period, limited to months between March and October (Fig. 4.1). Populations were dominated by juveniles and had relatively low proportion of adults throughout the year (also found in Welton 1979, see Appendix 4.2 for details). As the new juveniles were maturing and the overwintering adults dying, the reproductive output was, on average, smaller, and caused a distinct dip in the population size around August. By the end of the reproductive season, i.e. mid October to November, new adult females have grown and, thus, produced larger broods, causing a slight peak in population abundance (Fig. 4.1). For demonstration purposes, we also plotted a DR-population exposed for 24h to the predicted 24h-LC50 concentrations; after suppression in abundances, the population started growing, but did not fully recover by the end of the year (Fig. 4.1).

We divided the following section according to the two proposed aims.

Delayed effects on survival and consequences for population recovery

Calculations of cumulative survival probability from the different exposure scenarios yielded different outcomes for the TDM and the dose-response model (Fig. 4.2). By definition, the dose-response model yielded 50% decrease in survival in all exposure scenarios. The dose-response model was implemented in such a way that over a given exposure period 50% of the population would die and this mortality was equally spread over the entire period. The linear decrease in cumulative survival was, therefore, expected and evident (Fig. 4.2).

The TDM, however, calculated effects on survival by taking into account detailed toxicity processes that did not end with the exposure period. Decrease in survival after the exposure period was similar between the three AChE inhibiting insecticides, whereas for pentachlorophenol only limited additional adverse effects on survival were observed beyond the exposure period (Fig. 4.2).

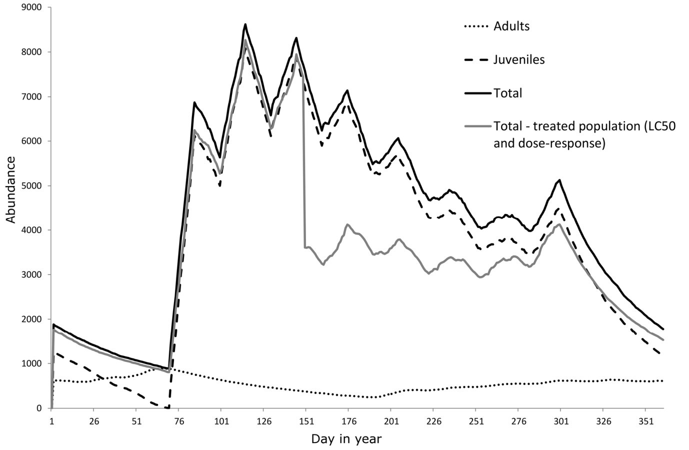

Figure 4.1. Yearly (x-axis) dynamics of control and treated *Gammarus pulex* populations, total population, adult and juvenile control abundance, and treated total populations (y-axis). Populations were exposed on Julian day 150; here showing a 50% abundance reduction in 24 hours, i.e. abundance after 24 h exposure to the predicted 24 h LC50 concentrations.

The adverse effects on individual survival were most notable for the 24 h exposure to the predicted 24h-LC50, which resulted in no predicted survival within three days after exposure for all pesticides except pentachlorophenol. 96 h exposure to the predicted 96h-LC50 concentrations of diazinon and chlorpyrifos resulted in almost no predicted survival within 20 days, whereas 96 h exposure to the predicted 96h-LC50 of carbaryl and pentachlorophenol resulted in cumulative survival probability of ca. 0.08 and 0.45, respectively. A long exposure (16 d) to the relatively low concentrations of the predicted 16d-LC50 resulted in the long-term cumulative survival probability of approximately 0.3 for diazinon and chlorpyrifos, 0.42 for carbaryl and 0.48 for pentachlorophenol.

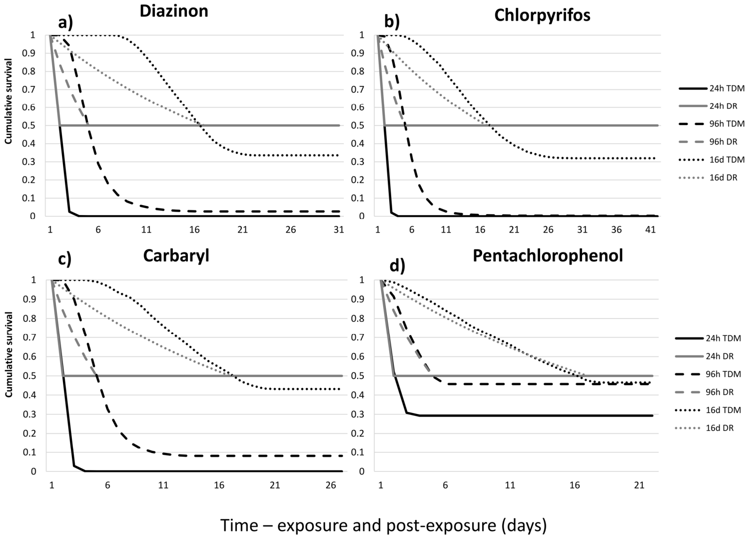

Figure 4.2. Cumulative survival probability curves calculated by the threshold damage and dose-response models for different exposure scenarios. Calculations are based on exposure to all four tested pesticides and do not include population dynamics of *Gammarus pulex*.

Interestingly, when exposure to the lower predicted concentrations, i.e. the 96h- and the 16d-LC50, was evaluated by the TDM, it took several days before the first adverse effects on survival emerged, in contrast to the dose-response model which predicted an immediate effect on survival probability (Fig. 4.2). This lag was especially visible in the case of 16 d exposure to diazinon where it took nine days after the first day of exposure for the survival to start decreasing in TDM populations. This was followed by a steep decrease in the survival probability curve and by day 21, five days after the exposure has ended, the cumulative survival was almost at its minimum, exceeding the one calculated for chlorpyrifos using the same exposure regime (Fig. 4.2). Comparison of their toxicokinetic parameters reveals that diazinon has a much lower uptake rate, k_{in}, than chlorpyrifos (Table 4.2), resulting in the time lags between the start of exposure and the time first adverse effects started occurring. However, it is the toxicodynamics that governed such a steep decrease in the survival curves, as diazinon has a higher killing rate,

k_k compared to chlorpyrifos. Out of the four pesticides, exposure to pentachlorophenol resulted in decreased survival most comparable to those calculated by the dose-response model. Pentachlorophenol has a very high recovery rate, k_r, which translates into almost immediate organism recovery as soon as the water concentrations went to zero (Table 4.2), making it the most comparable to the dose-response model which did not account for post-exposure effects.

Trends in cumulative survival observed in the different exposure scenarios propagated to similar trends in recovery of *Gammarus pulex* populations (Fig. 4.3 and 4.4). With the exception of pentachlorophenol exposure, TDM-populations always recovered slower when compared to DR-populations. The delayed effects calculated by the TDM suppressed population abundance, resulting in longer recovery times. We only showed the results of the 96 h exposure to the predicted 96h-LC50 for carbaryl and pentachlorophenol (Fig. 4.3) and the 16 d exposure to the predicted 16d-LC50 for all chemicals (Fig. 4.4) because for the other exposure scenarios the TDM calculated no individual survival (Fig. 4.2), resulting in the extinction of the modelled population due to the isolated nature of the modelled ditch. Exposure to the predicted 96h-LC50 of carbaryl resulted, according to the TDM, in less than 10% population survival and in a relatively long population recovery period, with the median time to recovery of more than 500 days, indicating that recovery occurred only at the end of the following reproductive season (Fig. 4.3). Recovery of TDM-populations after exposure to pentachlorophenol was comparable to the recovery of DR-populations (Fig. 4.3), resulting in the median value of 400 days, indicating that half of all recoveries were accomplished by the middle of the following season. Recovery of DR-populations did not differ based on the type of pesticide applied, as the dose-response model always calculated 50% decrease in survival within the exposure period. Therefore, for comparison, we plotted only one distribution of recovery times for DR-populations (Fig. 4.3).

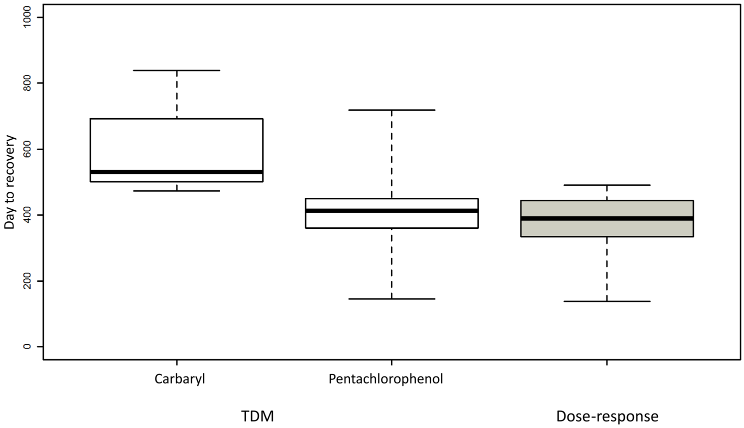

Figure 4.3. Population recovery times (y-axis) after 96 hour exposure to the predicted 96h-LC50 concentrations of carbaryl and pentachlorophenol (exposure to diazinon and chlorpyrifos resulted in population extinctions). Survival probabilities were calculated via the threshold-damage model (TDM) or a dose-response model for four pesticides (in grey). All distributions of recovery times are in boxplots, with a denoted median value and interquartile ranges.

Evaluation of the 16 d exposure to the predicted 16d-LC50 by TDM yielded recovery times that differed between the compounds and between the survival models. While the recovery times of DR-populations were exactly the same after exposure to different pesticides, for TDM-populations, median and ranges of recovery times differed between the compounds (Fig. 4.4). While medians were similar to those of DR-populations, their ranges of the distribution of the recovery time differed. The TDM calculated adverse effects for almost three weeks after the first day of exposure (Fig. 4.2) in which time the population kept on reproducing, as we did not account for any sublethal effects of different pesticides. There was, thus, constant compensation throughout the exposure period, resulting in the median time to recovery of 450 days for chlorpyrifos and 449 days for diazinon, 438 for carbaryl and 433 for pentachlorophenol, while the median day to recovery for the DR-populations was 437, indicating that 50% of treated populations recover by the end of next season. However, the ranges of recovery distributions differed, indicating that after exposure to diazinon, some TDM-populations took more than 800 days to recovery, whereas the maximum recovery time predicted using the dose-response model was 616 days.

The lower ranges of recovery time distributions after exposure to carbaryl and pentachlorophenol indicated that some of the treated populations recovered within the same season.

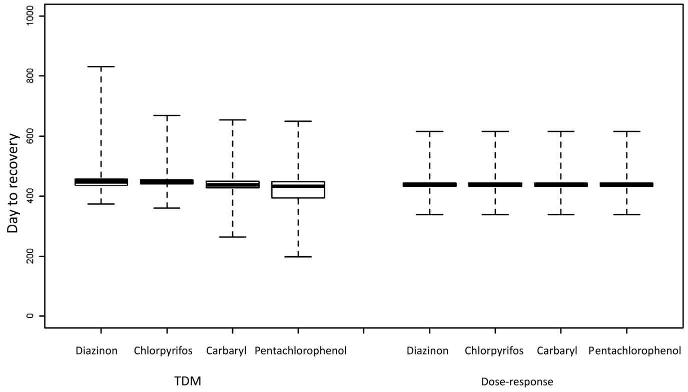

Figure 4.4. Population recovery times (y-axis) after 16 day exposure to the predicted 16d-LC50 of diazinon, carbaryl, pentachlorophenol and chlorpyrifos. Survival probabilities were calculated via the threshold-damage model (TDM) or a dose-response model for four pesticides. All distributions of recovery times are in boxplots, with a denoted median value and interquartile ranges.

Short-term exposure and population recovery

We then evaluated decreases in survival probability after exposure to six, 12, 24 and 48 hours to the predicted 96h-LC50 concentration of the four pesticides (Fig. 4.5). Exposure of only six hours resulted in decreased survival only for chlorpyrifos (stayed above 0.9, Fig. 4.5a), while doubling the period of exposure to 12 hours, yielded survival probabilities lower than 1 for all pesticides except diazinon. Survival remained above 0.9 for carbaryl and pentachlorophenol, but decreased to less than 0.7 in case of chlorpyrifos (Fig. 4.5b). Further extension of the exposure period resulted even in lower survival probabilities (Fig. 4.5c and 4.5d). However, in the case of diazinon, only exposure of 48 hours yielded a significant decrease in survival, where it decreased from 0.99 (24 h exposure) to 0.45.

Given the similarity of effects after exposure to diazinon and chlorpyrifos in different scenarios (Fig. 4.2), it would be expected that the effects on survival after short-term exposure to both pesticides would be consistent with previous findings. However, this was not the case as increasing exposure duration to chlorpyrifos consistently decreased the survival, whereas exposure to diazinon showed first adverse effects only after exposure of 24 h with a very steep increase when exposure was extended to 48 h (Fig. 4.5). The differences in the first occurrence of any adverse effects can be explained with toxicokinetics, where diazinon has a lower uptake rate, $k_{in,}$ and a higher elimination rate, $k_{out,}$ than chlorpyrifos (Table 4.2). However, the steep decrease in survival once the exposure is extended to 48 hours can be explained by the toxicodynamic process, i.e. a higher killing rate, k_k, than the one of chlorpyrifos.

Recovery of TDM-populations after short-term exposure (Fig. 4.6) followed the trends in calculated survival curves as shown in Figure 4.5, where chlorpyrifos consistently showed highest impact on survival and longest subsequent population recovery. Exposure of six hours to the predicted 96h-LC50 concentrations resulted in decreased survival only in case of chlorpyrifos. Since the survival probability remained above 0.9 (Fig. 4.5a), recovery of *G. pulex* populations was quick with a median of 21 days. However, recovery of DR-populations took much longer, with a median of 418 days, indicating recovery by the middle of the following season. Recovery of DR-populations is plotted for comparison with recoveries of TDM-populations. Please note that the recovery indicated for the DR-populations in Figure 6 is the same one as in Figure 4.3. Doubling the exposure time to 12 hours yielded longer recovery (median of 232 days for chlorpyrifos) and, almost immediate recovery, after 5 days for carbaryl and pentachlorophenol and no effects for diazinon (Fig. 4.6b).

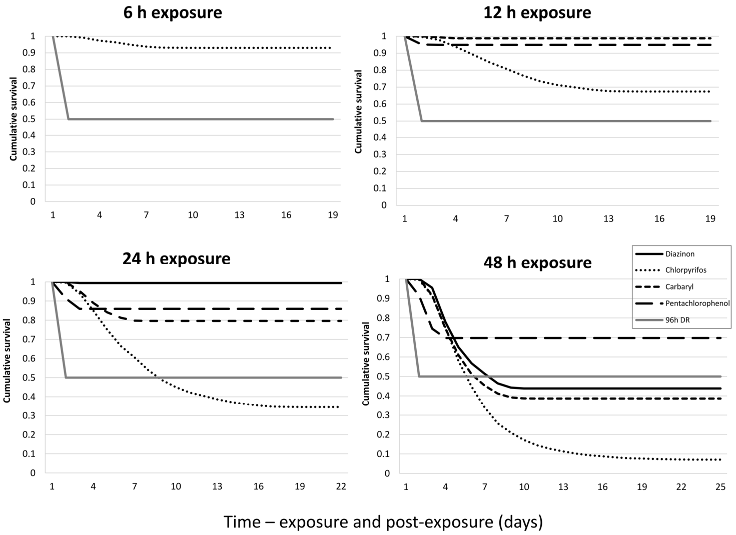

Figure 4.5. Cumulative survival probability curves calculated by the threshold damage model (TDM) for different short-term exposure scenarios, i.e. 6, 12, 24, and 48 h exposure to the predicted 96h-LC50 concentration. Calculations are based on exposure to all four tested pesticides and do not include population dynamics of *Gammarus pulex*.

Extending the exposure to 24 hours yielded longer recovery times for all pesticides (Fig. 4.6c), including first adverse effects after diazinon exposure, resulting in a median of 5 days to accomplish recovery (Fig. 4.6c). Finally, 48 hour exposure of the TDM populations to 96h LC50 of all tested pesticides, yielded longer (chlorpyrifos) or similar (diazinon and carbaryl) recovery times (Fig. 4.6d) as calculated for the DR-population, except in case of pentachlorophenol, for which TDM-populations recovered quicker (Fig. 4.6a and d). Pentachlorophenol has the highest organism recovery rate, k_r, when compared to the other three tested pesticides, which allowed quick organism recovery. Consequently, the recovery of half of the treated TDM-populations was accomplished within 200 days, whereas the recovery of DR-populations after exposure of 48 h was still at a median of 418 days. For the other three pesticides, it is the combination of toxicokinetic and toxicodynamic parameters that may explain larger adverse effects on survival (as described for diazinon and chlorpyrifos, Fig. 4.5) and, consequently, longer population recovery times.

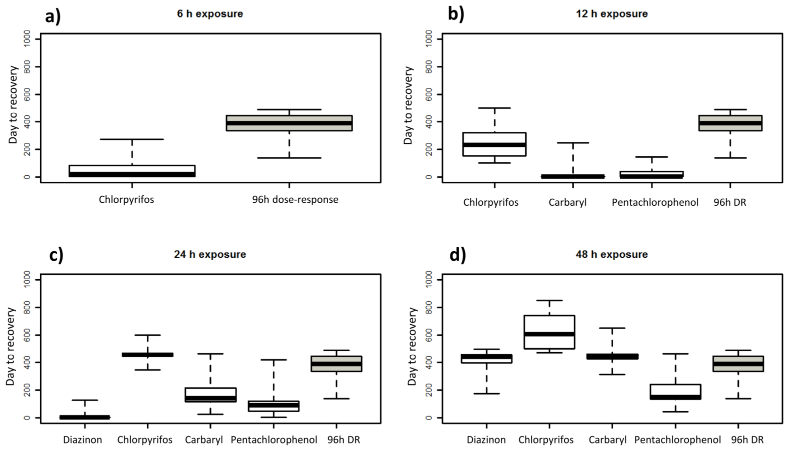

Figure 4.6. Population recovery times (y-axis) after short-term (6, 12, 24 and 48 hours) exposure to the predicted 96h-LC50 concentrations of diazinon, chlorpyrifos, carbaryl and pentachlorophenol. Recoveries of DR-populations are equal for all exposure scenarios and are plotted (in grey), for comparison, with recoveries of TDM-populations. All distributions of recovery times are in boxplots, with a denoted median value and interquartile ranges.

Populations of *Gammarus pulex* are considered to have high recovery potential due to quick colonization process governed by drifting individuals (Elliott 2002b; Maltby & Hills 2008). Liess and Schulz (1999), for instance, report a six month recovery time after the population, exposed to multiple run-off events, experiences a 50% decrease in abundances. Besides the reproductive potential by the survivors of the stress, such swift recovery, however, requires proximity of untreated parts of the landscape that serve as sources of individuals that enhance the population recovery process (Gore, Kelly & Yount 1990; Devine & Furlong 2007; Lake, Bond & Reich 2007; Galic *et al.* 2012a). In this study, we, however, assumed a closed or isolated population that was fully exposed in each scenario. This allowed us to focus exclusively on the comparison of predictions of adverse effects by the two survival models and the consequences for population recovery. Our recovery analysis, therefore, predicted relatively long recovery periods, as in such isolated systems, population recovery is based solely on surviving individuals and their offspring (van den Brink *et al.* 1995; Trekels, Van de Meutter & Stoks 2011a; Galic *et al.* 2012a). Finally, as we correct individual fecundity for modelling only female individuals, these recovery times are even further extended when compared to natural populations (Galic *et al.* 2012a) (see Appendix 4.2 for an analysis of the effects of reduced fecundity on population abundance and recovery).

Organism and population recovery

Organism recovery times differ from population recovery times as these are calculated using the TDM related to one endpoint, in our case survival, whereas population recovery times combine different life-history traits or endpoints of the species. Organism recovery times for the TDM (Ashauer, Boxall & Brown 2007a) are defined as the interval when the internal damage level falls below 5% of its maximum level after a 24-h pulse that kills 50% of the population after infinite time.

The TDM predicts 28 day organism recovery for diazinon (Ashauer *et al.* 2010a), and 25, 15 and 3 for chlorpyrifos, carbaryl and pentachlorophenol, respectively (Ashauer, Boxall & Brown 2007b). Organism recovery times are a product of both toxicokinetic and toxicodynamic processes. The TDM for diazinon explicitly simulates activation of diazinon to diazooxon, whereas the corresponding process is not simulated for chlorpyrifos, carbaryl and pentachlorophenol, because no information on biotransformation kinetics is available. The mechanistic explanation of the different values for organism recovery for the different pesticides is, thus, uncertain. The overall speed of organism recovery however is more certain, because the toxicodynamic parameters, which were fitted to survival time series, would compensate for errors in the toxicokinetic parameters (Hack 2006). Thus mechanistic interpretation of the parameter values is subject to uncertainty unless biotransformation is measured and modelled, as was done, for example, for diazinon (Ashauer *et al.* 2010b; Kretschmann *et al.* 2011a; Kretschmann *et al.* 2011b).

In our study, trends in population recovery times followed those of organism recovery times, where exposure to diazinon and chlorpyrifos yielded very similar effects on survival probability and subsequent recovery times (Fig. 4.2 and 4.4). Exposure to these chemicals yielded relatively long recovery times, compared to exposure to carbaryl and pentachlorophenol. However, the short-term exposure scenarios yielded some very interesting results, as only then the effects of the difference between toxicokinetic and toxicodynamic parameters of diazinon and chlorpyrifos on population recovery times became evident (Fig. 4.6). These results indicate, on one hand, that significant effects on survival probabilities are possible after short-term exposure to chlorpyrifos, as explained by toxicokinetics, and to a much lesser extent after short exposure to diazinon. On the other hand, once exposure to diazinon has exceeded certain duration, its toxicodynamics explain the very steep decrease in survival (Figure 4.5).

Implications for ERA

Our comparison of adverse effects of different pesticides on individual survival, calculated by the standardly used dose-response model and the TDM, and subsequent recovery of populations has potential implications for the field of ecological risk assessment of pesticides.

The TDM calculated effects on survival after 24 and 96 h exposure to the predicted 24h- and 96h-LC50, respectively, which were well beyond those calculated by the dose-response model (Fig. 4.2). Exposure to diazinon and chlorpyrifos in these two scenarios effectively left no survivors, whereas the dose-response model calculated a decrease of 50% in population abundance in all scenarios. This implies that a careful rethinking of the standard experimental setup might be necessary, where possible effects beyond the test duration should also be measured and evaluated (Reinert, Giddings & Judd 2002). Longer-term, or chronic, exposure to relatively lower concentrations (Fig. 4.4) shows that recovery of both TDM- and DR-populations is more comparable, indicating that using the dose-response model for chronic exposure might be protective for exposed biota. However, in our study, we disregarded the possibility of repeated pesticide applications, a common occurrence in agroecosystems. The three tested insecticides require relatively long organism recovery times, in absence of which accounting for carry-over toxicity (Ashauer *et al.* 2010a) will not be included using the dose-response, thus possibly underestimating adverse effects on survival.

Our results also indicate that the standard risk assessment practices are protective in short-term exposure scenarios, but only when exposure durations are relatively short (e.g. shorter than 50% of the time span used to derive the dose-response relationship, see Fig. 4.5 and 4.6). It is almost impossible to assign the differences in toxicity among the four tested compounds to one or two TDM parameters. The explanation that a high recovery rate of pentachlorophenol translates into quick organism, and population, recovery is straightforward. However, the differences in toxicity in scenarios of short-term exposure to diazinon and chlorpyrifos may only be explained with a combination of toxicokinetic and toxicodynamic parameters. The TDM predicts longest organism recovery times for these two insecticides, that marginally differ between each other (28 and 25 days for diazinon and chlorpyrifos, respectively; Ashauer *et al*., 2007c, Ashauer *et al*., 2010), and they both have the same mode of action, as they bind irreversibly to acetylcholinesterase (AChE). Exposed organisms, therefore, need to synthesize new AchE resulting in a low recovery rate, k_r, and longer organism recovery when compared, for instance, to carbaryl that binds reversibly to AChE resulting in quicker organism recovery (15 days, Ashauer *et al*., 2007c).

We, therefore, propose that in case of insecticides with specific modes of action, e.g. those that irreversibly affect the target sites, more detailed testing is conducted. Such tests should observe the toxicokinetics and toxicodynamics of the pesticide in the species of concern, in order to assess possible adverse effects on survival that occur beyond the exposure period..

The main disadvantages of TKTD models are that their parameterization is species and chemical specific, i.e. each new chemical has to be tested on a new species in a set of experiments. Currently, methods are being developed that may facilitate the extrapolation of TKTD parameters between chemicals and species (Rubach *et al.* 2010; Rubach, Crum & Van Den Brink 2011). Furthermore, different assumptions in models simulating toxicokinetic and toxicodynamic processes were brought together in the General Unified Threshold model for Survival (Jager *et al.* 2011), increasing the coherence of the field and enabling wider use for risk assessment purposes (Ashauer *et al.* 2011).

It is, therefore, expected that, in the coming years, we will gather more information about detailed toxicity processes (Ashauer *et al.* 2011), that we can integrate with the life-history traits of relevant species and evaluate their recovery potential under different exposure regimes and landscape characteristics. By developing population models, integration of different factors relevant for the assessment of the population recovery process is relatively straightforward (Forbes, Calow & Sibly 2008; Galic *et al.* 2010b; Galic *et al.* 2012b). It does, however, entail data on the life-history of the species, but also on landscape and possible inter- and intraspecific interactions (Galic *et al.* 2012a). Consequently, no matter how many challenges await, the final aim is rewarding as we are moving one step closer to a more realistic and ecologically relevant assessment of risk in the agroecosystem.

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Chapter 5

Persistence of aquatic insects across managed landscapes: effects of landscape permeability on recolonization and population recovery

Nika Galic, Hans M. Baveco, Geerten Hengeveld, Amelie Schmolke, Pernille Thorbek, Eric Bruns and Paul J. van den Brink

Abstract

Human practices in managed landscapes may often adversely affect aquatic biota, such as aquatic insects. Dispersal is often the limiting factor for successful re-colonization and recovery of stressed habitats. Therefore, in this study, we evaluated the effects of landscape permeability, assuming a combination of riparian vegetation (edge permeability) and other vegetation (landscape matrix permeability), and distance between waterbodies on the colonization and recovery potential of weakly flying insects. For this purpose, we developed two models, a movement and a population model of the non-biting midge, *Chironomus riparius*, an aquatic insect with weak flying abilities. With a movement model we predicted the outcome of dispersal in a landscape with several linear water bodies (ditches) under different assumptions regarding landscape-dependent movement. Output from the movement model constituted the probabilities of encountering another ditch and of staying in the natal ditch or perishing in the landscape matrix, and was used in the second model. With this individual-based model of midge populations, we assessed the implications for population persistence and for recovery potential after an extreme stress event. We showed that a combination of landscape attributes from the movement model determines the fate of dispersing individuals and, once extrapolated to the population level, has a big impact on the persistence and recovery of populations. Population persistence benefitted from low edge permeability as it reduced the dispersal mortality which was the main factor determining population persistence and viability. However, population recovery benefitted from higher edge permeability, but this was conditional on the low effective distance that ensured fewer losses in the landscape matrix. We discuss these findings with respect to possible landscape management scenarios.

Introduction

Human activities are changing aquatic ecosystems worldwide, by imposing multiple stressors to the aquatic compartment, either via physical alterations of the habitat, such as channelling of streams and rivers, chemical and nutrient runoff from agricultural practices, or introduction of invasive species (Dudgeon 2010). These occurrences led to severe degradation of aquatic environments, with negative consequences for ecosystem services provided for human benefit (Millenium Ecosystem Assessment 2005), such as quality potable water, biological diversity and community structure resulting in aesthetic, cultural and recreational value. To counter this trend, many of such degraded ecosystems are currently undergoing comprehensive restoration projects, with a goal of recovering the native biota, and restoring a functioning ecosystem. Unfortunately, the success rate of such projects has been quite limited (Bond & Lake 2003; Moreno-Mateos 2012). One of the desired processes in aquatic restoration projects is the recovery of the native biota, through the colonization of the restored or stressed habitat, occurring almost exclusively via dispersal of individuals from nearby areas (Bond & Lake 2003; Blakely *et al.* 2006; Trekels, van de Meutter & Stoks 2011b).

Species dispersal, therefore, has an especially vital role in ensuring population persistence across managed and disturbed landscapes. Dispersal is generally defined as moving away from the natal location or population, usually assuming crossing larger spatial scales, though the exact definition of dispersal has, however, often been left to the interpretation of different authors (Bowler & Benton 2005). Dispersal is found to be the limiting factor in many restoration efforts (Bond & Lake 2003; Blakely *et al.* 2006; Brederveld *et al.* 2011), as dispersing individuals might come across different barriers in the landscape that may limit their colonization success (Bond & Lake 2003; Blakely *et al.* 2006; Lake, Bond & Reich 2007; Spanhoff & Arle 2007). Besides physical barriers, i.e. dams, bridges or roads (Blakely *et al.* 2006), landscape connectivity (Sondgerath & Schroder 2002), and trophic constraints (Amarasekare 2007) may also limit the dispersal of the colonisers necessary to re-establish populations.

Freshwater ecosystems in managed landscapes harbour a variety of invertebrate species, where aquatic insects are one of the major contributors to overall biomass production (Huryn & Wallace 2000) and to the transfer of energy between the aquatic and terrestrial ecosystems (Jackson & Resh 1989; Chan, Zhang & Dudgeon 2007; Wesner 2010). Also, they represent one of the main successfully recolonizing taxa in streams after stress (Wallace, Huryn & Lugthart 1991).

Colonization and recovery of riverine insect populations typically follows the stream channel network, making, thus, the longitudinal connectivity essential (Wiens 2002). However, colonization of more isolated riverine systems requires lateral dispersal, i.e. across landscapes and away from the aquatic habitat (Brederveld *et al.* 2011). Many insect species are often weak, airborne flyers and seldom move laterally from their natal water body (Petersen & Winterbottom 1999; Petersen 2004; Smith, Alexander & Lamp 2009). Many species, e.g. various chironomids (Delettre, Tréhen & Grootaert 1992; Tokeshi & Reinhardt 1996; Delettre & Morvan 2000), use riparian vegetation as windbreaks (Whitaker, Carroll & Montevecchi 2000) and for completion of their life-cycles. Riparian vegetation is, thus, beneficial for the protection and persistence of individual insects (Briers & Gee 2004; Greenwood *et al.* 2011), but can, at the same time, limit lateral dispersal of those individuals that would be, for instance, otherwise carried by the wind (Delettre & Morvan 2000).

In this study we, therefore, evaluated the effects of landscape permeability, i.e. of riparian vegetation (edge permeability) and other vegetation (landscape matrix permeability), and distance between waterbodies on the colonization and recovery potential of weakly flying insects. We chose the non-biting midges, *Chironomus riparius*, as our model organisms, due to their importance in energy transfers in aquatic and terrestrial food webs (Berg & Hellenthal 1992), their global distribution and low flying capabilities. To investigate the interplay between landscape permeability, distance between water bodies, and individual movement and the consequences for re-colonization and population recovery after a stress event, we developed two models. With a movement model we predict the outcome of dispersal in a landscape with several linear water bodies (ditches) under different assumptions regarding landscape-dependent movement. The outcome of the movement model, in particular the probabilities of encountering another ditch (functional connectivity) and of staying in the natal ditch or perishing in the landscape matrix, is used in a second model. With this individual-based population model we assess the implications for population persistence (taking abundance as a proxy for viability) and in particular for recovery potential (i.e. time to recovery) after a stress event (e.g., pesticide application).

Material and methods

We developed spatially explicit models of dispersal and population dynamics of the non-biting midge, *Chironomus riparius*. Both models were programmed within the NetLogo platform (Wilensky 1999).

Dispersal model

Chironomids are considered to be relatively weak flyers, often carried by the wind (Armitage, Cranston & Pinder 1995). Chironomid dispersal usually includes three types of movement: initial dispersal after emergence to the resting site, swarming, i.e. mating, behaviour and ovipositing flight of females (Oliver 1971). In our model, we assume a single movement pattern to apply to all phases. Correlated random walks (CRW) (Barton *et al.* 2009; Hawkes 2009) combine a non-uniform distribution of turning angles with an exponentially decaying distribution of step lengths. Here we used the von Mises angular distribution (Best & Fisher 1979), i.e. a normal distribution on a circle, in which we vary the degree of angular correlation by altering the shape parameter, κ, which is the measure of concentration for this distribution and is analogous to $\frac{1}{\sigma^2}$ of a normal distribution. Smaller values of κ diffuse the distribution, while it becomes a uniform distribution at value 0, resulting in Brownian motion (also random walk). Larger values of κ result in the distribution centring more on the mean, which means that the movement will be more directed. Here we set the mean value to 0 and the value of κ to 6 (fairly correlated movement). Every time step, each adult individual was assigned a turning angle and a step from respective distributions (see Table 5.1 for details). Given the tiny size of our model organisms, we assumed one minute as a simulated time step, and a total dispersal period of 16 hours (960 minutes). Adult individuals were thus assumed to disperse only for one day.

The simulated landscape consisted of aquatic habitat, i.e. ditches, separated by the terrestrial (non-)habitat, in the following referred to as the landscape matrix (Fig. 5.1). A large number (10000) of movement paths was generated, all starting from the centre of one ditch (natal ditch in Fig. 5.1). The landscape impacted movement through edge and matrix permeability. Edge permeability refers to the probability of crossing the border between the natal ditch and landscape matrix, for a movement path that 'hits' this edge from the inside of the ditch. Note that the probability of crossing this edge in the opposite direction is set to 1. Matrix permeability refers to the extent to which the landscape facilitates movement (the reciprocal of 'resistance'), and is represented by a scaling factor on realized step size (or velocity, see above).

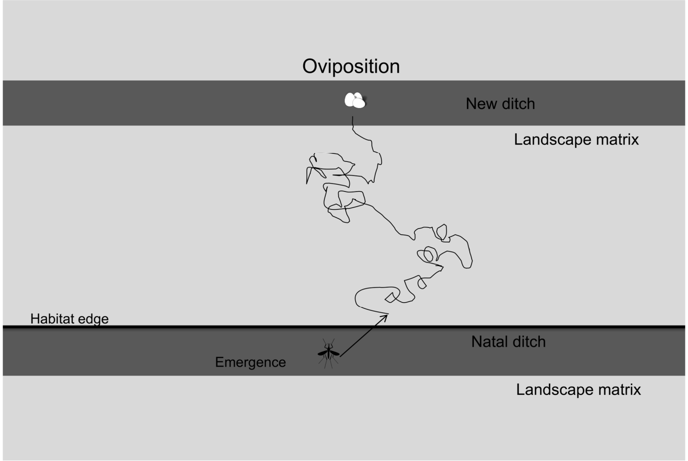

Figure 5.1. Simulated landscape in the dispersal model, consisting of the aquatic habitat, i.e. two 200 m ditches, and the landscape matrix. The distance between the ditches varies from 10 to 30 m, depending on the scenario, whereas the landscape matrix and edge permeability varied among spatial scenarios.

Movement continued for the full dispersal period, unless water (a ditch) was encountered. In that case, movement halted, but only outside the period of 'obligatory' movement, the swarming period. Dispersers that did not encounter any water at all were assumed to perish in the landscape matrix (dispersal mortality). Note that dispersers that encountered another than the natal ditch were always allowed to settle, even within the swarming period. We simulated movement for the following landscape configurations and landscape-dependent movement coefficients. The duration of the swarming period was set to 240, 480, 720 and 960 time steps. Distance between ditches amounted to 10, 20 and 30 m. Edge permeability values were 0.001, 0.005, 0.01, 0.05 and 0.1, while matrix permeability values amounted to 0.2, 0.4, 0.6, 0.8 and 1.0. Our definition of matrix permeability allowed us to combine matrix permeability and distance between ditches in one metric, effective distance (= distance / matrix permeability).

Each dispersal simulation produced three probabilities for use in the population model when run for the same spatial settings: 1) probability of staying in (or returning to) the natal ditch, 2) probability of encountering the other ditch (functional connectivity), and 3) probability of dying during the dispersal process (not encountering the aquatic habitat). In addition, for dispersers ending up in one of the ditches, from their x-coordinates one-dimensional dispersal kernels were estimated, defining the probability of covering a certain distance within a ditch. Note that given the setup for the movement model (movement starting from 1 ditch in a landscape with 3 ditches or 2 ditches with periodic boundary conditions, Fig. 5.1) the results refer to an ‘infinite’ landscape, where each ditch will have another neighbouring ditch on both sides.

Population model

Here we provide a short description of the population model processes following the ODD protocol (Grimm *et al.* 2006), while the full model description can be found in Appendix 5.1. We also provide a sensitivity analysis of the population model (Appendix 5.2).

Purpose. The main purpose of this model was to simulate the population dynamics of the non-biting midge, *Chironomus riparius*, and to evaluate the recolonization potential and population recovery after stress in relation to the landscape specific parameters.

State variables and scales. The entities of the model were the female individuals and the landscape. Chironomid females were characterized by the following state variables: age [days], developmental stage [larva, pupa or adult], body size of larvae [length in mm], reproductive status and fertility of female adults [number of offspring], dispersal status and their location [continuous X and Y coordinates].

The simulated landscape consisted of square cells on a 20x200 grid, where 400 cells represented the aquatic habitat. These cells formed two ditches, each consisting of a string of 200 cells. The state variables of ditch cells were the stress induced mortality probability and the density of individuals within once cell.

Only one ditch was subjected to stress. Treated populations were assumed to undergo extreme stress (100% mortality in the treated ditch) at day 150 (1st June); such extreme stress could represent a restoration or colonization effort of a newly built ditch.

The basic time step in the model was one day. There were 360 days in a year. The simulations ran for nine years or until there were no surviving individuals left. The first year of simulation was discarded to avoid transitional effects in the output, leaving, thus, eight simulation years for analysis. Processes in the model were executed in a prescribed order, but randomly within the population. All parameters and their distributions are provided in Table 5.1.

Process overview and scheduling. The model included different processes for different life stages of a chironomid population. Here we described the basic life-history as implemented in the model.

Only female individuals were modelled. The life-cycle started with the larval stage, which contained an inactive phase, mimicking the egg life stage (five days). Active larvae grew according to a temperature-dependent von Bertalanffy growth function (von Bertalanffy 1957). Once the larvae reached their maximum size, they pupated and stayed in this stage for two days after which individuals emerged as adults. Based on the dispersal simulation results (thus depending on ditch distance and landscape permeability values), dispersing adults had a probability of staying in the natal ditch, of moving to the other ditch and of dying in the landscape matrix. If an adult female was successful in dispersing (found a suitable aquatic habitat), she deposited a certain number of eggs/inactive larvae; the number of eggs/inactive larvae was drawn from a uniform distribution, the number of which was corrected for modelling only females (assuming 1:1 sex ratio). From here, the life-cycle started from the beginning.

Density-dependence

Including density-dependent mortality is an indirect way of modelling resource competition, as we do not explicitly account for resource dynamics in the population model. Chironomid populations are weakly regulated by their densities; populations can attain very high densities before density-dependent consequences are visible. (Pery *et al.* 2002) show that individual growth is hampered by increasing densities in their experimental system, with first effects visible at 10 individuals per beaker (14 cm^2).

In the population model, a linear increase in mortality was assumed (based on Van den Brink *et al.*, 2007, see Appendix 5.1 for more detail). This was based on the density of individuals within one cell where each individual had a certain effect on its conspecifics, governed by the mortality scaling factor (Table 5.1).

Temperature-dependent growth

Water temperatures, an exogenous process, were used as an input to our population model, and were based on year round data collection from ditches in the Netherlands (personal communication A. Veraart). Temperatures changed on a daily basis, but were kept equal for all cells in the modelled landscape, and no interannual variation was assumed (see Appendix 5.1 for more details). The growth function of larvae was set up in such a way that the increment in individual size (mm) exponentially increased with rising water temperatures (adapted from Lactin *et al.* 1995), with a maximum increment at a water temperature of 24° C (Pery, Mons & Garric 2004; Eggermont & Heiri 2011). Since the temperatures governed larval growth which regulated the generation time, the number of generations in one year was an emergent property of the model (the analysis of the temperature dependency is described in Appendix 5.2).

Table 5.1. Life-history parameters of *Chironomus riparius* used in the individual-based model and the CRW parameters from the dispersal model.

Submodel	Parameter	Distribution	Value	Unit	Reference
Mortality	background larval mortality probability	constant	0.0007	/day	Calibration estimate; also expert opinion
	adult lifespan	constant	1	days	Adapted from Downe (1973) and Charles *et al.* (2004)
	μ_1 - density-dependent mortality factor	constant	0.005		Based on Van den Brink *et al.* (2007)
Growth	gamma	constant	0.095	/ day	Calibration estimate; based on ca 15 days that it takes to reach maximum size of larvae before pupation
	female max size	constant	13.72	mm	Pery *et al.* (2002)
	initial larval size	normal	mean 0.002, SD 0.0001	mm	Adapted from Pery *et al*. (2002)
Duration of different stages	egg stage	constant	5	days	Expert opinion; adapted from Charles et al. (2004), Oliver (1971)
	pupal stage	constant	2	days	Expert opinion; adapted from Charles et al. (2004)
Reproduction	fecundity	uniform	50-150	eggs	Adapted from Pery et al. (2002) and Ducrot *et al.* (2004); corrected for modelling only females, assuming 1:1 sex ratio
Dispersal	turning angles	von Mises	mean 0, κ 6	°	Own estimation
	step length	exponential	mean 24	cm	Own estimation

Analysis of population recovery times

The model output from populations exposed to stress was compared with that from control populations. For the analysis of recovery times after each of simulated exposures, we used 20 replicate simulations of treatment and control. Daily abundances of 20 treated populations were compared to 20 replicates of control populations, yielding potentially 400 recovery times. A treated population was considered to be recovered once its abundance reached or was higher than certain percentage (default 95%) of abundance of the control population; if this condition was met for five days within a ten day period, we deemed the population recovered. The day of recovery was then noted to be in the middle of this 10 day period.

Results

Dispersal model output

Landscape-dependent movement parameters governed the dispersal and spread of individuals in the simulated landscape (Fig. 5.2). When effective distance was kept constant, lower edge permeability resulted in linear dispersal along the natal ditch, whereas increasing the edge permeability resulted in individuals moving through the landscape matrix. The distances covered by moving individuals were enhanced with the increase of the swarming duration (Fig. 5.2).

Dispersal simulations yielded individual probabilities of successfully colonizing the other ditch, dying in the dispersal process and the probability to remain in or return to the natal ditch (Fig. 5.3). Colonization probability increased mainly with smaller effective distance and higher edge permeability (Fig. 5.3a), but also slightly with increasing swarming duration. Mortality consistently increased with increasing edge permeability and effective distance (Fig. 5.3b), but also reached a higher level with longer swarming duration. With low edge permeability, mortality was low as most individuals were retained in their natal ditch. With small effective distances, dispersers always encountered a ditch (either the natal one or the other ditch). The probability of ending up in the natal ditch was consistently high for low values of edge permeability, but steadily decreased with increasing swarming duration (Fig. 5.3c). The increase of effective distance had less effect on the probability of staying, as it was mainly the edge permeability parameter that governed the process of leaving or staying in the natal ditch. However, in case of permeable edges, the probability of staying in the natal ditch was very low for small values of effective distance (Fig. 5.3c), due to the fact that the other ditch trapped many dispersers (interference between patches).

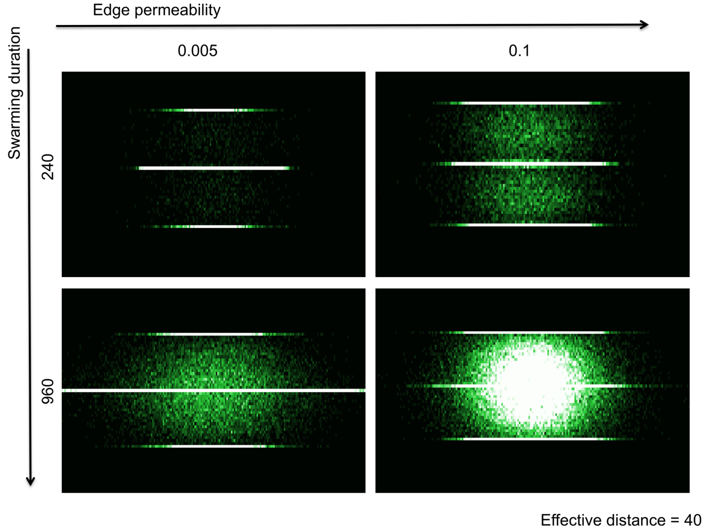

Figure 5.2. Density plots of individuals dispersing in a landscape where effective distance was kept constant. Lighter colours depict higher densities (black cells harbour zero individuals). Low edge permeability limits dispersal outside of the natal ditch, whereas increasing the edge permeability and swarming duration allows individuals to laterally disperse.

Midge population dynamics

Midge populations exhibited trivoltine yearly dynamics, i.e. had three generations (Fig. 5.4); population voltinism was based on the yearly water temperature measurements in the Dutch ditches (see Appendix 5.1 for details on temperature dependent growth). The population was dominated by larvae, abundances of which were controlled with density-dependent mortality; the larval dynamics curves overlapped with those of the total population (Figure 4).

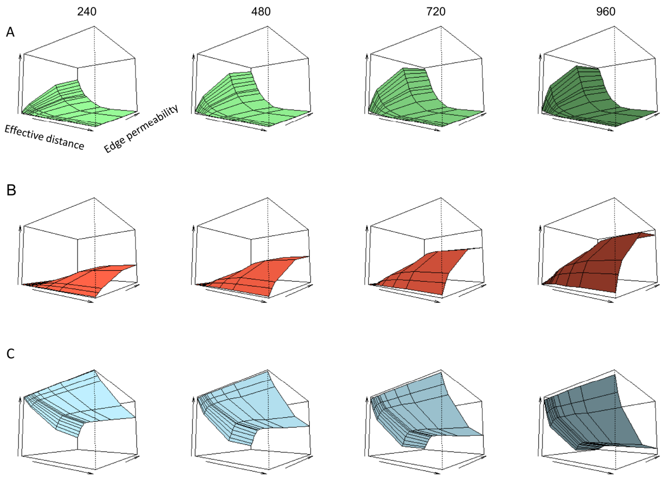

Figure 5.3. Dispersal model output, i.e. a) probability of colonizing the new ditch, b) probability of mortality in the terrestrial habitat and c) staying in the natal ditch (z-axis; not labelled for better visibility of axis values). The probabilities are dependent on the landscape attributes. The surface plots of the output are separated on the basis of the duration of the swarming movement, i.e. dispersal before individuals are allowed to settle in an aquatic patch. Values on z-axes in all surface plots are from 0 to 1.0. Effective distances are plotted on the x-axis and span from 10 to 150 m, while the edge permeability values are plotted on the y-axis and span from 0.001 to 0.1 (see text for more details).

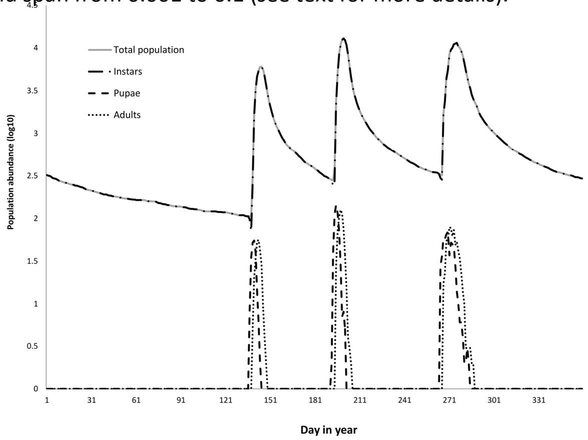

Figure 5.4. Simulated yearly dynamics of midge populations, life stages are distinguished. Abundances (y-axis) are log-transformed; larvae make up most of the total population, their abundances, thus, overlap with the curve depicting the dynamics of the total population.

Because the dispersal parameters affected the abundances of modelled populations, we show here the median abundances for a range of landscape parameters evaluated in the dispersal model (Fig. 5.5). The values in the surface plots were averaged over daily abundances of eight years of simulation and over 20 (reference) replicates.

Medians showed the same pattern as observed for survival probability (1 – mortality, see figure 3b). Combinations of landscape and movement attributes that lowered dispersal mortality risk consistently lead to higher (median) abundances. Higher mortality not only lowered abundances (Fig. 5.6), but also lead to lower population viability, as after a certain mortality value (ca. 0.4), populations became extinct.

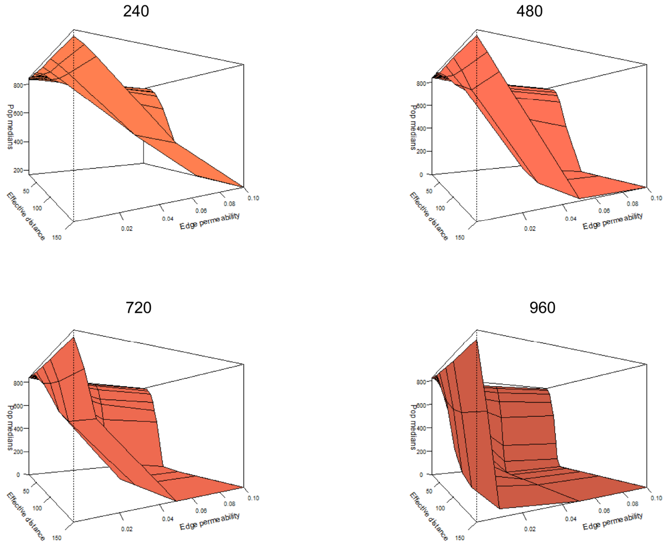

Figure 5.5. Medians of the total population abundance averaged over daily abundances of all simulation years and over 20 reference replicates, and based on evaluated landscape parameters in the dispersal model. Each of the surface plots represents a different duration of the swarming movement, i.e. dispersal before individuals are allowed to settle in an aquatic patch

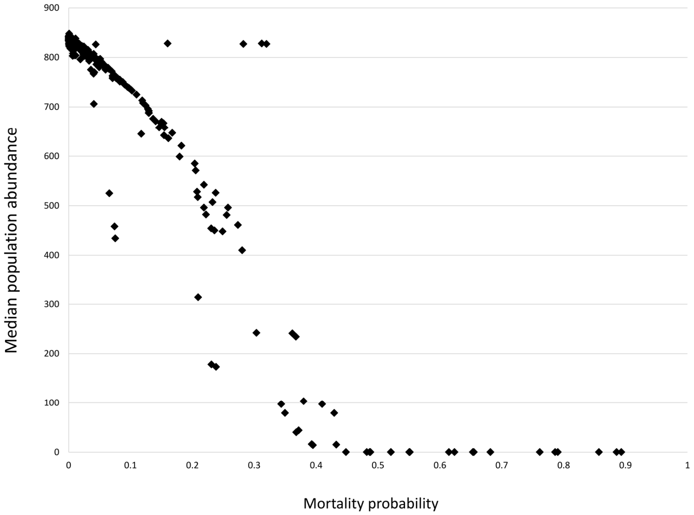

Figure 5.6. Realized median population abundances based on dispersal mortality. Most simulated populations became extinct when dispersal mortality amounted to 0.4.

Midge population recovery

Median time to recovery was shorter for high edge permeability and low effective distance (Fig. 5.7, note that the perspective of the surface plot is opposite than in other figures). Longer swarming duration further lowered the median recovery times. In a large part of the parameter space, with low edge permeability and/or high effective distance, no recovery was observed (median time longer than simulation duration).

Discussion

As dispersal appears to be the limiting factor for colonization of stressed habitats, thus hampering the success of many restoration projects (Blakely *et al.* 2006; Brederveld *et al.* 2011), we evaluated different landscape attributes governing the dispersal and colonization potential of organisms.

Our results apply to any organism living in linear habitat elements, with limited dispersal ability, a period of obligatory movement, and running a considerable risk when venturing out of its reproduction habitat. We capture the main effects of landscape on movement, by accounting for a) a possible reluctance to leave the reproduction habitat (mediated by properties of e.g. vegetation at the interface between habitat and landscape matrix) (Jackson & Resh 1989; Petersen & Winterbottom 1999; Delettre & Morvan 2000; Delettre 2005), b) effect of landscape matrix properties (e.g., vegetation, land-use) on movement, summarized in a possible slowing down of movement (smaller step length, lower velocity), and c) the distance between linear habitat elements (patches).

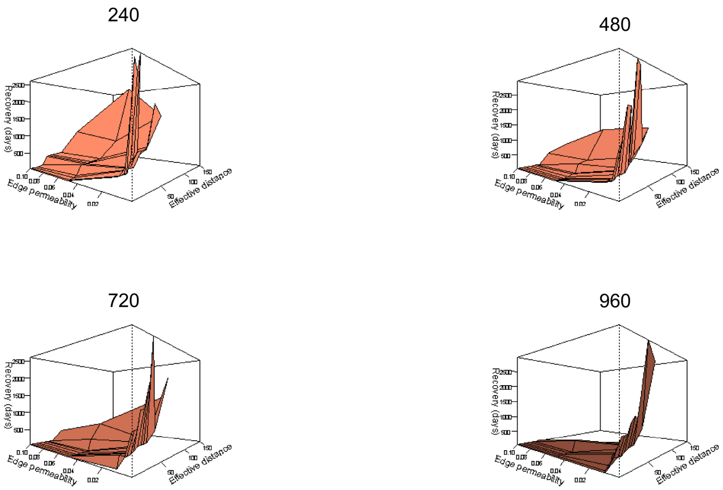

Figure 5.7. The time to recovery of successfully recovered populations. Surface plots represent a different duration of the swarming movement, i.e. dispersal before individuals are allowed to settle in an aquatic patch.

Our results show that the combination of these three factors (where distance and matrix permeability can be collapsed into one metric, effective distance), determines the fate of an individual disperser. Individual fate can be summarized in three probabilities that are relevant at the (meta)population level, being the probability to end up in another habitat patch (ditch), to end up at another location in the same patch, or to perish in the landscape matrix. Though the differences in the outcome in terms of individual fate may not seem that large, with the population model we show that for the (meta)population the balance between the probabilities of reproducing “here”, “there” or “not at all”, has a huge impact on its abundance, viability and recovery capacity. The main insight from the dispersal model is, therefore, that all three probabilities may vary widely depending on movement and landscape attributes, and none of them can be ignored in (spatial) population modelling of this type of organism (Elkin & Possingham 2008).

The population model shows that (meta)population size (abundance) is highly affected by dispersal mortality (Fig. 5.6). The balance between reproduction and mortality can shift in such a way as to lead to local populations with a high risk of going extinct, even in absence of any stress. Though this also implies that extinction risk for the whole metapopulation will increase, we should be aware that in reality metapopulation extinction risk depends on the number of patches (ditches) in the metapopulation (Bulman *et al.* 2007) – while we address only the situation with two patches. The population model output revealed that movement and landscape attributes can make out whether a population thrives in a landscape or not, and that this is mainly mediated by dispersal mortality risk.

The way we defined the stress event, as an extermination of one of the local patch populations, implies that for recovery both re-colonization of the empty patch and growth of the re-established population are required. Re-colonization chances are high (Fig. 5.3a) when effective distance between patches is low and edge permeability is high (or at least, not too small), i.e. when functional connectivity was high, which was consistent with many studies (Caquet *et al.* 2007; Elkin & Possingham 2008; Bowler & Benton 2009). Population growth rate, resulting from the balance between reproduction and mortality, was largely determined by dispersal mortality, and thus highest when mortality was low (Fig. 5.5 and 5.6), for low effective distance and/or low edge permeability. This implies that very closed landscapes, those with thick riparian and other vegetation, harbour high insect densities (Whitaker, Carroll & Montevecchi 2000; Briers, Cariss & Gee 2002).

As a result of recolonization chance and population growth rate, recovery times are, thus, expected to be shortest for the intersection of these areas in parameter space. Figure 5.7 shows that for the combination of low effective distance and edge permeability above a threshold value, recoveries do not take long. This likely bears witness to an overweighing importance of re-colonization in the recovery process (Elkin & Possingham 2008; Brederveld *et al.* 2011).

Landscape management

Management of riparian vegetation is one of the priorities in many restoration projects (Briers & Gee 2004; Dudgeon *et al.* 2006; Greenwood *et al.* 2011) as it benefits the biodiversity and ecosystem functioning (Hladyz *et al.* 2011). However, such vegetation also represents a barriers for lateral dispersal thus limiting colonization potential of many species (Delettre & Morvan 2000; Blakely *et al.* 2006; Smith, Alexander & Lamp 2009), as was also shown in our study. We showed that, for the type of organism we modelled, landscape management aiming at high population abundances (Fig. 5.6) should either promote a (very) low effective distance between habitat patches, OR a (very) low edge permeability, e.g. through riparian buffers. In other words, it should aim at impeding insect movement into the landscape matrix by impermeable edges, unless ditches are quite near to each other and the matrix is highly permeable.

On the other hand, if fast recovery of local populations is the main aim of landscape management, re-colonization is the key process and low effective distance AND high edge permeability are the factors promoting it. Thus, highly permeable edges, a permeable matrix and short distances are the aspect to focus on.

Our simulation study assumes landscape attributes that are constant throughout the year, whereas many environments are seasonal. Consequently, the landscape matrix permeability may also vary within a year, e.g. in the thickness or height of the vegetation cover. In seasonally dynamic landscapes, aquatic insects have been found to disperse further in the landscape matrix early in the season, whereas thicker vegetation in other parts of the season retains many individuals closer to their natal habitats (Delettre & Morvan 2000). These findings are comparable with our results where the combination of landscape attributes, through impermeable edges and landscape matrix, benefitted population abundance or, though increased functional connectivity and edge permeability, benefitted dispersal. However, a more thorough analysis of this phenomenon was beyond the scope of this study, but still remains an interesting research question.

In conclusion, we showed that a combination of landscape attributes determines the fate of dispersing individuals. Once the individual probabilities to stay in the natal habitat, colonize a new habitat or perish in the landscape matrix are extrapolated to the level of a population, the balance between reproduction and dispersal mortality will have a big impact on population persistence. Furthermore, population persistence and population recovery benefit from landscapes where the effective distance between reproductive habitats is very low. However, the level of edge permeability will benefit either persistence (low permeability) or recolonization and recovery (high permeability). Aims of landscape management may, therefore, need to be carefully considered and defined.

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Chapter 6

The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems

Nika Galic, Amelie Schmolke, Valery Forbes, Hans M. Baveco and Paul J. van den Brink

Abstract

Agricultural practices are essential for sustaining the human population, but at the same time they can directly disrupt ecosystem functioning. Ecological risk assessment (ERA) aims to estimate possible adverse effects of human activities on ecosystems and their parts. Current ERA practices, however, incorporate very little ecology and base the risk estimates on the results of standard tests with several standard species. The main obstacles for a more ecologically relevant ERA are the lack of clear protection goals and the inherent complexity of ecosystems that is hard to approach empirically. In this paper, we argue that the ecosystem services framework offers an opportunity to define clear and ecologically relevant protection goals. At the same time, ecological models provide the tools to address ecological complexity to the degree needed to link measurement endpoints and ecosystem services, and to quantify service provision and possible adverse effects from human activities. We focus on the ecosystem services relevant for agroecosystem functioning, including pollination, biocontrol and eutrophication effects and present modelling studies relevant for quantification of each of the services. The challenges of the ecosystem services approach are discussed as well as the limitations of ecological models in the context of ERA. A broad, multi-stakeholder dialogue is necessary to aid the definition of protection goals in terms of services delivered by ecosystems and their parts. The need to capture spatio-temporal dynamics and possible interactions among service providers pose challenges for ecological models as a basis for decision making. However, we argue that both fields are advancing quickly and can prove very valuable in achieving more ecologically relevant ERA.

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Introduction

The world's ecosystems are increasingly under pressure from various anthropogenic activities. For instance, agriculture is essential for sustaining the human population, but also directly disrupts ecosystem functioning (Power 2010). Some of the impacts associated with intensive agricultural practices include the conversion of natural habitats into agricultural fields, adverse effects of pesticides on non-target organisms through chemicals and nutrient runoff into adjacent water bodies. Ecological risk assessment (ERA) is a process that estimates potentially adverse effects and risks, to ecosystems or their components, from human activities and multiple human-induced stressors (Munns 2006). Theoretically, ERA is not limited to any specific activity, yet traditionally it has focused mostly on the assessment of adverse effects caused by toxic chemicals. Pesticides, for instance, are chemicals designed to be highly toxic towards specific organisms and are deliberately and regularly introduced into the environment. As such, they have to go through an extensive risk assessment process, including the provision of large toxicity datasets, to ensure minimal risks to the ecosystems and their biota (Hommen *et al.* 2010). Accordingly, this group of chemicals receives a lot of attention and an accompanying body of legislation that regulates its use in the environment. In Europe, current pesticide risk assessment is a tiered approach that, in its first tiers, focuses on measuring adverse effects from specific chemical compounds on a handful of chosen species, thought to represent the most sensitive species in the environment (SANCO 2002a; EC 2009).

In spite of its name, ecological risk assessment involves very little, if any, ecology because ecological data, such as species' life-history traits, population structure, density-dependent regulation, species composition and interactions, landscape structure etc., are commonly ignored (Van den Brink 2008; Forbes *et al.* 2009). Furthermore, the choice of standard test species is usually governed by practicality, i.e., geared towards species that are easily cultured in laboratories, such as *Daphnia* sp. and zebra fish. Neither the relation between the well-being of these species and the targeted ecosystem is well understood, nor do they represent the most vulnerable species in ecosystems. Accordingly, current ecological risk assessment is neither firmly based on scientific knowledge about ecosystems or their components, nor does it define ecologically relevant protection goals, although both aspects are required by European legislation, and are aspired to by experts in the field. Two main obstacles that prevent more ecologically relevant risk assessments are the lack of definition of concrete protection goals and the complexity of ecosystems that usually lies beyond feasible empirical testing.

Application of the ecosystem services concept as a basis for environmental management has gained momentum in recent years and offers promise as a valuable tool for setting meaningful ecological protection goals. Ecosystem services are the benefits people obtain from ecosystems and can be influenced directly or indirectly by drivers of change (Millenium Ecosystem Assessment 2005). Examples of indirect drivers are demography and policy while examples of direct drivers are land use and climate change. In this paper we show that models are not only very suitable for describing the mechanistic relationships occurring within ecosystems but also for how these relationships can be influenced by (external) drivers.

Ecological models have the potential to address the other problem that hinders ecologically relevant risk assessment: the inherent complexity of ecosystems. Modelling approaches may help overcome limitations of currently applied approaches to ecological risk assessment (Forbes *et al.* 2009; Thorbek *et al.* 2009; Galic *et al.* 2010a) as they allow the inclusion of both intrinsic sensitivity to a toxicant and various relevant ecological factors in a single study. Modelling studies allow for investigation of the impacts of various stressors on ecosystem components relevant for ecosystem services, and permit analysis at larger spatial and temporal scales than can be done experimentally. Subsequently, through extensive scenario testing, they can help to identify situations where risks are relatively higher (or lower) and thereby facilitate more efficient use of resources and identification of efficient mitigation measures. Such extended scenarios cannot be approached experimentally in practice, but are essential if larger ecosystem components, rather than individual organisms, are the focus of study.

In the following paragraphs, we briefly introduce the concept of ecosystem services and identify services relevant to ERA with a special focus on agroecosystems. Ecological modelling has been applied in the context of ERA and several different modelling approaches are available. After providing a short overview of the approaches, we discuss how models can be of particular value if ecosystem services are the protection goals of ERA. We provide three prominent examples of ecosystem services that are commonly affected by agricultural practices. We conclude the paper with a discussion of the challenges and give an outlook on potential future directions for research and legislation.

1.1 Ecosystem services framework

Hommen *et al*. (2010) reviewed European legislation related to chemical use and showed that environmental protection goals are very broadly and vaguely defined, mostly stating that "no adverse effects on the environment or species" should occur. This has usually been interpreted as protecting exposed populations, rather than individuals. However, in some cases the protection of individuals, such as vertebrates, or of specific ecological functions (e.g. water quality in rice paddy systems), instead of biodiversity parameters, are of interest (SANCO 2002a; Hommen *et al.* 2010). Recently the European Food Safety Authority (EFSA) suggested a new, more comprehensive approach for setting protection goals against adverse effects of pesticides using the ecosystem service framework (EFSA PPR 2010).

Ecosystem services (ES) are, in essence, functions of and provisions from ecosystems that are useful for and available to humans. The concept was first elaborated by Daily (1997) and Costanza *et al.* (1997), and its application in environmental policy was fostered by the Millennium Ecosystem Assessment project (Millennium Ecosystem Assessment, 2005). In the assessment, four main groups of services are distinguished, namely provisioning services, e.g. food, water, fibre and fuel; regulating services that include air quality, erosion, disease, pest regulation etc.; cultural services that pertain to non-material benefits such as recreation, cultural and religious values, and cultural heritage; and supporting services that provide a basis for all other services, and include processes such as photosynthesis and primary production, nutrient and water cycling. Some services can be provided by multiple ecosystems, and the same ecosystem provides multiple services; both of these issues are important since maximizing one service is likely to result in trade-offs on other services. For a more comprehensive and global analysis of the ecosystem services concept and ecosystems in general see the website of the RUBICODE project (www.rubicode.net, last accessed 15.01.2011.).

In agroecosystems, several services are essential for proper functioning of the system, but at the same time they can be negatively affected by standard agricultural practices (Power, 2010). These include pest control, pollination, nutrient cycling, soil structure and fertility, water provision, carbon sequestration and (genetic) biodiversity.

Most services are not typically delivered by an ecosystem as a whole, but rather by its distinct parts. This notion led to the introduction of the concept of service providing units (SPU) (Luck, Daily & Ehrlich 2003), that represent populations of species that provide the service at a certain temporal or spatial scale. This concept allows a direct link between the service and the part of the ecosystem that provides it to be made (Luck, Daily & Ehrlich 2003), where changes in the characteristics of a given SPU have consequences for service provision. The exact definition and extent of an SPU varies with the type of service and can be anything from a local population or community of species to a global distribution of a specific species. Kremen (2005) elaborates on this concept by introducing ecosystem service providers (ESP), covering the diversity of functions and traits found in populations, communities, and spatially or temporally disjunct networks that are necessary for service delivery.

In conclusion, the ecosystem services framework offers a different way to formulate protection goals that is especially relevant for ecological risk assessment. Rather than basing all our actions on practicality and several hand-picked species, the ES concept facilitates the identification of key services and service providers for a specific system. These key services can therefore be the focus of protection, i.e. protecting the service protects its providers. The spatio-temporal identification of the key services and service providers that will represent the protection goals of ERA will have to be conducted by scientists, regulatory authorities, industry, NGOs and other stakeholders working in collaboration.

Here we argue that well-chosen ecological models can be powerful tools to improve the links between what we measure in ERA and what we want to protect, using ecosystem services as specific protection goals.

1.2 Ecological models in ERA

All models, including ecological models, are by definition a simplification of reality, designed to study a given system. Historically, they were used for investigating ecological phenomena and were mainly developed by theoretical ecologists (starting with Malthus, 1798). Their assumptions can be tested in different scenarios, and thus, ecological models can foster mechanistic understanding of ecosystems and their parts.

Ecological models can encompass different levels of biological organization: from individual, population, metapopulation, community to ecosystem, and they can be spatially implicit or explicit. Complexity and amount of detail may be varied depending on the type of question under investigation. As a consequence of increasing computer power, it is becoming more and more feasible to incorporate larger spatial and temporal scales and to include more detail into ecological models. Combination of both biological and spatial dimensions can be necessary for specific questions, and the level of integrated detail depends on the system and the desired output of the model.

Ecological models of various spatial and biological resolution have been used for ecological applications, e.g. in the fields of conservation biology, wildlife and fisheries management (e.g. Starfield, 1997). In such applied fields of research, ecological models are increasingly used to predict future behaviour of tested systems. Some modelling studies are developed for projections beyond available datasets, where the consequences of multiple, e.g. chemical exposure or harvesting, scenarios are evaluated in terms of their effects on growth, abundance, structure, or some other population, community or ecosystem, characteristic in the future. Models used for such predictive purposes often require much more mechanistic understanding of the system, i.e. they include knowledge and assumptions about the functioning and underlying processes of the whole system and its parts. In order to confirm the suitability for the specific context, such models typically have to go through multiple comparisons with empirical data to test whether patterns observed in the model output are comparable with patterns observed in the field (Grimm *et al.* 2005).

In the realms of ERA, the added value of ecological models in obtaining more realistic assessments of risk has been argued (Forbes, Calow & Sibly 2008; Forbes *et al.* 2009; Galic *et al.* 2010a; Wang & Grimm 2010; Schmolke *et al.* 2010a). Several different modelling approaches have been applied specifically to questions related to chemical risk assessment (Galic *et al.* 2010a; Schmolke *et al.* 2010a); their development and use are not, however, restricted to the field of ERA. Differential equation models are typically used in simple assessments of unstructured population growth under different conditions or in more biologically complex systems, such as food web or ecosystem models, where the functional groups are assumed to be biologically unstructured. In matrix models, populations are divided into relevant classes (age, stage, size etc.) with class-specific survival and fecundity schedules. Matrix models are especially popular in chemical risk assessment studies, as they allow extrapolation of toxicity data available for different life stages of an organism to the dynamics of a population and also project population growth into the future, under the assumption that relevant life-history traits remain the same. Relatively straightforward sensitivity analysis, i.e. elasticity analysis, is based on matrix algebra and gives direct insight into the relative contribution of class-specific life-history traits to the overall population growth rate. In cases where more detail on the behaviour of individuals is relevant, individual-based models can be used. In typical pesticide risk assessment studies, the level of model complexity will depend on the population-level endpoint that needs to be assessed, whether the model is protective or aims toward more accurate prediction, and also on the extent to which conclusions drawn from the model are intended to be general rather than system specific (Forbes, Calow & Sibly 2008). All of the model types described above can be combined with explicit consideration of space for an assessment of effects of chemicals across spatial scales.

2. Ecological models for the assessment of ecosystem services

Ecological models are valuable tools that can be applied to achieve more ecologically relevant risk assessments, and that seem to be gaining in importance in this field (Grimm *et al.* 2009). However, models have to be developed around specific questions, in the context of ecological risk assessment, and to address particular protection goals. Current protection goals as specified in relevant legislation are not specific, but phrased in general terms that aim to keep impacts “acceptable” (Hommen *et al.* 2010). Application of the ecosystem services framework allows the general legislative protection goals to be translated into entities that can be quantified and hence modelled. More details on how this process can be implemented, using mostly pesticides as an example, can be found in other contributions within the Special Issue.

After a clear protection goal, i.e. service, has been defined, relevant service providers have to be determined, and their role in the service has to be understood and quantified. This will make data collection in the field necessary, but model approaches can greatly help in this venture by making the data collection more focused. The major assets of ecological models are the quantification of the service contribution by a service providing unit and quantification of the effects that various human activities have on these units. For instance, the service of biocontrol is delivered by a number of species belonging to related and unrelated taxonomic groups. Population models describing various bird, insect and spider species have already been developed and used to explore how changes in population dynamics can influence biocontrol and how human activities alter the population dynamics of the modelled species (e.g. Sherratt & Jepson 1993; Thorbek & Topping 2005; Topping *et al.* 2005). If the contribution of one specific species outweighs all the others, we can focus on modelling the population dynamics of that species. In case the contribution of several species to the same service provision is more or less equal, it will be hard to find modelling studies quantifying respective contributions of all service providers. Specific endpoints of a modelling study will depend on the service, service provider and relevant anthropogenic activity that is being assessed, e.g. seasonal abundance dynamics might be of relevance or the spatial distribution of the provider in a given region. Judgments will also have to be made about how detailed our quantification needs to be and the extent to which it is sufficient to have rough estimates of particular responses so that risks can subsequently be assessed. In some situations it might be sufficient to estimate the risk of an effect resulting in 50% mortality of a biocontrol agent that suppresses the pest populations by 20%. In other situations, more detailed and possibly multidimensional risk maps might be needed.

Quantification of service contributions facilitates a dynamic economic appraisal of service providing units. Research on the valuation of ecosystem services had been increasing in the last decade (Fisher, Turner & Morling 2009). Adding a monetary value to a given service provides a means for trade-off and cost-benefit analyses in the decision-making process, i.e. it makes the comparison of alternative scenarios possible (Daily *et al.* 2009). However, the field of environmental accounting has not realized its full potential mainly due to issues in classification of ecosystem services (Boyd & Banzhaf 2007; Wallace 2007), but also because many services are hard to define in monetary terms, such as the value of fresh potable water or some cultural services (Srinivasan *et al.* 2008; Daily *et al.* 2009). In spite of the obvious challenges, ecological models are the only tools that can dynamically capture changes in service provision and that can be linked with their economic counterparts for testing alternative scenarios of impacts of human activities.

2.1 Examples of relevant ecosystem services

In the following section, we describe three services delivered by agroecosystems that are potentially affected by human practices, identify the service providers and provide some examples of published modelling studies. These examples demonstrate that model approaches already exist and could be used as a starting point to address the specific needs of risk assessment related to agricultural practices. Table 6.1 summarizes the key points of presented modelling studies. We finish this section with published examples of models that combine ecological and economic aspects of service trade-offs.

2.1.1 Pollination

According to the Millennium Ecosystem Assessment (2003), pollination is a regulating service, provided by natural bee communities in the habitats surrounding crop fields. Pollination receives a lot of attention, partly because it is a service essential for agricultural production, where around 40% of animal pollinated crops depend on wild and domesticated pollinators (Power, 2010). Klein *et al.* (2007) analysed crop data from 200 countries and found that 87 major food crops rely on animal pollination. Also, pollination is one of the few ecosystem services that can be relatively easily quantified as its value is easily measured by estimating the change in crop production with changes in service delivery (Losey & Vaughan 2006). Pollination in agricultural crops is not delivered solely by wild bee populations, but mostly through managed honeybee populations. However, the managed honeybee stocks have been declining worldwide in the last several decades due to multiple factors such as disease (Watanabe 1994), parasites, pesticide use, socio-economic factors (van Engelsdorp & Meixner 2010), making the contribution of wild pollinators to crop production a research and conservation priority (Winfree *et al.* 2007). The honeybee issue boosted the development of ecological models relating to more general dynamics of honey bee populations and colonies (McLellan & Rowland 1986; Omholt 1988; DeGrandi-Hoffman *et al.* 1989; Makela *et al.* 1993; Amdam, Rueppell & Conn 2006; Schmickl & Crailsheim 2007; Becher *et al.* 2010) as well as those designed to investigate specific causes and dynamics of collapse (Martin 1998; Martin 2001).

The beneficiaries of pollination are local farmers, and native pollinator species are the providers of the service. Species contributing to pollination consist of around 50 bee species with a global distribution, and around 7 other invertebrate and vertebrate species (Klein *et al.* 2007). These species can be found in characteristic crops that are grown globally. In order to quantify the given SPU, local bee species have to be identified, their main characteristics determined and population dynamics of different species need to be considered to ensure spatio-temporal coverage of the service. Characteristics such as population size, density in an area, spatial and temporal dynamics, composition and diversity of necessary bee traits (preferred crop species, visiting frequency, foraging time and distance etc.) and diversity of habitats that ensure the presence of this complex all have to be properly investigated and quantified. Moreover, to evaluate the sustainability of a wanted ecosystem service, we have to integrate the sensitivity of various traits and complex characteristics to changes in land use, the application of chemicals and/or environmental factors.

Relevant drivers of change and pressures include agricultural intensification, habitat fragmentation and loss due to land-use change favouring agricultural crops rather than natural habitat. Global events such as climate change also need to be taken into account, as well as competition with domesticated bee species.

Ecological models developed for studying any of these aspects are the only tools available to integrate different levels of service provision in one study and to test various trade-off scenarios without massive time, energy and financial costs of field experiments. Kremen *et al.* (2007) developed a conceptual mobile-agent-based ecosystem service (MABES) model in which they integrated the biology of service providers, policies on land-use and market laws. Landscape structure is of pivotal importance here, as it impacts spatio-temporal dynamics of pollinators through availability of food, nesting, mating and overwintering habitat. Furthermore, they included various abiotic variables, such as increase in pesticide use, and biotic factors influencing the persistence of pollinator communities, such as foraging behaviour, internal species traits affecting dynamics (e.g. haplodiploidy and low fecundity, competition, parasitism). In this publication the authors did not present an actual ecological model, but rather developed a framework that clearly identifies areas where ecological models can be used for the quantification of effects of different land-use strategies on the pollinator complex.

Rands & Whitney (2010) developed a simple spatially explicit model to investigate how the pollinator’s wild flower foraging preferences are affected by monocultures. In a very simple modelling setting, where space was modelled as a two dimensional grid with discrete cell units, pollinators were allowed to forage within a radius from their nests, which were positioned within the managed field margins. Simulation output showed that the width and geometric design of the margins, together with wild flower density, will enhance pollinator visits to wild flowers, and increase the service in the monocultures too. These results have yet to be empirically verified, but their findings have direct implications for landscape management: the ecosystem service of pollination will benefit from increased wild flower density and from fewer, but wider field margins, as opposed to more numerous, but smaller margins. Both of these findings can be further tested and implemented in real case studies.

2.1.2 Biological control

Biocontrol is also a regulatory ecosystem service that is often evaluated within the field of ecological risk assessment especially in relation to pesticide use. It is very similar to pollination in that the service beneficiaries are local farmers, the service providers are usually assemblages of natural predator species whose viability, abundance and population density can be affected by pesticides, habitat fragmentation, agricultural intensification etc.

Bianchi *et al.* (2010) provide a theoretical investigation of how predator dispersal abilities and habitat configuration could govern the identification of locations where management strategies would have highest impact on service delivery. They developed a spatially explicit model in which the pest species populations grow exponentially within habitat cells and do not disperse, whereas the natural predators disperse across habitats, but show no population dynamics. An exponential power distribution is used as the dispersal function that produces a number of distributions by alternating one of the parameters; as a consequence predators become more or less mobile. Moreover, the model assumes that the time the predators stay in a single cell can be dependent (aggregating) or independent (non-aggregating) of pest densities, which, together with dispersal abilities, yields four theoretical species of predators in total for their analysis. They simulated the pest suppression over 1000 landscapes that varied in the arrangement of predator and pest cells and showed that the highly aggregating, mobile predators have highest pest suppression rates. Furthermore, landscapes with shortest distances between predator and prey cells show highest pest suppression. Their findings have implications for integrated pest management strategies that should aim at larger than one-field scales and should define distance of habitats to crops and ecological function of off-crop habitats, e.g. if it is a source of or sink for biocontrol agents. Finally, knowledge on biological traits of pests and natural predators will facilitate predictions about the areas prone to pest attacks and estimates of successful control by regionally present predators.

A more biologically detailed system was modelled by Visser *et al.* (2009) who developed a spatially explicit simulation model for a pest, the rape pollen beetle, and its parasitoid to investigate the role of off-crop habitat, including the amount, fragmentation and isolation, for parasitoid persistence. Both species can reside in a single habitat cell where the processes of reproduction, mortality and parasitation occur. Pest population dynamics are modelled using the Ricker function, with a yearly time step, and only females are modelled for both species. The distribution of parasitoid eggs is random and limited by individual fecundity. Both species are univoltine and die if they disperse to non-crop habitat or when parasitized. Parasitoid persistence was highest at intermediate isolation levels, but the parasitation rate was negatively correlated with isolation and fragmentation. This has clear landscape management implications for cases where natural habitat is scarce, in that either persistence of parasitoids or parasitation rate can be optimized, but not both simultaneously.

Another example of a simple, unstructured population model in a spatially explicit setting was developed by Bianchi, Honěk & van der Werf (2007) where the interaction between host plants, aphids as pests and ladybeetles as natural predators was investigated. The authors explored whether the historical changes in land use in the Czech Republic had any effects on decreasing populations of ladybeetles. Modelled landscape consisted of habitat maps with various crop species in which pests would realize their population dynamics. Aphid population growth was modelled with a logistic growth function, and the only population loss term was mortality that was dependent on the number of ladybeetles in one habitat cell. The ladybeetle population was composed of seven stages, consisting of an egg, four larval, a pupal and an adult stage. Each stage had stage-specific parameters for different processes, such as developmental and mortality rates, as well as search rates and handling times. The foraging activities of ladybeetles were governed by their energetic status, and the predation rate was described by a Holling type 2 functional response. Simulation results suggest that the steep decline in ladybeetle populations can indeed be explained by the decrease in aphid abundance due to agricultural de-intensification and lower fertilizer input. Ladybeetles seem to be following intensively cultured crops that harbour highest aphid densities. Once the aphids become less available, ladybeetles will become more dependent on off-crop habitat to meet their energetic needs, making the conservation of this type of habitat pivotal in sustaining their populations. Even though the service of aphid biocontrol might not always be necessary, ensuring high ladybeetle abundances provides insurance that, when necessary, aphid populations can be controlled.

Natural predator populations can also be modelled in a very detailed way: Thorbek & Topping (2005) developed a spatially explicit, individual-based model of a linyphiid spider, a typical predator in agroecosystems, to investigate the impact of landscape diversity and heterogeneity on the persistence of local populations. In this model, linyphiid spider individuals go through an egg, juvenile and adult phase. In different phases, they experience certain probabilities of development, dying, dispersing and reproducing, where each individual is unique and based on a number of given variables. Landscape was modelled according to a real Danish, intensely cultivated landscape with various crop and off-crop vegetation types. The authors show that the diversity of habitat types, especially presence of refugia from pesticide exposure with higher abundance of prey species, greatly influences the persistence of these predators, but that actual arrangement of these habitat types matters less, due to the species' high dispersal abilities. Implications for management include ensuring diverse crop rotation or leaving greater parts of the habitat unmanaged.

The modelling studies we described for the services of pollination and biocontrol need to consider spatial relationships, as the organisms that deliver the service depend on off-crop habitats that are spatially segregated from the location where the service is provided (the crop). To ensure delivery of both services, the amount of natural habitat, its geometry, quality and distance to crops are important aspects of management. Spatially explicit models, either more theoretical in nature or more region-specific, allow testing of the impacts of these aspects in various landscape management scenarios and possible trade-offs that may result. The necessary levels of biological detail and resolution will be dependent on the research question or protection goal relevant for the study.

2.1.3 Water quality

Good water quality in natural aquatic ecosystems provides multiple services, from good potable quality for local communities, making it a provisioning service, to ensuring certain levels of biological diversity and community structure that has aesthetic and recreational value, e.g. for sport fishing. Also, more indirectly, good water quality supports the functioning and stability of aquatic communities and food webs, which can play a role as nursery habitat or gene pool protection, making water and its aquatic communities also a supporting service. The multiple benefits of well-functioning water bodies are utilized by various beneficiaries, from local communities depending on the water source, to sports fishermen and tourists in the area. At the same time, aquatic ecosystems are under intense pressure from human activities and are considered to be among the most globally threatened ecosystems (Dudgeon, 2010).

Due to the wide variety of services that aquatic systems provide, it is impossible to cover them all in this paper. Therefore, we focus only on the eutrophication consequences in shallow lakes. Typically, shallow lakes, with a maximum depth of several meters, exist in two alternative stable states, a macrophyte dominated, clear water state, or a phytoplankton dominated turbid state. Excess nutrient loading, both phosphorus and nitrogen, can push the lake from a macrophyte to phytoplankton dominated state (Scheffer *et al.* 1993). It is considered that a turbid state has a lower value because the macrophyte community with its fish assemblages disappear, hereby decreasing overall biodiversity. The recovery of a lake after such a switch is not straightforward, as just reducing the nutrient loads is not sufficient, and frequently biomanipulation is necessary. This, however, also depends on lake size and climatic region (Jeppesen *et al.* 2007). The development of the PCLake model (Janse 1997; Janse *et al.* 2010) was inspired by agricultural intensification in Dutch lakes and the related effects that excessive nutrient loads had on the quality of lake systems, such as algal blooms. This complex ecosystem model takes into account nutrient and biota dynamics in a shallow lake. Essentially, it is a set of ordinary differential equations in which the biota are modelled as functional groups, a common practice for such complex systems. It was created to estimate the probabilities of shifting into an alternative stable state based on the observed nutrient loads, on the composition of the lake's communities and on management practices, in order to identify feedback mechanisms that hamper or enhance these transitions. The model has been extensively analysed and parameterized in a number of lakes, and it was implemented for various questions related to water quality management (see Mooij *et al.* 2010 for examples and references). Mooij *et al*. (2010) provide a review of the history and current uses of various lake ecosystem models developed for different management purposes.

Consequences of systems shifting to alternative states are far-reaching and long-term and thus deserve to be taken into account when assessing risks to the environment. The alternative stable states have been an interesting topic from a purely theoretical point of view, but with very strong implications for management, corroborated by the suite of lake models calibrated to various climatic conditions. If a lake ecosystem shifts to an undesired state due to agricultural intensification and increased nutrient load, ecological lake models can quantify various restoration activities, such as necessary reduction in nutrient loads or the extent of needed biomanipulation agents in order to recover the system quality. Biomanipulation usually includes drastic reduction of the fish stocks that, through trophic cascades, results in the re-establishment of the macrophyte dominated community. Such biomanipulation experiments have been implemented worldwide with differing success (Mehner *et al.* 2002) depending on the lake type, depth, complexity of the lake food web and various feedback mechanisms.

2.1.4 Trade-off analysis

Ecosystem service trade-offs take place when one service is valued over another, and when the delivery of one service reduces the delivery of another service. Agricultural activities that deliver provisioning services, such as food and fuel, have historically been favoured over services such as biodiversity and water quality, whereas supporting services (such as nutrient cycling or soil formation and quality) have been neglected (Rodriguez *et al.* 2006). The analysis of land-use change and the impacts on ecosystem services supports the development of various integrative modelling approaches (de Groot *et al.* 2010). For instance, Nelson *et al.* (2009) developed a model that takes into account ecosystem services, biodiversity conservation and trade-offs at landscape scales, especially in land use decision making. InVEST (Integrated Valuation of Ecosystem Services and Tools) can be applied to various systems, and the authors offer a case study of the Willamette basin in Oregon, US. They combine an ecological valuation of various services in the area with an economic valuation method. In their study, land use and land cover are the basis for ecosystem services, biodiversity conservation and commodity production. Biodiversity conservation is based on the species-area relationship (SAR) and marginal biodiversity value (MBV), the latter a more relative metric measuring the value of habitat in the area in relation to the habitat available for all species in the whole landscape.

Nalle *et al.* (2004) developed a simpler spatially explicit model for finding cost-effective strategies in timber production and endangered species conservation in a forested landscape. The ecological model here is based on the PATCH model (Schumaker *et al.* 2004) and consists of a matrix model for the great horned owl, *Bubo virginianus*, and the great porcupine, *Erethizon dorsatum* that includes life-history parameters such as survival and reproduction rates. Dispersal of individuals is modelled with maximum dispersal distances in a stochastic search procedure. The habitat preferences include data on the suitability of each land management unit as a function of vegetation cover and other landscape characteristics. The economic model calculates the current market value of timber harvesting, whereas the timber harvest is modelled through another modelling package that takes into account harvesting site quality and lists of trees no younger than 15 years of age. The authors demonstrate how the combined models can be implemented in a case study focusing on a part of the Willamette River Basin in Oregon. The whole study was envisaged as an example of how to link ecology and economics in a natural resources rich area where conflicts between exploitation and conservation could occur.

The choice of presented modelling studies reflects the diversity of applied ecological models related to risk assessment of different ecosystem services potentially affected by agricultural practices. Some of the presented studies are developed for risk management, rather than risk assessment. However, ecological models can be used both ways, to scientifically underpin ecological risk assessment as well as facilitate informed management decisions. For both fields, testing of different scenarios, possibility to ask if-then questions and to explore their consequences should prove to be very informative. It was shown that ecological models can capture population dynamics in a very simple, unstructured way, but also that population models can include a lot of biological detail and span over various spatial scales. Depending on the service, explicit consideration of space can be of lower or higher relevance. For instance, both pollination and biocontrol are delivered by organisms that are dependent on other habitats than the one where the service is provided. Thus, the need to take into account landscape composition and structure is reflected in the choice of models. On the other hand, explicit space might not be as relevant in well mixed systems, such as shallow lakes, where interactions between nutrients and various functional groups are more important in determining the dynamics of and changes in the system.

Table 6.1. Summary of presented case studies (without examples of trade-off analyses). RA: risk assessment, RM: risk management.

Service/protection aim	Service providers	Service beneficiaries	Potential risks	Modeling study	Study aim	Model type	Model output	Supporting empirical data	RA or RM
Pollination	Assemblages of native, wild pollinator species	Local farmers	Land use change, pesticides, competition with domesticated pollinators	Kremen et al. 2007	Assessing effects of land use change	Conceptual	/	/	Both
				Rands and Whitney 2010	Impact of monocultures on pollinator wild flower preference	Unstructured population	Pollinator preference	No	RM
Biological control	Assemblages of natural predator species	Local farmers	Pesticides, habitat fragmentation, agricultural intensification	Bianchi et al. 2010	Identifying locations for optimal management strategies	Unstructured population	Pest load	No	RM
				Visser et al. 2010	Role of off-crop habitat, for parasitoid persistence	Unstructured population (ricker function for the host population)	Host and parasitoid population size, parasitoid persistence and parasitation rate	No	Both

				Bianchi et al. 2007	Impact on land use change on ladybeetle abundance	Unstructured for the pest, stage-structured for the ladybeetle population	Ladybeetle population size and energy status in different crops	Yes	RA (retroactive)
				Thorbek and Topping 2005	Impact of landscape diversity and heterogeneity on the persistence of local spider populations	Individual-based model of spider population	Spider abundance in different landscapes /crops	Yes	Both
Water quality - multiple services	Aquatic communities	Local human population	Multiple - agriculture, flow regulation, pollution	Janse 1997	Impact of excessive nutrient load on Dutch lake water quality	Ecosystem (composed of unstructured functional groups)	Nutrient load, total P and N, amount of chlorophyll and submerged vegetation	Yes	Both

3. Challenges and outlook

The ecosystem services framework offers a novel way to approach and conduct conservation of our ecosystems. It also provides an effective means for operationalizing general legislative protection goals into targets that can be quantitatively assessed. Ecosystem services are, per definition, important for humans and deserve to be protected, or their loss has to be thoroughly weighed against the gain of the human activity that may cause such a loss. If ecosystem services that are affected directly or indirectly by agricultural practices can be identified, their well-being or swift recovery could be a meaningful protection goal for ecological risk assessment. It might not be straightforward to define all relevant aspects of a protection goal, such as temporal and spatial scales for the provision of the given service, but at least the aim of protection should be based on more than just results of toxicity tests performed with species that can be easily cultured in laboratories. There is a big discrepancy between measurement endpoints and protection goals since most ecosystem services are performed by distinct units of ecosystems, i.e. populations or communities, while most tests mandated by the relevant legislation and supporting documentation, e.g. Technical Guidance Documents, focus on organism-level effects of a few standard species. Ecological models are powerful tools that can link the measurement endpoints with relevant protection goals. With clearly defined goals, ecological models can help to investigate impacts on various ecosystem components, such as service providing units, also incorporating extended temporal and spatial scales if necessary. Their characteristic advantage, over empirical approaches, is their extrapolative power. They are highly useful for extrapolation across levels of biological organization (e.g. from individual-level effects of toxicants, to population level consequences), and across spatial and temporal scales (e.g. for estimating recovery or accounting for spatio-temporal variability in exposure). They are also useful for the analysis of indirect effects and bioaccumulation, both within and across trophic levels (Munns 2006; Forbes, Calow & Sibly 2008; Galic *et al.* 2010a; Hommen *et al.* 2010).

Still, challenges remain for the ecosystem service concept itself and for model development. Firstly, the valuation of ecosystem services is not yet fully developed nor globally accepted (Armsworth & Roughgarden

2003; Boyd 2007; Boyd & Banzhaf 2007; Wallace 2007; Wallace 2008). Furthermore, some services may not have been identified yet, and multiple interactions, feedbacks and outcomes in various service combinations have not received much attention (Bennett, Peterson & Gordon 2009). Norgaard (2010) argues that a more comprehensive restructuring of relevant governing and economic institutions is necessary to accomplish the full potential of the proposed framework; otherwise we will not move fast enough in the direction of sustainability.

Secondly, knowledge on the structure and functioning of agroecosystems is still limited, despite the wealth of published information. A lot of the observations and experiments published in the literature are very context specific, and few authors have dared to make generalizations on ecosystem structure and functioning. The structure and functioning of ecosystems, and effects of various drivers on them, may very well be context specific to a certain extent and therefore difficult to capture in general ecological models. This is especially true when “real” ecosystems are modelled to evaluate the effects of certain drivers in specific ecosystem case studies. From a review of the literature, Daam & Van den Brink (2010) concluded that the sensitivity of tropical aquatic ecosystems does not seem to be very different from temperate ones, but that recovery patterns and indirect effects can be expected to be very different between climate regions. This means that it should be very clear from the start which specific service in which ecosystem is being captured by the model. Model outputs cannot be easily transferred between contexts, but rather a thorough reconsideration of model assumptions, structure, and parameterization is necessary if a model is applied in a context outside of its intended purpose (e.g. for a different climatic region, for the assessment of new protection goals, etc.).

Thirdly, the required level of complexity of ecological models remains an issue. Decisions on what exactly to quantify and with how much biological detail can be hard to make when a specific service is delivered by many providing units. To perform an ecologically relevant risk assessment, a lot of ecological detail is necessary. However, simulating the natural world is neither realistic nor desired. Finding the right balance between model complexity and ecological realism/relevance remains a crucial challenge and requires precise definition of protection goals which is achievable only through broad stakeholder dialogue combined with collaboration between ecologist and economists. Furthermore, modelling service provision adds another dimension of extrapolation and complexity, especially when a given service is provided by multiple providers. While in ERA practices the extrapolation of effects from the individual to the level of a population could be sufficiently informative, focusing on service provision means that the spatio-temporal dynamics of service providers have to be taken into account, as well as possible interactions with populations of other species. Moreover, the general definitions of ecosystem services make quantification very difficult. It might be necessary to break down general services into more manageable units, for instance, instead of the service of biocontrol we might look into suppression of aphids in cereals in a given climatic region. For many services, including biocontrol and pollination, explicit consideration of space is essential and is expected to result in the increased development of spatially realistic population models. Again, the right balance between the amount of spatial and biological detail will have to be found.

Finally, the execution and implementation of some applied modelling studies has not always been successful (Pilkey & Pilkey-Jarvis 2007), possibly due to too much reliance in the predictive power of models (Hall 1988), lack of transparency and bad judgment in model assumptions or parameter choice (Comiskey, Eller & Perkins 2004; Gross 2005; Patterson & Murray 2008). Accordingly, there is a need for much more transparency, especially in ecological models used for decision making. In the field of pesticide risk assessment, steps are currently being taken to standardize approaches and reduce scepticism around the development, use and results obtained from modelling studies developed for the purpose of pesticide registration (Schmolke *et al.* 2010a; Schmolke *et al.* 2010b). Consequently, acceptance of ecological models for ERA and decision making is expected to grow in regulatory spheres. For example, pesticide risk assessment is currently taking significant steps toward developing and promoting the use of ecological models for the purposes of product registration (Forbes *et al.* 2009; Grimm *et al.* 2009; Thorbek *et al.* 2009).

In spite of many challenges, the link between measurement endpoints and services as protection goals is feasible only with the help of ecological models. We do not propose abandonment of empirical approaches, indeed, the two are complementary. Necessary parameters can only be extracted from field or experimental data, and the outputs of ecological models, especially those used in decision making, need to be tested against independent datasets to show that they are indeed recreating a part of the system of interest. Only then can they be fully trusted and used for comparing alternative management scenarios.

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Chapter 7

Synthesis and general discussion

There is no denying that the human pressures on the environment may result in detrimental consequences. With the exponentially increasing human population and its needs for food, housing, energy etc., ecosystems worldwide are under escalating pressures, resulting in damaged ecosystems, disturbing declines in vital natural resources, e.g. fish stocks, and an alarming and continuous loss of biodiversity (Millenium Ecosystem Assessment 2005). In the agroecosystem, a balance between food production and ecosystem functioning is a legal requirement and a quest of the field of ecological risk assessment. In this thesis, I add to the general knowledge on factors contributing to population recovery after stress, such as exposure to pesticides. I focus on aquatic arthropods inhabiting edge of the field water bodies in agroecosystems. For this purpose I developed population models which prove to be excellent tools for supporting environmental decision-making. A part of this thesis, therefore, contributes to the application of ecological models in the ecological risk assessment.

7.1 Recovery of disturbed systems

If anthropogenic pressures persist beyond a certain critical threshold (Scheffer *et al.* 2001), an ecological system might enter an alternative stable state (Lewontin 1969) where some of its characteristics might be qualitatively different from the original state (Scheffer *et al.* 1993; Persson *et al.* 2007). However, ecological systems have the capacity to withstand certain pressures that allows them to recover from such disturbances (Holling 1973). The time to recovery varies based on the magnitude of the perturbation, but also on the type of the system, e.g. terrestrial systems recover much slower than aquatic ones, even when corrected for the disturbance magnitude (Jones & Schmitz 2009).

Factors influencing the success or failure of system recovery are of great interest for the fields of restoration ecology, conservation biology and ecological risk assessment (ERA). The recovery of populations is mainly governed by various ecological, evolutionary and disturbance factors (Gardmark *et al.* 2003), but the definition of recovery vary greatly among different stakeholders (Gore, Kelly & Yount 1990; Niemi *et al.* 1990; Stone & Wallace 1998; Gardmark *et al.* 2003; Greathouse, March & Pringle 2005). Even the term disturbance or stress calls for its own definition, and can constitute the discrete removal of organisms due to en event or an unusual or unexpected deviation from normal conditions (Gore, Kelly & Yount 1990). Long-term, i.e. pressed, disturbance will eventually result in either (genetic) adaptation or extinction of the population, while it is considered that short-term, i.e. pulsed, disturbance will eventually stop and allow disturbed populations to return to their nominal, pre-disturbance behaviour (Yount & Niemi 1990). Knowledge about the system before disturbance occurred is, therefore, required in order to assess recovery, including data on annual and interannual dynamics and differences.

From here on, I will concentrate on **recoveries after pulsed exposure to chemical stress**, mainly focusing on the effect of pesticides, and will disregard evolutionary factors benefiting population adaptation to new environmental conditions. The choice of recovery endpoints to study, depends on the system, but also on the available pre-stress and post-stress data (Niemi *et al.* 1990). In other words, the reference state the system is expected to recover, or revert, to depends also on our knowledge about the reference state itself. Recovery endpoints include recovery of average individual size, recovery of densities or total biomass, recovery of species composition, or first reappearance (Niemi *et al.* 1990).

7.2 Pesticide risk assessment and population recovery

Within the European legislation on placing plant protection products (i.e. pesticides) on the market, some adverse effects on the non-target species are allowed if recovery of their populations can be accomplished (EC 1991; SANCO 2002a; EC 2009). However, the guidelines do not provide a clear definition of recovery, and is mostly translated by risk assessors and managers as the recovery of abundances to levels expected in unstressed systems, especially for organisms such as algae, zooplankton and macroinvertebrates (SANCO 2002). Consequently, I also considered only recovery in abundances of the local and total populations. Furthermore, I evaluate how different factors affect the recovery process of modelled populations.

The central premise of this thesis is that a combination of **species-specific**, **stressor-specific** and **landscape-specific** factors determines the potential for, and time to, recovery of non-target populations after exposure to chemical stress (Fig. 7.1).

7.2.1 Population recovery and species specific factors

It is well established that certain life-history traits of species strongly influence the recovery process (Gardmark *et al.* 2003), especially fecundity and generation time play a major role. High reproductive output ensures fast increases in suppressed abundances, resulting in species with a very short generation time and multiple generations per year (multivoltine species) recovering relatively faster than other species in the community (Van den Brink *et al.* 1996; Gardmark *et al.* 2003; Stark, Banks & Vargas 2004b; **Chapter 3** and **5**). However, some species, e.g. some fish, have difficulties finding mates at very low abundances, leading to depensatory dynamics, i.e. Allee effects (Stephens, Sutherland & Freckleton 1999), that hamper recovery or even drive populations to extinction. In systems exposed to chemical stress, insensitive life stages represent survivors of the chemical impact that give the recovery process a quicker start (Pieters & Liess 2006; Devine & Furlong 2007). Such stages may include ephippia of daphnids which aid the recovery of a crustacean otherwise very sensitive to pesticides (Van den Brink *et al.* 1996).

Good dispersal abilities ensure persistence of species across landscapes, and are especially important in the metapopulation and metacommunity context, as they allow dynamic presence of species across landscapes (Hanski 1998; Frank 2005; Elkin & Possingham 2008; Altermatt, Pajunen & Ebert 2009). Most natural populations are spatially structured, forming, thus, a metapopulation consisting of local populations (Hanski & Gaggiotti 2004). It is assumed that stress is buffered in the metapopulation context as not all local populations are stressed at the same time (Devine & Furlong 2007). Consequently, such populations will provide individuals that colonize vacant landscape patches, enhancing the recovery process after stress (Tronstad, Tronstad & Benke 2007; Trekels, van de Meutter & Stoks 2011b; **Chapter 3** and **5**).

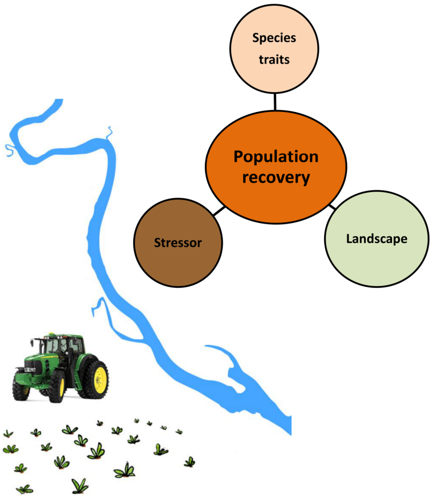

Figure 7.1. Schematic representation of the main premise of this thesis – a combination of species, stressor and landscape characteristics determines the potential and speed of recovery of arthropod populations.

However, dispersal of, for instance, aquatic insects, especially those considered to be weak flyers will depend on the structure of the landscape, but also on the amount of e.g. wind. Permeability of the habitat edges such as riparian vegetation will determine the dispersal rates, laterally from the water body (Jackson & Resh 1989; Petersen & Winterbottom 1999; Delettre & Morvan 2000; Delettre 2005), be it due to inability to move through them or just preference for the vegetated habitat. Very impermeable edges will enhance linear dispersal along the water body (Wiens 2002). Furthermore, the permeability of the landscape matrix, i.e. vegetation (or lack thereof) or human made barriers, will further enhance or hamper dispersal of insects (Delettre & Morvan 2000) and will control the potential to recolonize and recover other habitats (Blakely *et al.* 2006; **Chapter 5**).

Intraspecific interactions, may have negative consequences on individual survival, through high local densities of individual organisms (as implemented in **Chapter 3, 4 and 5**). However, if subsequent reduction in population densities allows survivors access to less limited resources, thus, enhancing their survival and recovery (De Roos, Galic & Heesterbeek 2009).

Interactions between species bring another dimension to the recovery process, as they might hamper or facilitate recovery of affected species (Spanhoff & Arle 2007). The role of **interspecific interactions** in the recovery process is especially relevant when a stressed prey population is being further suppressed by a natural predator, e.g. the abundances of cod fisheries remains low due to natural predation from seals (Bundy 2001). Furthermore, the recovery of a predator after the stressor has been removed, will depend on the abundance of its prey (Gardmark *et al.* 2003). Competitive interactions are the major structuring force (Menge & Sutherland 1987; Leibold *et al.* 2004) of ecological communities and determine the biodiversity patterns and community composition. Species can compete among themselves or with other species, typically for resources, such as food, space, etc. As such, competition can affect recovery after stress, especially when species are not equally susceptible to the stressor (Foit, Kaske & Liess 2012). For instance, both *A. aquaticus* and *G. pulex* (**Chapters 3** and **4**) can co-exist in freshwater ecosystems, though, under certain conditions, *G. pulex* negatively affects the physiological status of *A. aquaticus* (Hargeby 1990); often these species are in a predator-prey relationship and/or exhibiting some interference competition (Bengtsson 1982; Pontin 1982). In presence of different pollutants in the aquatic environment, the feeding rate of *G. pulex* on eggs of *Artemisia salina* was reduced by the presence of *A. aquaticus* that was, subsequently, excluded in some treatments (Blockwell *et al.* 1998). The physiological stress due to the presence of *G. pulex* and the toxicity of the test system significantly affected survival of *A. aquaticus*. However, in presence of a different pollutant, the trends of survivorship and species dominance were reversed (Blockwell *et al.* 1998). Colonization is often facilitated by biotic, interspecific interactions (Milner *et al.* 2008), whereas in some cases just the presence of a species affects the life-history of another one, e.g. in *ad libitum* conditions, individuals of

Asellus aquaticus excluded those of its congener, *Asellus meridianus* (Hynes & Williams 1965). Competitive interactions can also facilitate the coexistence and persistence of several predator species, by specializing on different stages of the same prey species (De Roos *et al.* 2008).

Clearly, there are still a lot of interesting and relevant questions, that go beyond the focus of this thesis, to be answered regarding the effects of intra- and interspecific interactions on the recovery process.

7.2.2 Population recovery and landscape factors

Dispersal abilities of different species directly interact with landscape factors influencing the recovery process, as, for instance, distances between preferred habitats will be perceived differently by strong and weak flyers. Vicinity of unstressed areas, presence of refugia at the site of the impact and overall functional connectivity of the landscape typically ensure rapid exchange of individuals on which population recovery is based (Niemi *et al.* 1990; Brock *et al.* 2010b; Trekels, van de Meutter & Stoks 2011b). The recovery is quicker in well-connected landscapes, but this is only true if the stress is heterogeneously distributed (**Chapter 3**). In other words, if the population abundances are equally suppressed across the whole landscape then connectivity, but also dispersal, plays a lesser role as a certain number of individuals will remain in each landscape patch (**Chapter 4**); these individuals will then enhance the recovery process. Individual drift, i.e. passive movement via stream currents, is a common mechanism of movement among many aquatic arthropods, including crustacean species, such as *Gammarus pulex*, a notorious drifter (Elliott 1970), and various aquatic insect species. It is generally considered that drifting is a very strong colonization mechanism (Brittain & Eikeland 1988; Yount & Niemi 1990), as it carries many individuals fairly quickly, from upstream reaches to the impact site, and quickens the recovery of their populations. However, this is only true for the parts of the system that have been depleted, as an analysis of the total system, including the unstressed parts of the landscape, reveals that drifting is a mere spatial redistribution of individuals (**Chapter 3**), and constitutes only the first step in the recovery process. The total population (including all individuals of the whole landscape) will take longer to recover, as it will recover only in the following reproductive season. Furthermore, it has been shown that movement to stressed areas, depletes populations from unstressed parts (Brock *et al.* 2010b) or induces changes in the population size structure (Greathouse, March & Pringle 2005). Therefore, the actual contribution of drift, but also movement in general, has to be carefully considered if we are to assess risks to the whole system.

7.2.3 Population recovery and stressor factors

Lastly, and especially relevant for the field of chemical risk assessment, are the stressor specific factors influencing the time needed for populations to recover. These include the persistence of the stressor, which can be physical or chemical, in the environment, as this affects the recovery of the habitat, a prerequisite for population recovery (Crutchfield & Ferson 2000; Vieira *et al.* 2004), but also the timing of stress in the field. Persistence of pesticides in the water compartment can be assessed by their fate in different waterbodies, which is determined by the physical and chemical properties of the pesticides and the hydrology and environmental conditions of the water body. Determining the toxicity of different chemicals, such as pesticides, by performing standard toxicity tests on different organisms is the main activity of ecotoxicology. Standard toxicity tests provide information about the magnitude of lethal and/or sublethal effects across different exposure concentrations (Brock *et al.* 2010a), The results of these tests are analysed using dose-response models in order to obtain dose-response relationships that describe the occurrence of a certain response (mortality, immobility, etc.) over a range of exposure concentrations. From these dose-response relationships, statistics such as EC50 and LC50, i.e. concentration that affects or kills 50% of tested organisms, are used in first tiers of prospective risk assessment for deriving conservative “safe concentrations” and in the retrospective risk assessment to assess the toxicity of existing concentrations (SANCO 2002). Such tests are performed at constant concentrations maintained for fixed periods of time, and are regulated within legal documents (EC 2009). Consequently, they might underestimate risks since possible effects occurring after the testing period, i.e. delayed effects, are not taken into account (Reinert, Giddings & Judd 2002). Toxicokinetic-toxicodynamic (TK-TD) models allow predicting the combined effects of concentration and duration of exposure. Uptake and elimination from the environment constitute the toxicokinetic process, while organism damage and recovery constitute toxicodynamics. For instance, the threshold damage model (Ashauer, Boxall & Brown 2007), TDM, includes both toxicokinetic and toxicodynamic processes, and assumes stochastic death once the level of damage exceeds a given threshold. The combination of all TDM parameters, which are species and chemical specific, determines the magnitude of effects in exposed organisms. The comparison of the TDM and dose-response calculated mortality reveals that in most cases the TDM predicted substantially larger adverse effects, with longer population recovery as a consequence, indicating that using the dose-response model for survival might underestimate the adverse effects of pesticides (**Chapter 4**).

New generation pesticides tend to have very low persistence (Wijngaarden, Brock & Brink 2005) and their presence in the water column may be a matter of hours (e.g. pyrethroids, see Laskowski 2002). In such instances, standard risk assessment practices use a 96 h dose-response model in order to assess risk from short-term exposure (measured in hours). This practice is protective if the exposure is quite short (**Chapter 4**). Accounting for toxicokinetic and toxicodynamic processes allows for individual differences between different tested pesticides to become visible. Occurrences such as effects beyond the exposure period, but also toxicity dynamics that differ among the chemicals and organisms (Ashauer, Boxall & Brown 2006b; Ashauer *et al.* 2010a; Rubach *et al.* 2010; Rubach, Crum & Van Den Brink 2011) are not captured by standard tests and TKTD approaches may help overcome such shortcomings and improve risk assessments.

Timing of stress, be it pesticide applications in agroecosystems or any other stress event, in relation to species phenology is an important factor governing population recovery (**Chapter 3**). This characteristic of the recovery process is especially relevant for species with few generations in a year (Niemi *et al.* 1990; Whiles & Wallace 1992; **Chapter 3**). Populations exposed early in the season, e.g. before the onset of reproduction, tend to recover within the same season, depending on the level of imposed stress (**Chapter 3, 4 and 5**). However, populations exposed late in the year, after the reproductive season, may take much longer to recover (**Chapter 3**).

7.2.4 Population recovery analysis and time to recovery

The only defined acceptable recovery period in the legislation relates to mesocosm studies, where an eight week period is required for recovery of affected taxa (SANCO 2002). When stress levels are in line with what is expected in regulated agroecosystems, the recovery of zooplankton species can be expected to occur within the defined period (Van Wijngaarden, Brock & Douglas 2005). Recovery of aquatic macroinvertebrates, that might have only a few defined generations within a year, can take much longer (**Chapter 3 and 4**). Clearly, this is very much dependent on the level of imposed stress (Van den Brink *et al.* 1996; **Chapter 4**).

Therefore, the legislation is quite flexible about prescribing the required periods to accomplish recovery in systems exposed to pesticides (SANCO 2002). In order to properly define the period needed for recovery, one has to take into account the role of the affected species in the food web or ecosystem and characteristics of its life-cycle. Assigning biota in ecosystems a role, i.e. group them in units that provide a certain service that is of interest and benefit for the human population, will put the maximum period for recovery into a wider and ecologically more relevant context. The ecosystem service framework offers promise for the fields of ecological risk assessment of pesticides, by operationalizing the very general protection goals from legal documents to manageable targets that can be assessed, quantified and protected (Nienstedt *et al.* 2012).

7.3 Ecosystem services in ERA

Ecosystem services are generally defined as benefits obtained from ecosystems that are essential for sustaining the human population (Costanza *et al.* 1997; Daily 1997; Millenium Ecosystem Assessment 2005). There are four groups of services: provisioning services, including food, water and fuel, regulating services, including regulation of air and water quality, pest regulation and pollination, climate and disease regulation, supporting services, such as nutrient cycling, soil formation, primary production and, finally, cultural services relating to non-material goods, such as recreation, cultural and aesthetic values and heritage (Fig. 7.2). Some services can be provided by multiple ecosystems while, at the same time, some ecosystems can provide multiple services. Such correlations, and especially, interactions, feedback and outcomes among various service combinations are very relevant for sustainable service provision and ecosystem health, but have not yet been well researched (Bennett, Peterson & Gordon 2009). When a service is valued over another in the same system, or when the delivery of one reduces the delivery of another one, ecosystem service trade-off takes place (Rodriguez *et al.* 2006). In agroecosystems provisioning services have historically been valued over others, e.g. food production over pollination (Nienstedt *et al.* 2012).

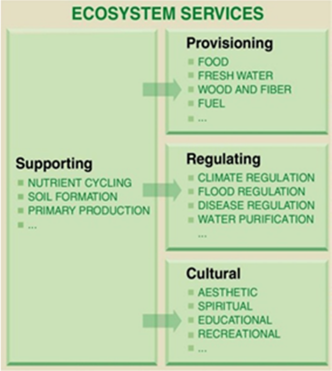

Figure 7.2. The ecosystem services framework distinguishes four groups of services: provisioning, regulating, cultural and supporting. (source: Millennium Ecosystem Assessment Synthesis Report, http://www.maweb.org/)

Ecosystem services are typically provided by parts of the system, so called service providing units (SPU) (Luck, Daily & Ehrlich 2003). The definition of a SPU is dependent on the type of service, and spans from one species with special cultural or aesthetic values, such as tigers or elephants, populations of, e.g., spiders delivering the service of pest regulation to a set of functional groups, providing services such as nutrient cycling or pollination. A definition of ecosystem service providers (ESP) extends the SPU concept to allow for the diversity of traits and functions found in populations, communities and spatio-temporally disjunct networks, such as metacommunities, necessary for service provision (Kremen & Ostfeld 2005). Both definitions are very useful because they allow for a direct link between the wanted service and parts of the ecosystem that provide it to be identified and quantified.

The field of ecological risk assessment may greatly benefit from defining its protection goals in the currency of ecosystem services (Nienstedt *et al.* 2012), while ecological models can play a big role in the linking of the two (**Chapter 6**). Besides food provision, several services provided by agroecosystems are essential for humans, such as pest control, pollination, nutrient cycling, soil structure and functioning, water provision etc., but they can also be disrupted by agricultural practices (Power 2010; **Chapter 6**). Extending the protection goal set for some species which are chosen for their ease to culture them in the laboratory, to a broader set of species that deliver a certain service of interest contributes to increased ecological relevance of the risk assessment. However, it does not simplify the process and will instigate many new and important questions (**Chapter 6**). For instance, at which spatial and temporal levels is the service of biological control needed, which pests and predators are present in the unstressed system and can predators survive outside the crop season? Consequently, the protection of service of biocontrol in agroecosystems might have to be broken down in more manageable and context specific units, such as suppression of thrips in a certain crop type in a certain climatic region. Furthermore, a spatial and temporal scale has to be defined in which the service is needed and can be delivered. Finally, as some services are provided by many interacting providers, their interaction dynamics also have to be considered. Since agroecosystem functioning and the processes governing them are still under-researched and understood, the lack of proper information about dynamics and distribution of different service providing units further complicates protecting relevant services, which are proposed by different stakeholders in the risk assessment field (Nienstedt *et al.* 2012).

A fair and important question arises: **how does recovery of single species in this thesis relate to the provision of ecosystem services?** Most of the species were chosen based on the availability of data, at least for the parts of their lifecycle, and on their demonstrated sensitivity to pesticides. However, both *Asellus aquaticus* and *Gammarus pulex* have very prominent roles in the ecosystem function of decomposition of leaf material, i.e. part of the nutrient cycling service. Both are leaf shredders whose activities facilitate decomposition by microbial organisms (Jonsson & Malmqvist 2000), though both have also an opportunistic feeding preference, not shying away from cannibalism and predation in case of the amphipod (McGrath *et al.* 2007). It is, therefore, hard to determine whether their role in the leaf litter decomposition process is exclusive or shared with other species in the community, allowing for compensatory dynamics to occur (Gonzalez & Loreau 2009). In species impoverished systems, a common characteristic of agroecosystems, such functions might be carried only by one species, emphasizing the need for the time to recovery to be relatively short in order for the system to function properly. However, in species diverse systems, where biodiversity, through functional redundancy, can serve as an insurance against stress (Loreau, Mouquet & Gonzalez 2003), other species within similar functional groups can take over, under the assumption that not all species are equally susceptible and/or exposed to imposed stress. Furthermore, functional connectivity of the ecosystem allows for spatial exchanges across stressed landscapes, thus maintaining the provision of relevant services (Loreau, Mouquet & Gonzalez 2003; Trekels, van de Meutter & Stoks 2011).

An important challenge for risk assessment is defining both spatial and temporal scales for acceptable recovery times. It is especially important to define the spatial scale of recovery, as local populations (in a part of the exposed system) may recover quicker than the total population landscapes (**Chapter 3**). Such quick recovery is often accomplished due to simple spatial redistribution of organisms, and should not be understood as “real” recovery in abundances, but as a first step in the recovery process followed by reproduction of the species and increase in suppressed population abundances. Furthermore, redistribution of individuals presumes that these individuals arrive from unstressed parts of the system, leaving them relatively depleted. Such “action at distance” has been observed in both experimental (Brock *et al.* 2010b) and natural systems (Greathouse, March & Pringle 2005). This has important implications for assessing population recovery in the field, and implies that several locations outside the stressed area, serving as source of individuals, should be consistently monitored for changes in their expected dynamics and trends. This is of even greater importance since waterbodies in typical agroecosystems might be stressed multiple times per year.

Accounting for different spatial and temporal scales important for recovery of various species or communities which deliver wanted services goes beyond the scope of most laboratory or semi-field studies. The isolated nature and limited duration of such studies do not allow inclusion of important processes, such as dispersal, or completion of multiple species life-cycles. Field studies that could account for e.g. dispersal and recolonization of stressed areas might suffer from other issues. Especially for chemical risk assessment, applying a toxicant over larger areas might raise ethical concerns, especially when systems are not fully researched nor understood as unexpected outcomes might occur due to natural variability of the systems. Also, even if such studies would be carried out, it is very unlikely that the number of replicates would yield sufficient statistical power to draw any firm conclusions, i.e. those beyond anecdotal evidence. The potential and scope for use of ecological models is proving to be increasingly important in chemical risk assessment (**Chapter 2 and 6**).

7.4 Ecological models and risk assessment

Recent years have generated great interest and publications promoting the use of ecological models for ERA (Forbes, Calow & Sibly 2008; Forbes *et al.* 2009; Thorbek *et al.* 2009; Schmolke *et al.* 2010a; Schmolke *et al.* 2010b). This thesis and in particular **chapters 2 and 6** represent my contribution to these efforts.

The advantages of using ecological models include: meaningful extrapolation of laboratory or semi-field derived results beyond their context, including more ecology into fields of ecotoxicology and ecological risk assessment and cost-effective comparison of the effects in alternative scenarios (Forbes, Calow & Sibly 2008; Forbes *et al.* 2009; Schmolke *et al.* 2010a; **Chapter 2**). Standard risk assessment practices include the results of laboratory tests that evaluate the effects of a certain chemical on different endpoints on a handful of individuals of standard test species. However, most protection goals aim at the level of populations and communities. The relevant life-cycle processes of the species of concern and the effects of the chemical on their tested endpoints can be integrated into one modelling study in order to enable a straightforward extrapolation of effects and projections over longer time scales (Forbes, Calow & Sibly 2008).

Extrapolation pertains to different exposure regimes, but also assessing effects of exposure beyond the testing period. Currently, a group of individual level models that is most suited for such extrapolation are toxicokinetic-toxicodynamic (TKTD) models as, once parameterized, they can account for spatial and temporal variability in exposure, due to e.g. aerial drift, leeching or drainage of pesticides from crop areas (Ashauer, Boxall & Brown 2006b; Ashauer, Boxall & Brown 2007a; Ashauer *et al.* 2011). These models are still typically developed on the level of individuals (Ashauer, Boxall & Brown 2006b; Ashauer, Boxall & Brown 2007a), but are easily integrated into population, especially individual-based, models (**Chapter 4**). Extrapolation of TKTD parameters between chemicals and species, based on, for instance, their correlations with physical, chemical and toxicological characteristics of a given pesticide and the phenotypic or ecological characteristic (traits) of species, is a promising, yet challenging, research direction (Rubach, Baird & Van Den Brink 2010; Rubach, Crum & Van Den Brink 2011).

The extrapolation of recovery processes over temporal or spatial scales is a prominent topic in ecological risk assessment (**Chapter 3, 4 and 5**). Ecological models are here particularly useful, as integration of the dispersal abilities of various species, but also evaluation of different landscape contexts relevant for recovery, goes well beyond capabilities of most experimental systems. This is especially important when different landscape and species factors may need to be contrasted (**Chapter 5**), as ecological models are very suitable for comparing outcomes of alternative scenarios (**Chapter 6**). The same is valid for the duration of e.g. mesocosm studies that are usually much shorter than is needed for a proper consideration of all life-cycle processes relevant for population recovery.

Different experts in the field of risk assessments are recommending inclusion of more ecological processes into standard testing procedures (Van Straalen 2003; Forbes, Calow & Sibly 2008; Van den Brink 2008), and the tools mostly mentioned that are capable of accomplishing this are indeed ecological models. In fact, ecological models are the only practical tools that can really link the measurement endpoints, obtained via standard tests with relevant protection goals defined within the ecosystem service framework (Nienstedt *et al.* 2012; **Chapter 6**). Even in relatively simple cases where we want to assess effects on the population level from data gathered on the individual level, more ecological information is needed, such as longevity of the species, fecundity, background mortality and/or density-dependent processes. Thus, one can say, that inclusion of ecological data and theory related to higher levels of organization (population, community, ecosystem) is inherent to the modelling process itself. However, the right balance between the amount of biological and spatial detail has to be acquired and constantly re-assessed (**Chapter 6**).

Once an ecological model has been parameterized, validated and properly analysed for a certain system of interest, it can be used for answering various questions, possibly unrelated to the ones that prompted its development (Forbes, Calow & Sibly 2008). For instance, a population model developed for comparison of the consequences of calculating individual survival probability via two survival models in different exposure scenarios and the consequences for population recovery times (**Chapter 4**) may be used beyond the initial research questions for which it was developed. It might be used to evaluate, e.g. recovery under realistic exposure regimes in different spatial contexts, i.e. different types of waterbodies such as streams or ponds. Obviously, some slight modifications or addition of relevant parameters are required. However, one should be very cautious as such extrapolations should be based on deep understanding of mechanisms and empirical data.

Furthermore, the model can easily evaluate the effects of different mitigation options in case risk was found to be unacceptable. Clearly, these types of models can also be used to assess population level consequences of exposure to new chemicals. This would, of course, require basic toxicity information about the new chemical. Using ecological models, thus, has the advantages of a) applying them beyond the initial aims, b) comparing alternative scenarios in the same study and c) using them for risk management. In fact, there is a very fine line between using models for risk assessment and management, as they are most often used simultaneously for both (**Chapter 6**).

Using ecological models to support environmental decision making has not been without problems, since the implementation of some studies was not very successful (Hall 1988; Comiskey, Eller & Perkins 2004; Gross 2005; Pilkey & Pilkey-Jarvis 2007). These failures are probably a result of a lack of transparency in model assumptions and parameterization and too much reliance on predictive abilities of models. It is tempting to put a lot of trust in model output, however, it should never be considered in absolute terms, as the error propagation in models originates from different levels of the modelling process and so its results should be interpreted with caution (Bartell *et al.* 2003). The risk of use out of context or misinterpretation can be reduced by making all parts of the modelling process transparent, including the domain of applicability (Schmolke *et al.* 2010b) and scrutinized by peers. In the European pesticide risk assessment field, serious steps are currently being taken to standardize modelling approaches and provide useful and coherent documentation of the whole modelling process (Grimm *et al.* 2009; Grimm *et al.* 2010; Schmolke *et al.* 2010b). This will, in return, increase the trust of institutions in charge of pesticide registration, i.e. the users of such modelling studies. In the end, only transparent communication between all stakeholders in the risk assessment process will ensure proper ecosystem assessment and management (Nienstedt *et al.* 2012; **Chapter 6**).

7.5 Final conclusions and outlook

The field of ecological risk assessment (ERA) is going through significant changes in the last decade (Van den Brink 2008). As with any living organism, constant adaptation is necessary for survival. The same goes for scientific disciplines, especially those playing a major role in balancing human needs and preserving Earth's support systems. As human pressures on the environment increase and more sensitive measurement tools detect chemicals all around the world, the field of risk assessment is adopting novel methods, such as ecological models, for estimating risks. Ecological models are already in use for long by different branches of environmental sciences, including ecology. Ecological models have proven to be useful in a variety of studies relating to wildlife and fisheries management (Starfield 1997; De Roos, Galic & Heesterbeek 2009; Mooij *et al.* 2010) and conservation biology (Resit Akcakaya 2000;

Bulman *et al.* 2007). They have been heavily advertised in the field of ecological risk assessment due to their extrapolative power, as vessels to include more ecology and for comparing alternative scenarios and risk management (Forbes, Calow & Sibly 2008; Forbes *et al.* 2009; Grimm *et al.* 2009; Thorbek *et al.* 2009; **Chapter 2 and 6**). I am happy to have been a part of this motivating group. The time has now come to really put models into practice and show successful examples of models being used for ecological risk assessment and management efforts.

The question of recovery is becoming increasingly relevant in the current state of the environment, and clear definitions of spatial and temporal scales for recovery will have to be made soon. Many species and system specific factors that influence recovery are still unknown, including the role of density dependence in mortality, fecundity and growth, impact of intra- and interspecific biotic interactions, abiotic interactions etc. This makes estimations of recovery uncertain and reliance on limited information not recommendable. In the field of pesticide risk assessment, clear guidelines have to be developed on what constitutes recovery for different species.

Temporally, recoveries should at least be accomplished within the year of application, to avoid effects building up over time. This might be especially relevant for species impoverished system, such as the agroecosystem. Within season recovery may prove to be difficult for some species, especially the univoltine ones. Consequently, some effort has to be put into developing mitigation scenarios that would allow populations to recover within the given, acceptable period. Ecological models are really well suited for this job, which starts with modelling the risk for the population, determining the length of times required for population recovery and testing alternative mitigation, i.e. management, scenarios that will yield the acceptable windows for recovery. Both risk assessors and managers should be aware of the spatial scale at which they assess recovery, as was shown that “action at distance” may deplete populations from adjacent, unstressed areas (Brock *et al.* 2010b; **Chapter 3**). In frequently stressed landscapes, such as agroecosystems, this depletion might add to significant yearly population losses in supposedly unstressed areas. To counter this, biological monitoring could be performed inside and outside the exposed area in order to detect changes in population trends.

Currently, clear guidelines are lacking on development of ecological models, but, more importantly, also on which species are relevant for assessment of adverse effects, and subsequent recovery of their populations. Here I focus only on aquatic macroinvertebrates and their role as providers of relevant ecosystem services, as accounting for relevant species across different ecosystems goes beyond the topic of this thesis.

In order to harmonize the pesticide risk assessment process across Europe, several relevant macroinvertebrate species should be identified. These species have to be relevant for their role in the ecosystem, i.e. ecosystem service provision. These should also be species that are relatively sensitive to pesticide exposure. Other life-history traits, especially those proven to be relevant for the recovery process, need to be taken into account. For instance, the freshwater amphipod, *Gammarus pulex*, is a good representative of a species that is sensitive to a myriad of chemicals, and plays an important role in the decomposition process in the aquatic environment. However, species that are important for transfer of energy between the freshwater and terrestrial ecosystem are aquatic insects; many other species depend on them. Several insect species with different life-history traits, based on the specific service they might provide, should, therefore also be taken into account. Bearing in mind that ecological zones in Europe are well studied, such decisions should be feasible. A harmonized and coherent risk assessment process, thus, needs to develop several climatic or ecological scenarios which would provide basic guidelines on expected ecology of the species or the system. Similar efforts have been done in the field of pesticide fate assessment (Forum for Co-Ordination of Pesticide Fate Models and Their Use 2001), but clearly with the exclusive focus on assessing fate in different regions of Europe. For assessing risks to biota, defined temperature (water and air) scenarios will ensure that risks are assessed on species exhibiting the realistic number of generation. This is especially relevant for flexible species, such as the water louse, *Asellus aquaticus*, known for its ability to increase the number of generations, from uni- to multivoltine, in one year, depending on water temperatures. Therefore, for the purposes of ERA in southern parts of Europe, ecological models should include more generations, if not even the continuous reproduction for this species. However, in southern regions, the lack of precipitation in summer months results in total desiccation of water systems, imposing another type of stress to populations exposed also to chemicals. By simply assuming continuous reproduction, ecological factors relevant for a realistic risk assessment might be omitted. Currently, such factors are not commonly taken into account, leaving room for standardization and improvement of the risk assessment process. A European wide agreement on the important ecological characteristics of chosen species should be the first step to bridge these deficiencies.

Strictly defining the relevant ecological knowledge on species of interests, and landscape and regional contexts should not limit the development of new tools and methods including ecological models. In other words, regulatory guidelines should prescribe which aspects of the species, including interactions with its abiotic and biotic environment, need to be taken into account, but should allow researchers to develop tools as they deem necessary for a scientifically underpinned ecological risk assessment. Healthy competition in the field of ERA might, in the coming years, yield interesting modelling solutions for current issues and challenges.

In conclusion, the ecological risk assessment of pesticides has moved forward from simple laboratory studies to include more ecology, making it a more exciting and a more complex field. The issue of recovery assessment requires knowledge on species traits, landscape and toxicant characteristics and their interactions. It is a very challenging and timely issue that needs to be tackled by all stakeholders in the ERA process.

Appendices

Appendix 3.1.

Description of the population model of the water louse, *Asellus aquaticus*

The model description follows the ODD protocol for describing individual- and agent-based models (Grimm *et al.* 2006; Grimm *et al.* 2010).

Purpose

The purpose of the model is to assess the effects of stress on population dynamics of the water louse, *Asellus aquaticus*, especially in terms of how population recovery potential depends on the landscape structure and timing of stress, i.e. pesticide exposure.

Entities, state variables, and scales

Entities in the model are waterlouse individual females and square cells comprising the habitat. For individual females we distinguish between juvenile and adult stage.

Individual state variables are individual's age [days], size [length in mm], hatching date [day in the calendar year], lifespan [days] and location [continuous X and Y coordinates] in the landscape. Adults, i.e. individuals older than 44 days, have additional variable reproductive status which takes on the value of either 0 (= not yet reproduced) or 1 (= reproduced, i.e. released its offspring).

We simulate three types of habitats (figure 1):

a) Ditch - consists of a string of 100 cells representing the aquatic habitat
b) Stream – consists of a string of 100 cells representing the aquatic habitat, with drift as an additional type of movement
c) Fragmented landscape – where 100 cells representing small waterbodies are randomly dispersed in a grid of 50x50 cells (see below)

The state variable of cells is the local mortality of *Asellus* induced by pesticides and by the density of individuals in the patch. Each cell represents 1 m^2.

The time step in the model is one day. There are 365 days in a year. Simulations start on day 0 (Jan 1) and go for 6 years or until there are no surviving individuals left. The output is evaluated only after the second year to avoid transitional effects. The table with all parameters and their distributions is provided at the end of this document (table 2).

MASTEP is programmed within the NetLogo platform (Wilensky 1999).

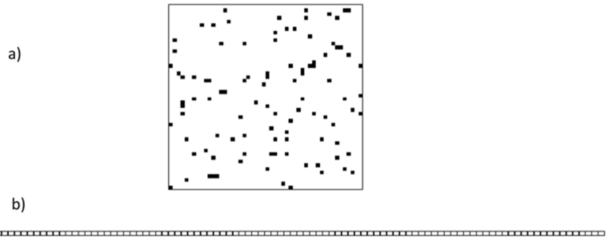

Figure 1. A picture representing a) fragmented habitat and b) the ditch in the model. The fragmented habitat consists of 100 aquatic cells (black) randomly positioned in a 50x50 cell grid. Ditch consists of a string of 100 aquatic cells

Process overview and scheduling

Every time step (day), the following processes, or submodels, are scheduled for all individuals in a randomized sequence for each process; state variables are updated immediately (asynchronous updating):

Aging (Increase age of individuals by one time step)

If **Mortality** of juveniles and adults (background and density- dependent)

Delete from the population

Else

Move – same for all

Move-drifters – only in the stream

Grow – both juveniles and adults grow until they reach maximum size

Mature – when they reach 45 days, juveniles become adults

Reproduce - once per each individual adult, 2 generations in 1 year

Pesticide mortality

Update plots and outputs

Design Concepts

Basic principles. The model relies locally on a phenomenological representation of density-dependent effects, i.e. density-dependence is based on observation, but not on mechanistic representation. Individuals will be affected by their conspecifics in a single habitat cell. Another principle explored is the effect of movement on recovery, and of metapopulation and rescue effects, i.e. of individuals immigrating from other, unstressed areas.

Emergence. Population dynamics and in particular the response of the population following pesticide-induced mortality arise from individual behaviour (reproduction and movement) and local, within-cell density-dependent effects.

Interaction. Individuals interact indirectly via local density-dependent effects on growth, reproduction, and mortality, where growth and reproduction are decreased whereas mortality is increased with increasing density in the cell where the individual is located (see details sections for more information).

Stochasticity. Values of most parameters are drawn from probability distributions obtained from literature data to represent natural variability observed in waterlouse populations. All parameter values and distributions are shown in Table 2.

Observation. For model testing and analysis, the dynamics of the local (10 cells) and total population (all 100 aquatic cells), population death rate and size distribution of the whole population are observed. Furthermore, time to recovery, i.e. the number of days needed for exposed population to reach 95% of the reference population, which had not been exposed to pesticides was calculated.

Initialization

The initial population of adult individuals is set to 300, 3 individuals per cell, each with a given size, drawn from a normal distribution (mean 3 mm, SD 0.2, based on Chambers (1977)). Individuals are randomly distributed within their aquatic habitat and have their variables defined at the start of the simulation (Table 1).

The following pseudo-code gives an overview of the initialization process:

```
initialize all cells:
      set pesticide mortality level…
  initialize Asellus individuals within the cell
               set size
               set age
               set location …]]
```

<u>Pesticide exposure</u>

Cells in the habitat can be exposed to pesticides or not; those that are exposed simulate a 24h LCX (where x can be from 1 to 100%) on different dates, resulting in 1 time (1 time step) effects on the population. Fate of pesticides in the environment is not considered in this version, i.e. mortality is only cased on the day of application.

Input data

The model does not include external input, i.e. there are now external drivers of system behaviour such as temperature, rainfall etc.

Submodels

There are four submodels in the population model: mortality, dispersal, growth and reproduction.

MORTALITY

Individuals suffer from three types of mortality: background, density-dependent and pesticide induced. Mortalities and their probabilities are sequential, and not additive.

First is the background or natural mortality, based on the lifespan of *A. aquaticus* in NW Europe (up to 600 days in Vitagliano *et al.* 1991). Natural mortality is related to age, reproductive status, predation, and we assume juveniles experience a higher mortality rate than adults (Van den Brink *et al*. 2007). Because the shape of the survival function is not known, we follow the assumption by Van den Brink et al. (2007) and we assign each individual a lifespan from an exponential distribution with a mean 90, resulting in less than 1% of individuals surviving longer than 400 days. Once the number of time steps in the simulation reaches an individual's lifespan, it will die and be erased from the population.

Including density-dependent mortality is an indirect way of modelling resource competition, because we do not model resource dynamics. Even though underlying mechanisms of density dependence are not known for this species, it is known that populations of *A.aquaticus* are regulated to a certain level by their densities (see e.g. Adcock 1979; Iversen & Thorup 1988; Van den Brink *et al.* 2007); we follow the mortality based on local densities, μ_{dd}, from Van den Brink *et al*. (2007), where

$$\mu_{dd} = \mu_1 \cdot N \qquad \text{eq. 1}$$

where μ_1 is a parameter governing the steepness of the density dependence (m^2/ind*d) and *N* is the local density (ind/m^2). Density-dependent mortality is cell based, so all individuals in one cell have the same probability of dying due to overcrowding.

Eq. 1 is the simplest assumption on effects of density, where each individual has a certain effect on the survival of each of its conspecifics within the cell. We provide a sensitivity analysis of the model output in relation to various density-dependent mortality functions.

In this version, mortality due to a hypothetical pesticide is implemented as a cell specific mortality probability (i.e. all individuals in a given cell have the same probability of dying), which range from 0 to 1. The pesticide is assumed to only be toxic on day of application (see table 3 for more information on application days).

MOVEMENT

Very little data exists on movement patterns and speed of *A.aquaticus* individuals. Van den Brink *et al*. (2007) calculate the mean residence time of individuals in one cell of 1 m^2 to be 51 minutes, of which one third is spend moving and two thirds are spend resting. Englund and Hamback (2004)(Englund & Hambäck 2004) describe the step length frequency distribution of individuals of *A. aquaticus*, where the majority of steps fall between 0 and 4 cm, both downstream and upstream. Yet, no estimations are made on the daily step frequency; therefore it is not known how much individuals of this species can move in one day. As movement is important for recolonization and recovery dynamics (Niemi *et al.* 1990; Holomuzki & Biggs 2000; Albanese, Angermeier & Peterson 2009), we estimated daily movement distances in the following way.

Active movement in the ditch

In this model, we assume that individuals move one step per minute, and that they move 480 minutes of the day (1/3 of 1440 minutes in 24 hours). As the exact details on *Asellus* movement are unknown, we assume they follow the correlated random walk (CRW) rules where each new orientation of an individual depends probabilistically on the previous orientation, i.e. there is a preference to continue in a similar direction, depending on the defined angle of a circular distribution. This approach seems to work for many animal species where exact movement patterns were analysed (see (Turchin 1998)).

We used the von Mises probability distribution, a normal distribution on the circle, given by the following equation

$$f(x) = \frac{e^{\kappa \cdot \cos \cdot (x-\mu)}}{2\pi \cdot I_0(\kappa)} \qquad \text{eq. 2}$$

where $I_0(\kappa)$ is the modified Bessel function of order 0. μ is the mean of the distribution, while the variance is defined by κ. The smaller κ, the more diffused the distribution is and resembles a uniform distribution at value 0. The larger values of κ are, the distribution centers more around the mean, which means that if used in CRW procedure, the movement will be very directed. For our purposes, both μ and κ are estimated from experiments (*pers.comm.* Van den Brink, see Table 2).

Once the new turning angle is drawn from the afore defined distribution, each individual moves the distance of the chosen step length. Based on the work of Ruijter et al. (*pers.comm.* Van den Brink) we approximate a step length distribution (see table 2).

Because small, individual movement occurs on a very fine time scale (in minutes), while the basic time step in the model is 1 day, we chose to simulate the fine dispersal separately and include only the distances covered after 24 hours in the population model.

We simulated dispersal of 100 000 individuals in a ditch, for 480 minutes (under the same assumption that individual move one third of their time), all starting from the same position in one cell, counted the number of individuals in each of the cells after the simulation and from that, estimated the probability distribution of distances each individual is expected to cover in one time step (fig 2.). See table 2 for all the parameter estimations.

In the population model, all of the individuals of the initial population and their subsequent offspring are positioned randomly within a cell. In each time step, each individual will be assigned a random number from the simulated distribution and will change its x coordinate accordingly, by moving to the left or to the right from their initial position. In that way, individuals move from cell to cell, but keep the same location within the cell. Since conditions within each cell are uniform, location within each cell is not considered important.

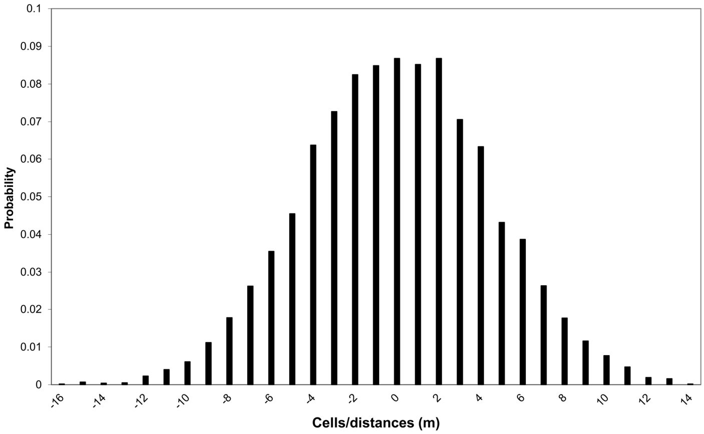

Figure 2. Distribution of distances covered from cell 0, movement 1/3 of one day (480 minutes).

Active dispersal in the fragmented landscape

The fragmented landscape represents a network of small habitat cells, out of which some are connected and some not. There are 20 simulation landscapes that we test that differ in the position of aquatic cells within the terrestrial matrix. Thus, individuals draw a random number from the same distribution obtained from small scale dispersal simulation (as described in previous section, Table 2) and use this as a radius in which they can find an aquatic cell. If they draw a number lower or equal to 1, they stay in their current cell. If they draw a larger value, they look in that radius for an adequate cell.

In this way, we obtained a dynamic metapopulation, with common local extinctions and colonisations.

Passive dispersal

In the modeled stream landscape, individuals can also go through passive movement, i.e. drift. Drift is a common mechanism of passive dispersal in many aquatic arthropod taxa and refers to downstream transport in stream currents (see e.g. (Elliot 1967; Waters 1972), and a review by Brittain and Eikeland 1988). It is, thus, considered to be a very important mechanism of recolonization in disturbed lotic environments (Lake 2000).

In our model, a certain percentage of individuals drift to a distance (z) that is specific for each individual, i.e. from x to x + z. This drifting distance is assigned to each individual from an exponential distribution with a mean of 10 m at each drift event (based on vd Brink et al. 2007).

We provide a more thorough sensitivity analysis of model output with respect to different movement parameters.

GROWTH

Individuals grow following the von Bertalanffy growth equation (von Bertalanffy 1957), leading to a logistic growth curve which is observed in most isomorphs under constant food conditions:

$$l(a) = l_{\max} \cdot (1 - e^{-k \cdot a})$$ eq. 3

where l_{max} is the maximal length an individual can reach, κ is the daily growth rate and a is age (days). The maximum size of individuals varies depending on the region, between 11 and 12 mm in the publication by (Økland 1978), (Chambers 1977)reports 9 mm, (Arakelova 2001) 10 mm and (Marcus, Sutcliffe & Willoughby 1978) up to 12 mm.

The newly hatched individuals are assigned an initial size, normally distributed with a mean of 1 mm and SD of 0.2 mm (Adcock 1979). Following the growth function (with a growth rate as in table 2), an individual starting with 1 mm length needs 145 days to reach 95% of the maximum given size, i.e. 11.4 mm.

Daily growth increment is then the derivative of eq.3

$$\frac{dl}{da} = \kappa \cdot l \cdot \left(\frac{l_{\max}}{l} - 1\right)$$ eq. 4

We assume that growth is density dependent, and decreases exponentially with high densities in a patch (figure 3). The density dependent growth factor< *DDG*, is expressed as

$$DDG(density) = e^{-y/K} * density$$ eq. 5

where y is the scaling factor of the function, and K is the local (cell specific) carrying capacity.

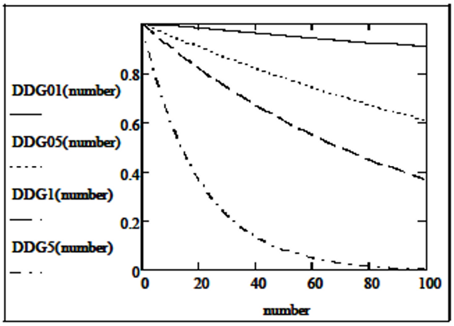

Figure 3. The strength of individual growth dependence on local densities is expressed with a scaling parameter. The carrying capacity in this figure is 100 individuals, and 4 different values are depicted, namely 0.1, 0.5, 1 (the default value) and 5.

The reasoning behind implementing density-dependent growth is the publication of (Hynes & Williams 1965) who experimentally show that waterlice populations produce more offspring when housed in larger jars; even though the amount of food in their experiments was the same, the lower productivity indicates certain effects of, possibly interference, competition resulting in lowered production.

We approximate the effect of less preferred habitat or scarce resource by including the effects of density on daily size increments, i.e. individual growth rate, in such a way that when the density in a cell reaches the assigned carrying capacity, each individual has a decrease of 60% in size of its increment (green line in fig. 4).

Figure 4 shows (mean individual) growth trajectories at different constant densities (density dependent scaling parameter is set to 1, there are 50 individuals in the population), where the carrying capacity of the system varies. At K=100, population abundance of 50 individuals is at the middle of its capacity, at K=50 population of 50 individuals is just at its capacity, and, finally, at K=10 the population is five times over its capacity.

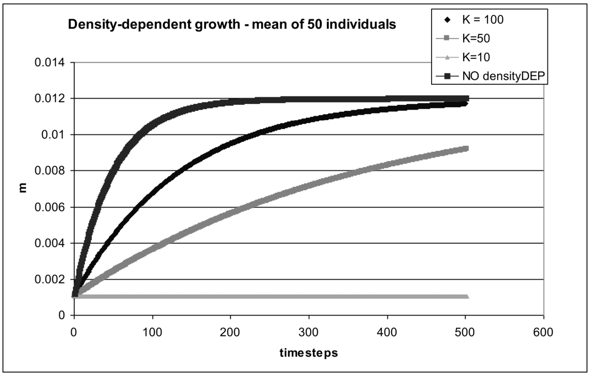

Figure 4. Mean values of individual growth trajectories of populations under different densities. *m* is the size in meters, and “timesteps” are in days. There are 50 individuals in this population (that only go through the growth procedure), their growth is modeled under no density-dependent effects, and under set K of 10, 50 and 100.

With no density dependent effects, individuals reach their maximal size by day 200, whereas it takes them around 300 days longer in case when the density is half of the set carrying capacity (K=100), and much longer in case the population is at its K (K=50). If the density exceeds carrying capacity by 5x (K is 10, fig 4.) individuals almost stop growing.

In the default parameter set, cell carrying capacity is fixed to 100 while on average there are between 10 and 60 individuals per cell. Individuals change their position in each time step and the effect of densities on individual growth rate is calculated with new densities each new time step.

We performed a sensitivity analysis of the model output with respect to presence and absence of density-dependent effects on growth.

REPRODUCTION

Voltinism, i.e. number of generations in a year, of aquatic arthropods is typically governed by environmental conditions, mainly through water temperatures. As we do not include external temperature data in the model, we introduced two periods in a year when individuals are able to reproduce. The reproductive periods start in the beginning of May (Julian day 210) and mid-July (Julian day 200), and they last 28 and 45 days (Table 1), respectively. In these reproductive periods each individual female releases its offspring once such that each adult female is assigned a random number from a uniform distribution, corresponding to the length of each reproductive period, that represents the day after the onset of each reproductive period at which she will release her offspring. For instance, after winter, an adult female is assigned a number 12 (from a uniform distribution between 1 and 28) and it will release its young at day 132 (onset 120 + 12). The same goes for the spring generation, individuals hatched in spring whose reproductive period starts at day 200. Such an individual is assigned a value, e.g. 20, from a uniform distribution (between 1 and 45) and will release its offspring on day 220.

Fecundity

Individuals are allowed to reproduce only once in their lifetime, as this is most commonly observed (Chambers 1977). The number of offspring (clutch size) is size-dependent and is positively correlated with size (Chambers 1977)(fig 5)

$$Noffspring = (\_\frac{current\_size}{\max imum\_size}) \cdot \max imum\_clutch\_size \qquad \text{eq. 6}$$

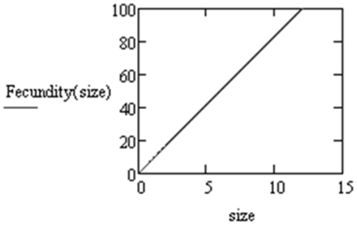

Figure 5. Relationship between size and number of offspring each female releases in 1 reproductive cycle.

Each adult, thus, gives birth to a given number of juveniles and dies immediately after. Females from the winter generation are bigger and will have more offspring per female, but are fewer to start with; summer females are smaller, as by the time they start reproducing (after around 80 days and less), they will be maximum 9 mm long (according to Okland 1978, summer females are up to 7 mm in length).

Different authors report different clutch sizes in water lice females with a size of 12 mm, ranging from maximum of ca. 100 (Arakelova 2001), 125 (Graça, Maltby & Calow 1993), 250 (Ridley & Thompson 1979) to more than 300 (Tolba & Holdich 1981). Here we fixed the maximum clutch size to 100 individual females (we do not model male individuals), but the realized clutch size, averaged over the whole year, in the modeled population reaches 75 individuals per female.

Table 1. Table with the initial parameter set.

Parameter	**Distribution**	**Value**	**Unit**	**Reference**
Size (length)	normal	mean 3, SD 0.2	mm	Okland (1978), Arakelova (2001) Marcus et al. (1978)
Lifespan	exponential	mean 90	days	adapted from Vitagliano (1991)
First reproduction day	uniform	1 to 28	days	adapted from Chambers (1977)
Second reproduction day	uniform	1 to 45	days	adapted from Chambers (1977)

Table 2. List of model parameters.

Submodel	Parameter	Distribution	Value	Unit	Reference
Habitat	system carrying capacity, K	constant	10 000	ind	Constant K per patch (growth related)
Mortality	lifespan	exponential	Mean 90		adapted from Vitagliano (1991)
	µ1	constant	0.001		Based on vd Brink et al. (2007)
Reproduction	onset of 1st reproductive cycle	constant	120 (April/May)	day	mimicking western European conditions
	onset of 2nd reproductive cycle	constant	200 (July)	day	
	maximum clutch size	constant	100	ind	Adapted from Tolba and Holdich (1981)
	length of 1st reproduction period	uniform	1 to 28	day	Adapted from Chambers (1977)
	length of 2nd reproduction period	uniform	1 to 45	day	Adapted from Chambers (1977)
Growth	maximum size	constant	12	mm	Okland (1978), Arakelova (2001), Marcus et al. (1978)
	minimum size	distribution	mean 1, SD 0.2	mm	Adcock (1979)
	kappa, k	constant	0.02	/ day	determined by calibration
	age at maturity	constant	45	day	(Williams 1962)
	density-dependent factor, *y*	constant	1		own estimation (see sensitivity analysis)
Dispersal	drift distance	exponential	mean 10	m	based on vd Brink et al. (2007)
	κ, variance of von Mises distribution	constant	1.73	rad	Pers. Comm. Van den Brink, de Ruijter 2006
	μ, mean of von Mises distribution	constant	0.5201	rad	Pers. Comm. Van den Brink , de Ruijter 2006
	step length	lognormal	Mean – 2 .83, SD 0.92	m	Pers. Comm. Van den Brink , de Ruijter 2006
	daily dispersal distances	normal	Mean 0.004, SD 4.444	m	Own simulation (more in Dispersal simulations)

Table 3. Simulated model experiments (the difference between the ditch and stream modeled landscapes is solely in allowing individuals in the stream to drift, thus it is expressed through individuals' attributes, rather than environmental factors).

Scenario	Landscape	Pesticide toxicity	Exposure	Stress events
1.	Ditch	LC50 LC100	100% 50% of landscape	110 160 210 260
2.	Stream			
3.	Fragmented			

Appendix 3.2

Sensitivity analysis of the Asellus model

We tested the robustness of model output to changes in parameters and functions. Due to a lack of information and data on density-dependent processes, resulting in various assumptions in the model, these functions have been especially tested. Since the recolonization process is dependent on the movement ranges of the species, we also looked into how different movement distributions affect the final output. To make it a bit simpler, we only used the ditch habitat for the analysis.

All the comparisons and results are presented in the form of violin plots, and Wilcoxon rank test was used to check for differences between the new and standard parameter set.

Violin plots are a combination of boxplots and kernel density plots; they are very similar to boxplots, but show the probability density of data at different values. We chose to present data in this form as they show more information than just boxplots, especially relating to the period of recovery, where in some cases they clearly show a bimodal distribution of recovery times, meaning that one part of simulated populations recover within one period, and the other within another. All the violin plots include a marker denoting a median value, and also the exact value of the median.

1) **daily movement distances**

Here we checked whether changes in the parameters of the von Mises distribution, step size and the time spent moving significantly change the model output. We simulated several scenarios with new parameter combinations (movement simulations described in detail in model ODD) (Table 1), all the other parameters remain as in table 1 of the ODD.

Daily movement is assumed to take place only one third of the day so we tested this assumption by doubling the time of daily movement, from 480 to 960 minutes (increased movement time scenario). This yielded a daily movement distribution with a standard deviation of 6.28 m that was used in the population model.

Similarly, we increased the step size, obtained a standard deviation of 10.91 m for the daily movement distribution that was implemented in the population model (increased step size scenario). The means were kept as in the original parameter set. Increasing the mean and standard deviation of the von Mises distribution yielded a standard deviation of the movement distribution that fell in between the standard run and the one with increased movement, i.e. 5.12, so this was not included in further analysis.

Finally, we decreased the standard deviation of the movement distribution to 1.44 and looked for differences.

Table 1. All movement scenarios.

Scenario	min	vM mu	vM kappa	Mean stepSize	SD stepSize	**Resulting distr (mean ± SD) m**
standard	480	0.5201	1.73	-2.83	0.92	**0.03 ± 4.44**
timeVar	**960**	0.5201	1.73	-2.83	0.92	**-0.09 ± 6.28**
50%+vM	480	**0.7801**	**2.59**	-2.83	0.92	**0.27 ± 5.12**
+1ssM	480	0.5201	1.73	**-1.83**	0.92	**-0.19 ± 10.91**
Small SD						**0.03 ± 1.44**

Increased movement time scenario (SD of 6.28 m) yielded similar results to standard runs (fig. 1 for the total population, fig. 2 for the 10 m population).

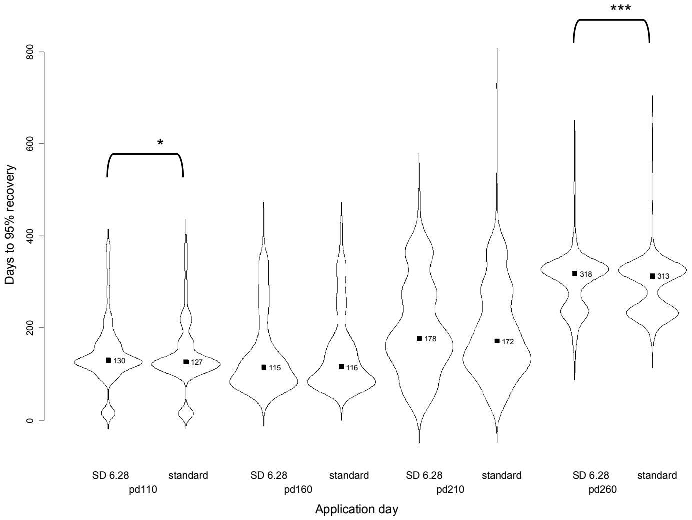

Figure 1. Comparison of the recovery times for a total population after stress events at 4 different times in one year, increased movement (SD 6.28) versus standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

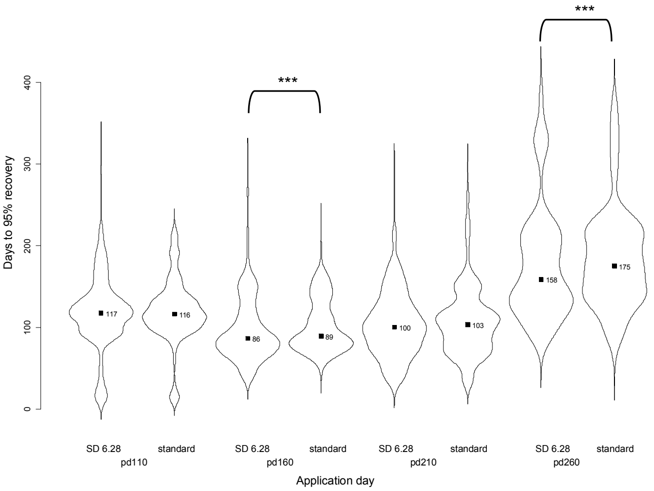

Figure 2. Comparison of the recovery times for the 10 m population after stress events at 4 different times in one year, increased movement (SD 6.28) versus standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

Similar results were obtained with even higher standard deviation of movement, in the increased step size scenario (SD of 10.91 m) (fig 3 for the total, fig 4 showing the 10 m population recovery).

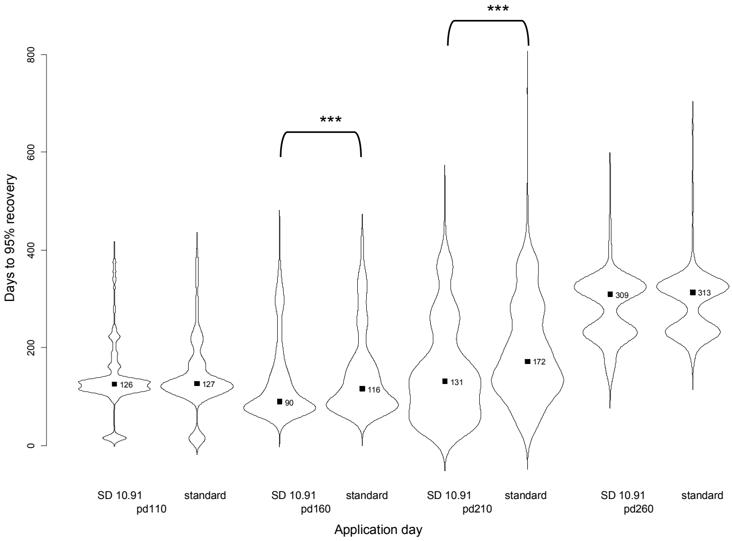

Figure 3. Comparison of the recovery times for the total population after stress events at 4 different times in one year, increased movement (SD 10.91) versus standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

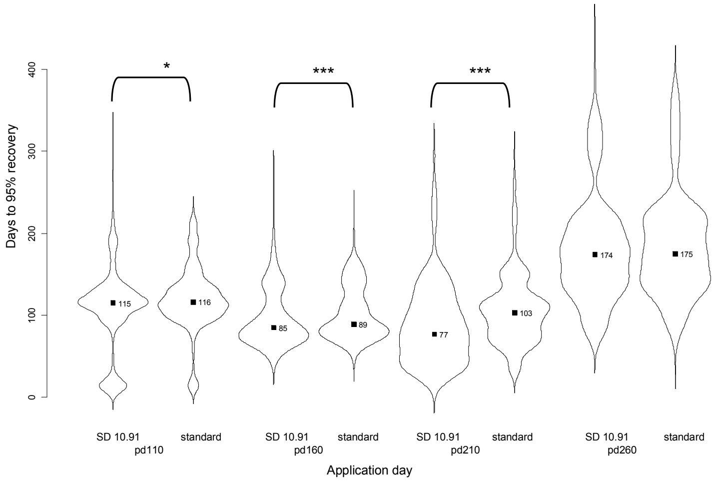

Figure 4. Comparison of the recovery times for the 10 m population after stress events at 4 different times in one year, increased movement (SD 10.91) versus standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

These results show that there are some differences in the final output, i.e. recovery times, of the standard and changed parameter set. However, these differences are not very consistent. For instance, figures 1 and 3 show the comparison of recovery times of the total population with 2 different standard deviations of the movement distribution. In the increased movement time scenario (fig. 1), recovery after the first and the last application day differ between the standard and changed parameter set. In the increased step size scenario (fig. 3), recovery times after the two applications in the middle differ significantly. Because the main difference between the two is the extent of the standard deviation of movement (which is bigger in both cases), it is expected that the differences would also be consistent. This leads to the conclusion that these differences occur not only due to the changed parameters and that the standard movement distribution results in a well-mixed system, making the final output relatively robust to increased movement.

However, decreasing daily extent of movement (SD 1.44) results in very clear and significant changes (figures 5 and 6). Most profound differences occur in the 10 m stretch, as it takes populations in the 10 m stretch much longer to recover due to limited movement. Though the differences are somewhat smaller, the same effects are visible on the level of total population (fig. 6).

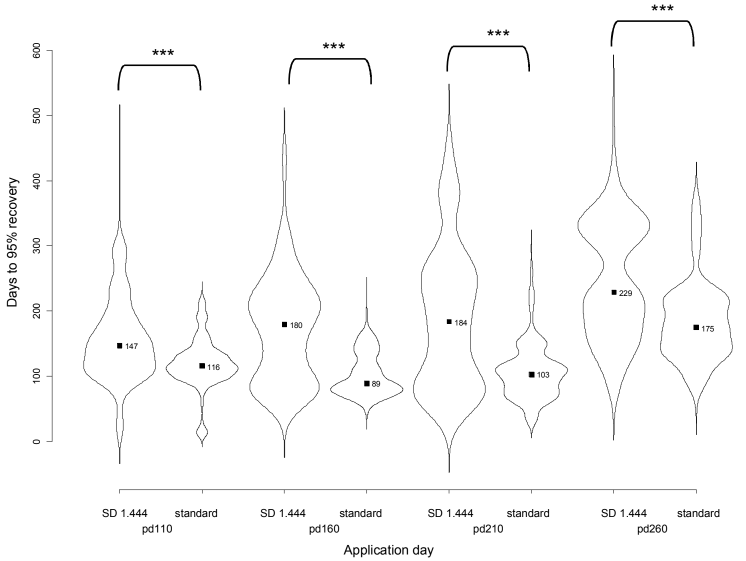

Figure 5. Comparison of the recovery times for the 10 m population after stress events at 4 different times in one year, decreased movement (SD 1.44) versus standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

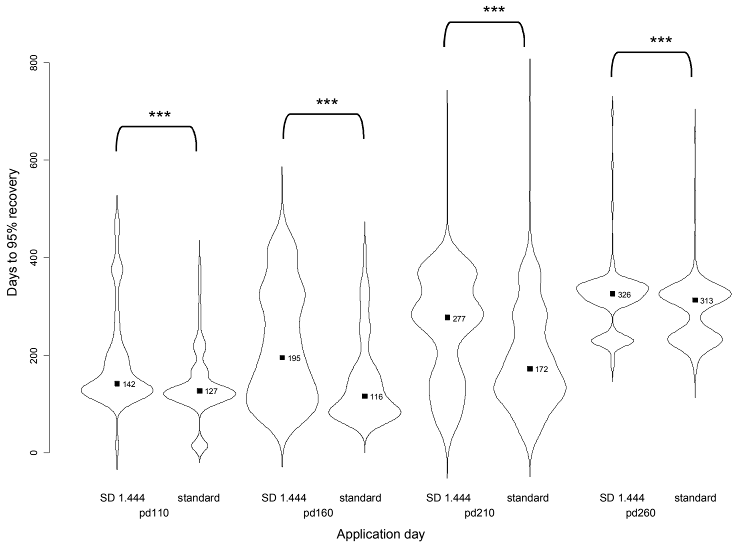

Figure 6. Comparison of the recovery times for the total population after stress events at 4 different times in one year, decreased movement (SD 1.44) versus standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

2) density dependent mortality

Due to a total lack of any data on density dependent processes that might be regulating waterlouse populations, we are forced to use functions with estimated parameters in order to have a certain control over the total population growth. We tested how the form of the function affects the final output.

We tested whether the final output is different when we implement a different function, namely the logistic function of density-dependent mortality (fig. 7 depicts both the standard, linear function and the logistic one).

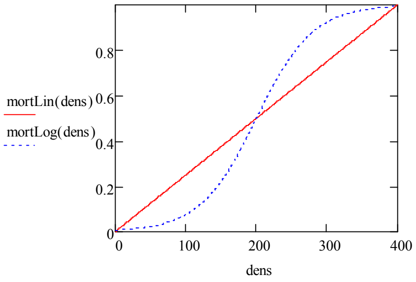

Figure 7. Linear density-dependent mortality function (red line) and the logistic form of density-dependent mortality (blue dotted line). Both functions result in mortality probability of 0.5 at carrying capacity (here at density of 200 individuals).

Figure 8 shows that there are significant differences in the final output where the logistic function was implemented, in comparison with the linear. It is also clear that the implementation of the logistic function consistently yields longer recovery times.

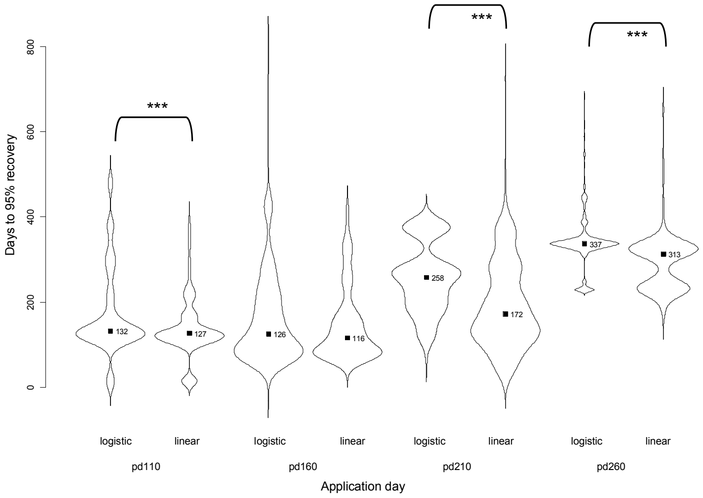

Figure 8. Comparison of the recovery times for the total population after stress events at 4 different times in one year, logistic density-dependent mortality function versus standard, linear function. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

The decision to use the linear function in the population model was supported by the fact that the density regulation using the logistic function has very little effect when the abundances are very low, and very strong effects if the abundances are very high in one time step (see fig. 5 for the form of both functions). This often resulted in total mortality of all individuals in a single cell due to, for instance, the release of offspring. For the reason that the actual density regulation is not known for this species, we decided to use the simplest form of density regulation, the linear function.

Additionally, we changed the density regulating parameter, resulting in higher abundances obtained in the population model. Figure 9 shows the final output for the standard and changed parameters regulating densities in the model.

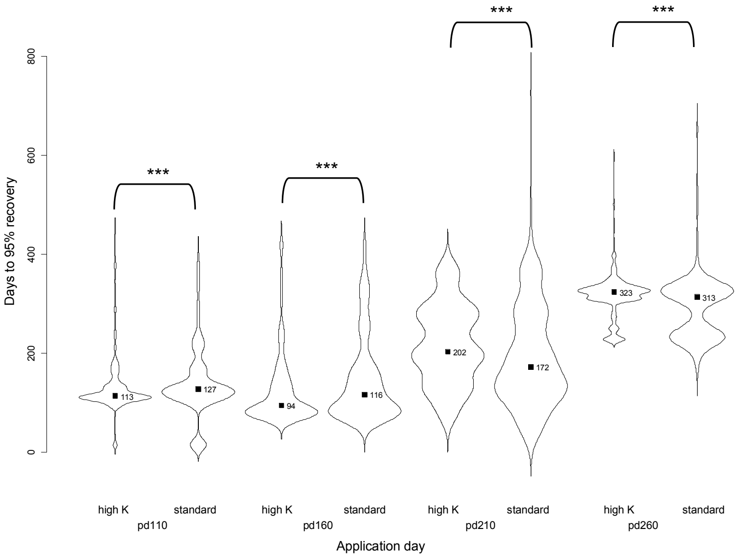

Figure 9. Comparison of the recovery times for the total population after stress events at 4 different times in one year, changed parameter regulating densities (0.0005) versus standard parameter (0.001). Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

We expected no differences due to higher attained densities of individuals in the model, but the results show there are differences for each of the stress events. However, the differences are not consistent, for the first two events, the median number of days needed for populations to recover is smaller for populations experiencing higher densities, whereas for the second two events, recovery takes longer.

Finally, we increased the value of the density regulating parameter (from 0.001 to 0.0015) which resulted in smaller overall abundances, but no major differences in recovery times. When the same parameter was increased even further, i.e. to 0.002, some populations failed to recover in the given time, whereas at the value of 0.003, some went extinct, thus showing the effect of small abundances being under strong influence of demographic stochasticity.

We only show the results of recovery of the total population, comparing the standard parameter set with increased density regulating parameter (figure 10).

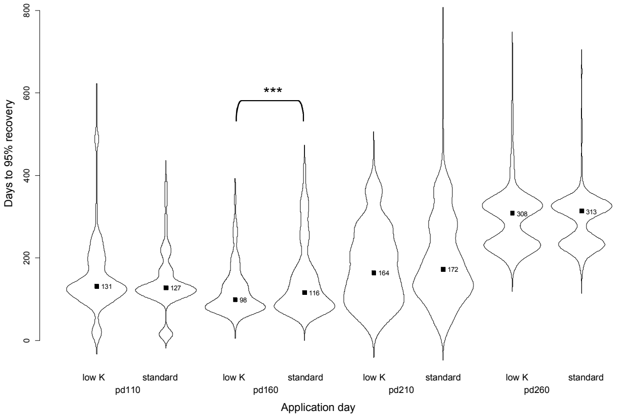

Figure 10. Comparison of the recovery times for the total population after stress events at 4 different times in one year, changed parameter regulating densities (0.0015) versus standard parameter (0.001). Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

3) density-dependent growth

The standard model includes density dependent effects on individual growth, a phenomenon observed in many species (such as fish) where the resource deficit results in decreased individual growth rates. Due to a lack of data for this assumption in our model, I tested whether there is a difference in the final model output when the individual growth is density independent. Figure 11, shows the plotted recovery times for the total population, comparing the density independent growth (termed DinD) and density-dependent growth of individuals.

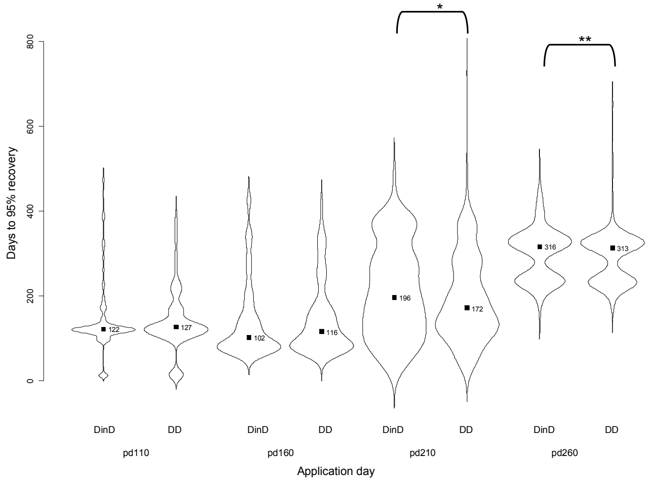

Figure 11. Comparison of the recovery times for the total population after stress events at 4 different times in one year, density independent individual growth (DinD) versus standard, density-dependent growth of individuals (DD). Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

There are no differences for the first two events, and some difference for the last two events. Even with smaller effects of density independent growth on recovery, we can conclude that, with the current parameter set, densities regulated growth does not have a substantial effect on the final model output, i.e. time to recover.All differences between medians of the standard and altered parameter set are shown in table 2. It represents a summary of all the above depicted analyses.

Table 2. Differences in median values of recovery times, after four application periods and for populations in both 10 and 100 m^2 ditch stretches. + or – signs indicate whether the median recovery value is smaller or larger than in the standard parameter set. Wilcoxon rank test, *, P< .05; **, P < .01; ***, P < .001.

	10 m population				**100 m population**			
	pd110	**pd160**	**pd210**	**pd260**	**pd110**	**pd160**	**pd210**	**pd260**
SD 6.28 (fig 1&2)	0.8%+	3.4%-(***)	3%-	10%-(***)	2.3%+(*)	1%-	3.4%+	1.5%+
SD 10.91 (fig 3&4)	0.9%-(*)	4.5%-(***)	25.3%-(***)	0.6%-(***)	0.8%-	22.5-(***)	23.9%-(***)	1.3%-
SD 1.44 (fig 5&6)	27.3%+(***)	202%+(***)	179%+(***)	131%+(***)	12%+(***)	40.5%+(***)	62%+(***)	4%+(***)
logistic DD (fig 8)	/	/	/	/	3.9%+(***)	8%+	50%+(***)	7.2%+(***)
higher K (fig 9)	/	/	/	/	11.1%-(***)	19%-(***)	17%+(***)	3%+(***)
lower K (fig 10)	/	/	/	/	3%+	21%-(***)	5%-	2%-
DD growth (fig 11)	/	/	/	/	4%-	13.7%-	14%+(*)	1%+(**)

Appendix 4.1

Description of the population model of the freshwater amphipod, *Gammarus pulex*

The model description follows the ODD protocol for describing individual- and agent-based models (Grimm & Railsback 2005; Grimm *et al.* 2006).

Purpose

The purpose of the IBM was to quantify the effects on survival after exposure to four different pesticides and the consequences of this reduced survival for population recovery of *Gammarus pulex*. Both the TDM and the dose-response model were implemented as different submodels to translate pesticide exposure to effects on individual survival.

State variables and scales

Entities in the model are individual females and square cells comprising the landscape. Individual state variables are age [days], size [length in mm] and location [continuous X and Y coordinates] in the landscape. We distinguish between a juvenile and an adult stage. Adult females, i.e. individuals bigger than 6.5 mm, have in addition a counter that counts the number of broods realized (from 0 to 5 or 6).

We simulate one type of landscape, namely a ditch, consists of a string of 200 cells of aquatic habitat (Figure 1). The state variable of cells is the mortality probability induced by pesticides and by the density of individuals in the patch. Each cell represents 1 m^2.

The basic time step in the model is one day, whereas the TK-TD process is modelled in 5 minute time steps. There are 360 days in a year. Simulations start on day 0 (Jan 1) and go for 10 years or until there are no surviving individuals left. Populations are exposed in the third year of the simulation, and the first two years of the simulation are discarded to avoid transitional effects in the output. All species- and pesticide-relevant parameters and their distributions are listed in Tables 1, 2 and 3.

The model is implemented in the NetLogo platform (Wilensky 1999).

Figure 1. The landscape consists of a string of 200 aquatic cells.

Process overview and scheduling

Every time step (day), the following processes, or submodels, are scheduled for all individuals in a randomized sequence for each process; state variables are updated immediately (asynchronous updating):

Aging (Increase age of individuals by one time step)

If **Mortality (background + density dependent)**

Delete from the population

Else

Move – same for all individuals

Reproduce – only adults

Grow – both juveniles and adults until they reach maximum size

Pesticide induced mortality

Update plots and outputs

Design Concepts

Emergence. Population dynamics and in particular the response of the population to pesticide-induced mortality arise from individual behaviour (movement) and local, within-cell density-dependent effects.

Interaction. Individuals interact indirectly via local density-dependent effects on mortality. Probability of dying increases with increasing density, based on the carrying capacity, of individuals in a local cell.

Stochasticity. Values of most parameters are drawn from probability distributions obtained from literature data to represent natural variability observed in gammarid populations. All parameter values and distributions are shown in Table 1.

Observation. For model testing and analysis, the dynamics of the total population, population death rate, age and size distribution, and mean individual size of the whole population are observed. In addition to pesticide concentrations, TKTD related processes, such as mean internal concentration, damage and hazard rate are also monitored. For the analysis of recovery times, we use daily abundances of 20 reference and 20 populations for each of the treatment scenarios.

Initialization

Data obtained from field research suggest that the most abundant size class of adult females and juveniles in January is 7 - 10 mm and 3 - 6 mm (Hynes & Williams 1965), or with means of 9 mm and 6 mm (Hultin 1971), respectively. According to these authors, proportion of juveniles in a population is around 15% at the same period. In our model, the initial population consists of adult females whose size is normally distributed around a mean of 9 mm with 1 mm SD, and of juveniles with length normally distributed around a mean of 5 mm and 1 mm SD. Proportion of juveniles is also adjusted to be 15%.

Individuals are randomly distributed within the landscape and have their variables defined at the start of the simulation.

The following pseudo-code gives an overview of the initialization process

```
initialize all cells:
      [set carrying capacity
    set pesticide mortality level…
          initialize Gammarus individuals within the cell
               [ set size
                set age
                set location …]]
```

<u>Pesticide exposure</u>

Cells in the ditch can be exposed to different pesticides, for different time periods and with varying intervals between exposure (simulation experiments are described in detail in the manuscript). Recovery after exposure to following pesticides was assessed: chlorpyrifos, carbaryl, pentachlorophenol and diazinon; all relevant toxicity parameters can be found in Tables 2 and 3. Fate of pesticides in the environment is not considered, we assume conditions similar to laboratory experiments, i.e. constant concentrations and total disappearance of the pesticide after exposure period.

Input

The model does not include external input for environmental variables, i.e. environmental variations are not considered.

<u>Submodels</u>

There are four submodels in the population model: mortality, movement, growth and reproduction.

MORTALITY

Individuals suffer from three types of mortality: background, density-dependent and pesticide induced.

Background mortality

Ashauer et al. (2007) estimate the daily background mortality probability to be 0.0071. Sutcliffe et al. (1981)(Sutcliffe, Carrick & Willoughby 1981) estimate a typical lifespan to be 350-450 days, where some individuals lived up to 700 days. Demyanov et al. (2006)(Demyanov, Wood & Kedwards 2006) also introduce background (or basic) mortality, which differs among instar stages, spans from 0.0014 to 0.03 and is, on average, 0.009.

Here we use 0.01 probability to die on a daily basis, which translates into, on average, 1% of the initial population of 1000 individuals, surviving until 540 days (Figure 2), which is in accordance with observations from Sutcliffe et al. (1981).

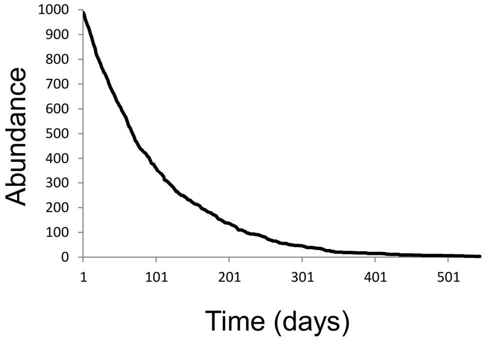

Figure 2. Survival of a population consisting of a 1000 individuals, with a 0.01 daily mortality probability. Time (days) on x-axis, abundance (individuals) on y-axis.

Density-dependent mortality

Not much is known about the density-dependent mortality in *Gammarus pulex* populations. Densities found vary based on the time of the year (with higher densities within reproductive events, and low in winter time), and reach densities of 200 to 20000 per m^2 (Welton 1979). (McGrath *et al.* 2007)find that juveniles are more sensitive than adults to densities, due to cannibalism. In the model, we assume that only juveniles are affected by local densities, i.e. each individual juvenile in a local cell is affected by the presence of its conspecifics, both juvenile and adult, in the following way (Van den Brink *et al.* 2007)

$$\mu_{dd} = \mu_1 \cdot N_{local} \qquad \text{eq. 1}$$

where μ_1 is the strength of the density-dependence and N_{local} is the density of a single cell (see Table 1 for parameter values). This term results in the same density-dependent mortality probability for all juveniles in a local cell per time step. We analysed the effects of different values of μ_1 on population abundance and population recovery time (see Appendix 4.2).

Pesticide induced mortality

Individuals are exposed to different concentrations of four pesticides in different exposure scenarios(see manuscript for the details). Mortality after exposure is modelled with two survival models:

a) Dose-response function – describes a change in effect, i.e. mortality, based on the pesticide exposure concentration. The sigmoidal model used in this model corresponds to (ref?)

$$mortality(Conc) = \frac{1}{1 + e^{slope\cdot(\ln Conc - \ln LC50)}} \qquad \text{eq. 2}$$

The LC50 and slope values used in the model were calculated using the parameterized TDM model (see below) for four different pesticides in order to avoid possible sampling errors while using published experimental data. Relevant parameters are listed in Table 3.

b) Threshold damage model (Ashauer, Boxall & Brown 2007a) – a TK-TD model that is more mechanistic than dose-response function and it accounts for individual recovery, i.e. recovery from a sublethal damage. It includes the following processes: uptake and elimination in the toxicokinetic part, damage and recovery in the toxicodynamic part of the model, and a hazard rate which is a probability that an organism dies at a given time step.

$$\frac{dC_{\text{int}}(t)}{dt} = k_{in} \cdot C(t) - k_{out} \cdot C_{\text{int}}(t) \qquad \text{Toxicokinetics} \quad \text{eq. 3}$$

$$\frac{dD(t)}{dt} = k_k \cdot C_{\text{int}}(t) - k_r \cdot D(t) \qquad \text{Toxicodynamics} \quad \text{eq. 4}$$

$$\frac{dH(t)}{dt} = \max[D(t) - threshold, 0] \qquad \text{Hazard rate} \quad \text{eq. 5}$$

In case of diazinon, the activation of its metabolite diazoxon is also included in the toxicokinetic process; the submodel is adjusted accordingly (Ashauer *et al.* 2010a).

All relevant parameters are listed in Table 3.

MOVEMENT

Elliott (2003) found that the distance (median ± 95% CL) *G. pulex* move within one day is 1.00 ± 0.12 m upstream and 0.94 ± 0.10 m downstream (max up 6m, max down 1.5) with stream flow from 0.04 - 0.35 m/s (mean 0.135 m/s). In another study, downstream dispersal/drift has been found to be 0.28 ± 0.10 m (water flow 0.032m/s) - 7.52 ± 0.74 m (water flow 0.962m/s) ^{4}.

In this model, all individuals are assigned a value form a normal distribution with a mean 0 and SD of 6 m. This translates into each individual starting from its cell position, which is 0, in the ditch and moving up or down, the movement length depending on the assigned value. Exact position within each cell is assigned at birth and only the x-coordinate changes throughout an individual's lifespan.

This model does not treat drifting separately from small scale movement. Some studies suggest that drift might be important factor determining local population densities while some found that only a small percentage of individuals is drifting (seven out of 280 ind = 2.5% (24-h), [3]). In many cases, drifting distances are rather small (2.88-5.66m [5]) and they are within distances of active dispersal. Therefore, drifting can be thought as already included in the movement process.

GROWTH

Individual growth of *Gammarus pulex* through its life span follows a logistic growth curve (Sutcliffe, Carrick & Willoughby 1981). According to different authors (Welton 1979; McCahon & Pascoe 1988a; Taylor, Rees & Pascoe 1994) newly hatched animals are 1.3 – 2 mm in length. Maximum size that females can reach at the end of their life is about 12 mm (Hynes 1955; Welton & Clarke 1980) or 13 mm (Maitland 1966; Welton 1979).

We implemented the individual growth function from Sutcliffe et al. (1981), but adapted for growth in lengths (mm), which also showed sigmoidal growth (Welton & Clarke 1980), rather than wet weights (mg)

$$l(a) = \frac{l_{\max}}{1 + e^{-r \cdot (a-i)}} \qquad \text{eq. 6}$$

where l_{max} is maximal length that females can reach (13 mm, Welton 1979); r is the individual growth rate (day^{-1}); a is age of individuals in days; and i is age of sexual maturity (set between 120 and 133 days), which is also the inflection point of the growth curve. Because McCahon and Pascoe (1988) found that individuals need 130 days at 13°C and Hynes (1955) found that 120 days are needed to reach sexual maturity at room temperature, in the model we assumed that individuals become adults and sexually mature at 6.5 mm.

Following eq. 6, if the life span of an individual is e.g. 450 days, it reaches the body length of 12.9 mm (figure 3).

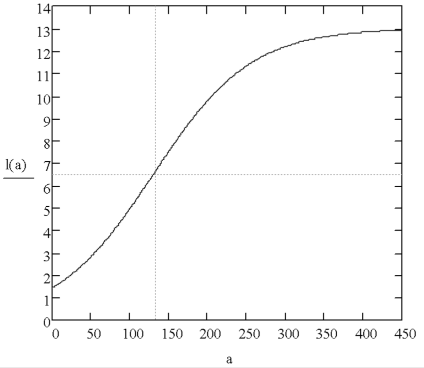

Figure 3. Individuals' logistic growth curve describes animals growth. They start growing at size (l) of around 1.5 mm, and until reach the age (a) of 450 days they are 12.9 mm in length.

REPRODUCTION

In NW Europe, breeding usually occurs from March till September (Hynes 1955, Welton 1979). Positive assortative pairing - that is large males paired with large females and small males with small females - usually occurs in G. *pulex* in the field ((Ward 1988)and references therein) and mating is sexually selected (Crane 1994). The reproductive behaviour of *G. pulex* is characterized by a precopulatory guarding phase which plays a key role in the reproductive cycle (Malbouisson, Young & Bark 1995). It is a complex ritual which ensures that insemination can occur as soon as the female moults and is ready to realize eggs into the brood pouch. The female is carried beneath the male, and the pair swim together for a few days until the female moults, and copulation takes place, normally within a few hours of release of the female's exuvium. Following fertilization the pairs separate, and the fertilized eggs are carried in a brood pouch on the ventral side of the female until hatching. Hynes (1955) has described that hatching occurs after some days and the young leave the mother's pouch after a day or two. Female becomes attractive to males again at, or slightly before, the time of hatching her eggs, and is often to be found in precopula while unhatched eggs remain in her pouch. Finally, three reproductive phases are distinguishable: precopula (ends with ovulation and copulation), incubation of eggs (ends at hatching juveniles in a brood pouch), and brooding of the newly hatched juveniles in the brood pouch. The number of broods produced by a single female can be 5 – 6 (Hynes 1955; Welton & Clarke 1980).

In the model, we assume reproduction takes place from mid-March until the end of October, i.e. from day 70 until day 300. We also simplify the reproductive phase and behaviour of gammarids, by, first of all, not including males in the population. Secondly, we merge the three phases into one at the end of which females release the young. The length of this phase is temperature dependent (Figure 4) (Nilsson 1977).

	1°C	**5°C**	**10°C**	**15°C**
Precopula	25±2.4	10±2.5	3±1.2	2±0.6
Incubation	110.5±6.6	59.3±4.9	33.6±2.2	20.6±1.7
Posthatch	12±3.8	6±2.4	2±0.4	/
n	12	18	21	23

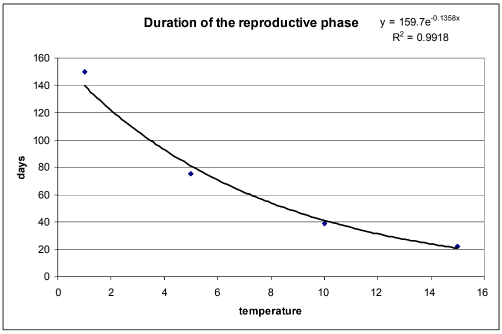

Figure 4. Dependency of the reproductive phase duration on water temperatures (from Nilsson 1977)

We simplify even more by not including temperature dependency and assume that the reproductive phase takes 30 days, as the average ditch water temperature in the Netherlands is ca. 11.4 degrees (personal communication). Sensitivity of the model output is analysed with respect to the duration of the reproductive phase (see Appendix 4.2).

Females reach sexual maturity at length of 6 mm (Hynes 1955) and 7 mm (Welton 1979), or, as has been said before, at reaching 14 – 16 antennal segments (McCahon & Pascoe 1988b). Experiments at room temperature by (Mottram 1993) and Hynes (1955) have shown that *G. pulex* needs 100 and 120 days respectively to reach maturity. To reach the length of 6 mm Welton & Clarke (1980) have found that *G. pulex* needs 133 days at 15° C and 87.5 days at 20° C, and according to McCahon & Pascoe (1988a) 130 days on 13° C. Under summer conditions (temperature 10 – 15° C) *G. pulex* take 3 - 4 months to mature, and under winter conditions (5 - 10° C) about 7 months (Hynes, 1955).

The size of the brood is dependent on the length of individual females (Figure 5) (Hynes 1955).

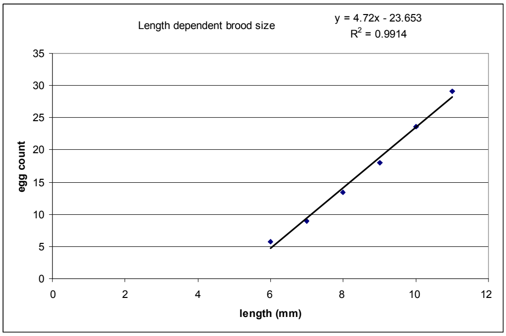

Figure 5. Length dependent brood size (Hynes 1955).

With the regression

$$BroodSize(length) = \frac{(4.72 \cdot length - 23.653)}{2} \qquad \text{eq. 7}$$

That is corrected for modelling only female individuals by assuming a 1:1 sex ratio

In the model, we assume that females reach maturity at 6.5 mm and after they start reproducing, each female will have from 5 or 6 broods, with 30 days in between them, assuming water temperatures of ca. 12 degrees.

Finally, (Pockl & Humpesch 1990a) show that the survival of eggs in two gammarid species, *Gammarus fossarum* and *G. roeseli*, is very dependent on water temperatures. At water temperatures of 10° C the survival of eggs in *G. pulex* is 65% (Pockl & Humpesch 1990a). In the population model, we assume constant water temperatures of 12° C, and therefore disregard the decreased egg survival. We do, however, analyse the model output and time to recovery with respect to decreases egg survival (see Appendix 4.2).

Table 1. List of species specific model parameters.

	Parameter	Distribution	Value	Unit	Reference
Mortality	Background mortality probability	onstant	0.01		Estimated from Sutcliffe *et al*. (1981)
	μ_1, density-dependent scaling factor	constant	0.0005	/ind	Based on vd Brink *et al*. (2007)
Reproduction	Number of broods per female	constant	5 or 6	broods	Hynes (1955), Welton&Clarke (1980)
	Mature size threshold	constant	6.5	mm	Adapted from Hynes (1955), Welton (1979)
Growth	Maximum length, l_{max}	constant	13	mm	Hynes (1955), Welton (1979), Welton&Clarke (1980)
	Individual growth rate, *r*	constant	0.016	/day	adapted from Sutcliffe *et al*. (1981)
	Reaching maturity, *i*	uniform distribution	120 - 133	days	Hynes (1955), Welton&Clarke (1980), McCahon&Pascoe (1988)
Movement	Distance distribution	Normal	0 ± 6	m	Own estimations, based on (Elliott 2002b; Elliott 2003)

Table 2. Dose-response function (eq. 2) parameters for four different pesticides. Below (table 2a) is the table with the comparison of simulated and published data on 2D LC50 values.

Pesticide	**Parameter**	**Unit**	**Value (simulated)**
Chlorpyrifos	1D LC50	nmol/L	130.7
	1D slope	/	-1.509
	4D LC50	nmol/L	3.449
	4D slope	/	-1.67
	16D LC50	nmol/L	0.2558
	16D slope	/	-2.235
Carbaryl	1D LC50	nmol/L	2882
	1D slope	/	-1.635
	4D LC50	nmol/L	120.1
	4D slope	/	-2.027
	16D LC50	nmol/L	19.65
	16D slope	/	-3.535
Pentachlorophenol	1D LC50	nmol/L	105989
	1D slope	/	-1.568
	4D LC50	nmol/L	19306
	4D slope	/	-1.895
	16D LC50	nmol/L	6880
	16D slope	/	-3
Diazinon	1D LC50	nmol/L	1237
	1D slope	/	-1.852
	4D LC50	nmol/L	75.13
	4D slope	/	-2.784
	16D LC50	nmol/L	-5.674
	16D slope	/	14.25

2a)

Pesticide	**Parameter**	**Unit**	**Value (simulated)**	**Value (published)**	**Reference (published data)**
Chlorpyrifos	2D LC50	nmol/L	19.66	9.69; 0.649	Ashauer et al. (2007); Rubach, Crum & Van Den Brink (2011)
Carbaryl			517	148	Bluzat & Seuge (1979)
Pentachlorophenol			40874	21026	Ashauer *et al.* (2007)
Diazinon			260	27.83	Ashauer *et al.* (2010)

Table 3. TDM parameters for four pesticides.

Pesticide	**Parameters**	**Unit**	**Value**	**Reference**
Chlorpyrifos	kin	L/(kg*d)	747	Ashauer *et al.* (2007)
	kout	1/d	0.45	
	kk	g/(pmol*d)	0.000047	
	kr	1/d	0.169	
	threshold	-	0.022	
Carbaryl	kin	L/(kg*d)	23.4	Ashauer *et al.* (2007)
	kout	1/d	0.27	
	kk	g/(pmol*d)	0.0000845	
	kr	1/d	0.97	
	threshold	-	0.067	
Pentachlorophenol	kin	L/(kg*d)	89	Ashauer *et al.* (2007)
	kout	1/d	1.76	
	kk	g/(pmol*d)	0.0000162	
	kr	1/d	66	
	threshold	-	0.037	
Diazinon	kin diazinon	L/(kg*d)	118.9	Ashauer *et al.* (2010)
	kout diazinon	1/d	8.464	
	k activation	1/d	0.896	
	kout diazoxon	1/d	3.278	
	kk	g/(pmol*d)	0.000897	
	kr	1/d	0.11	
	threshold	-	0.197	

Appendix 4.2

Sensitivity analysis of the *Gammarus pulex* population model

We analysed the model output with respect to changes in parameters. Here we focused on the factor governing the density-dependent mortality, on the length of the brood development period and on the decreased egg survival. We exposed all populations for one day to a LC50 of a hypothetical pesticide, resulting in 50% population mortality within one time step. All treated populations are exposed at day 150.

As the result of different parameter sets, both the abundance of control populations and population recovery times are presented. Daily population abundances were averaged over eight years of simulation. All the results are presented in boxplots, with denoted median and interquartile ranges.

This sensitivity analysis relates to the version 1.2 of the *Gammarus* population model, implemented in the NetLogo platform (Wilensky 1999).

1) Density-dependent mortality

Due to a lack of data on density dependent processes that might be regulating gammarid populations, we used a function with estimated parameters in order to have a certain control over the total population growth and abundance (relevant for the simulation speed). In the population model, a very simple, linear function is used to control population abundances (based on Van den Brink *et al.* 2007). Here we tested how the magnitude of the function constant affects the final output.

The default parameter in the population model is set to 0.0005 /ind, resulting in linear increase in local (at the level of one cell) mortality which results in 1 if there are 2000 individuals in the cell.

We tested the model output by increasing this parameter by one order of magnitude, i.e. setting it to 0.005, and decreasing it by one order, i.e. setting it to 0.00005. Increasing the parameter increases the strength of density-dependent processes resulting in lower total population abundance (Figure 1), while decreasing the parameter value will result in much weaker density-dependence and, consequently, higher total abundances.

Relaxing the effects of density (factor 0.00005) resulted in overall abundances that are several magnitudes higher than the default set. Similarly, making the effects of densities even more stringent (factor 0.005), decreased the overall population abundance (Figure 1).

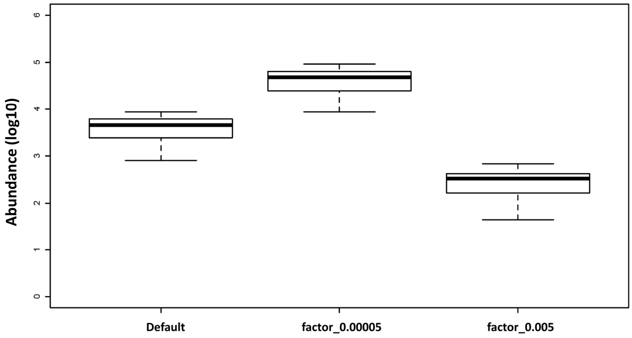

Figure 1. Comparison of the total population abundances (on a log10 scale) with the default and changed density- dependent factors.

However, the trends of population recovery do not differ as much as the abundances do (Figure 2). Large numbers of individuals ensure that the population is not under great impact of stochasticity, resulting in a very narrow distribution of recovery times (Figure 2 – middle boxplot). Conversely, those with very strong effects of densities, resulting in small populations, are more prone to effects of environmental or demographic stochasticity. In our analysis this translates into a larger range of recovery times, indicating that some populations take more than four years (ca. 1300 days) to recover. Therefore, the density-dependent mortality parameter on time to recovery acts indirectly through populations being more or less susceptible to stochastic events.

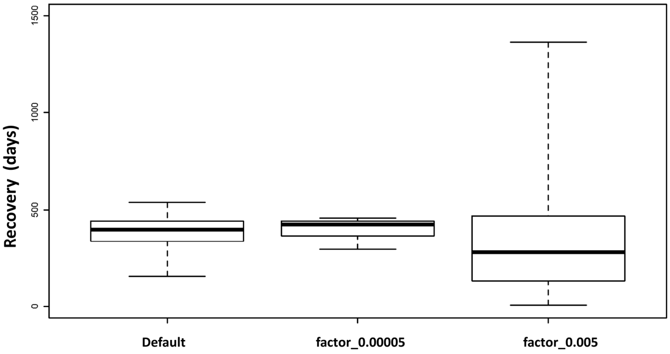

Figure 2. Time to recovery after exposure to 50% mortality – effects of densities on time to recovery. Default density-dependent mortality factor is 0.0005 /ind.

The tested endpoints, i.e. population abundance and recovery time distributions, are within expectations. It is expected that allowing higher densities (factor 0.00005) will result in high abundance and that such populations are less prone to effects of stochasticity in the field but also in our simulated system. The same is valid for increasing the effect of density, resulting in lower abundances, that are more prone to be affected by stochasticity.

2) Length of the reproductive phase/brood development time

The reproductive behaviour of *G. pulex* is characterized by a precopulatory guarding phase which plays a key role in the reproductive cycle (Malbouisson, Young & Bark 1995). It is a complex ritual which ensures that insemination can occur as soon as the female moults and is ready to realize eggs into the brood pouch. The female is carried beneath the male, and the pair swim together for a few days until the female moults, and copulation takes place, normally within a few hours of release of the female's exuvium. Following fertilization the pairs separate, and the fertilized eggs are carried in a brood pouch on the ventral side of the female until hatching.

Hynes (1955) has described that hatching occurs after some days and the young leave the mother's pouch after a day or two. Female becomes attractive to males again at, or slightly before, the time of hatching her eggs, and is often to be found in precopula while unhatched eggs remain in her pouch. Finally, three reproductive phases are distinguishable: precopula (ends with ovulation and copulation), incubation of eggs (ends at hatching juveniles in a brood pouch), and brooding of the newly hatched juveniles in the brood pouch. The number of broods produced by a single female can be 5 – 6 (Hynes 1955; Welton & Clarke 1980).

In the model, we simplify the reproductive phase and behaviour of gammarids, by, first of all, not including males in the population. Secondly, we merge the three phases into one at the end of which females release the young. The length of this phase is temperature dependent (Nilsson 1977).

The default value in the population model is set to 30 days, based on the average water temperatures of 12° C, as the average temperature of Dutch ditch water is 11.4° C.

Here we test how the duration of reproductive phase affect the model output, in both total population abundance and recovery after stress.

Decreasing the reproductive phase (e.g. to 20 days) time increases the population turn-over (leading to more generations in one year) and allows for higher population abundance than with the default parameter set (Figure 3). Still, as the abundances are mainly governed by the magnitude of the density-dependent mortality factor (Figure 1), the overall differences are not very big and all populations have a median between 3900 and 4600 individuals.

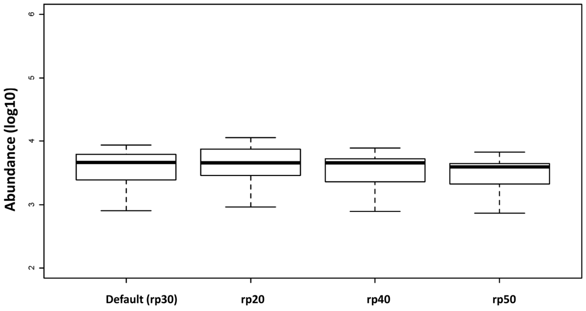

Figure 3. Differences in the total population abundance (log10) dependent on the length of the reproductive period or brood development time.

However, lengthening or shortening the reproductive phase results in much more distinct, but expected, differences when it comes to population recovery (Figure 4).

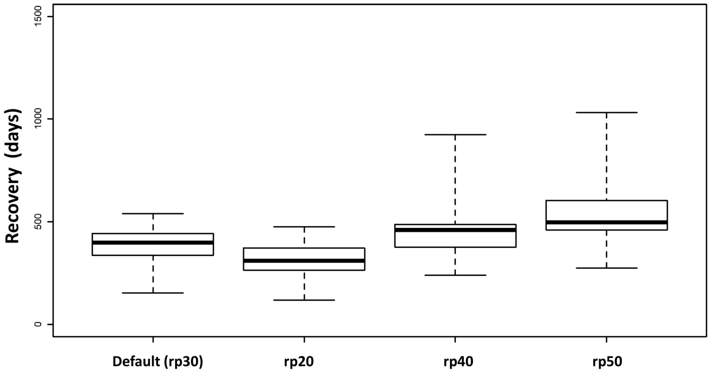

Figure 4. Time to recovery based on different durations of the reproductive phase/brood development time. Shorter phases result in higher population turnover, allowing for quicker recovery of the total population (e.g. rp20).

Shortening this phase is equal to adding new generations to the yearly population dynamics (i.e. increasing voltinism), therefore increasing the population growth rate, resulting in quicker recovery after stress (Fig. 4, rp20). Equally, increasing this period is translated into fewer generations within one reproductive season and longer periods until population recover after stress.

3) Egg survival

Pockl and Humpesch (1990a) show that the survival of eggs and brood development time in two gammarid species, *Gammarus fossarum* and *G. roeseli*, is very dependent on water temperatures. At water temperatures of 10° C the survival of eggs in *G. pulex* is 65% (Pockl & Humpesch 1990a). In the population model, we assume constant water temperatures of 12° C.

Here we tested the effects of lower egg (offspring) survival on the population abundance and recovery. Decreasing egg survival, i.e. decreasing individual fecundity, inevitably leads to lower realized abundances, under equal conditions of density dependence (Figure 5).

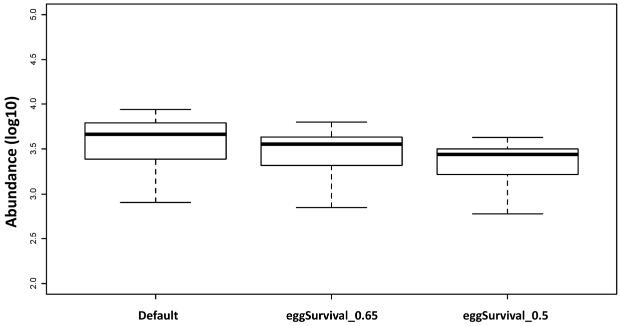

Figure 5. Effects of decreased egg/offspring (only 65% and 50%surviving until hatching) survival on total population abundance (log10 scale).

By limiting egg survival, an individual's reproductive output is decreased, resulting, thus, in longer recovery times (Figure 6). Since we here model an isolated system, reproductive effort of surviving individuals after stress is the sole mechanism of population recovery. Any life-history or environmental parameter that affects the reproductive output will thus have an effect on population recovery.

Again, by decreasing egg survival, the population growth rate is reduced, leading, thus, to longer recovery times and wider ranges of recovery time distributions (Figure 6).

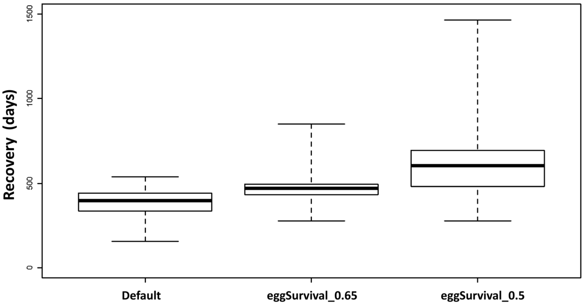

Figure 6. Effects of decrease in reproductive output, by limiting egg survival (65% and 50% survival), on population recovery after stress.

Comparing population patterns in real and simulated populations

Here we attempt to compare model patterns with field obtained data. Welton (1979) reports seasonal dynamics of *Gammarus pulex* in a stream in UK, its yearly abundance dynamics and dynamics of the size structure distributions. We plotted the simulated yearly population dynamics together with data from Welton (Figure 7). Note that the modelled population abundance relates to the total system, while the natural population density is expressed per m^2. Furthermore, only females are modelled, so the comparison with natural populations also includes only females. In Welton (1979), the gender of juveniles is not distinguished, we, therefore, assumed a 1:1 sex ratio and plotted only half of the juvenile abundances.

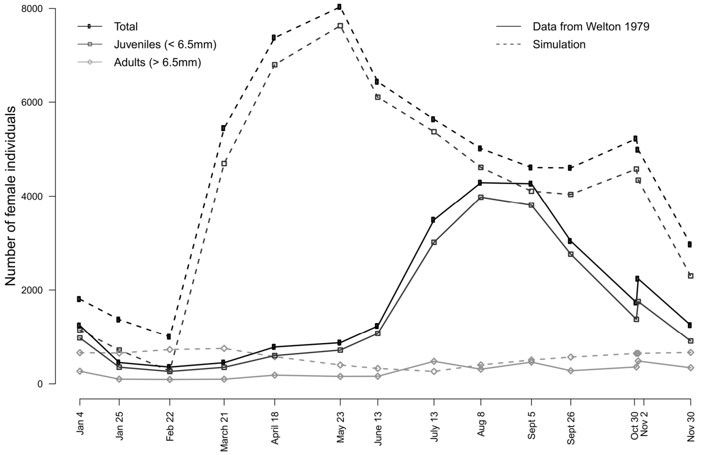

Figure 7. Comparison of the yearly dynamics of a natural (Welton 1979) and simulated populations.

With the exception of a much earlier start of population growth in the modelled population (end of February/ beginning of March vs. June in the natural population), the shape of dynamics of both populations fits rather well. Both populations are dominated by juveniles, with more or less constant, small fraction of adults. Gammarid dynamics, as well as all other freshwater macroinvertebrates, is largely governed by water temperatures, the rise of which will signal the onset of activity, i.e. reproduction. In the population model, temperature dependencies are not explicitly modelled, but assumed that around March temperatures are high enough for individuals to start reproducing (based on expert knowledge about the Dutch ditch system). We, thus, assume that in March temperatures rise above 10° C (and remain at 11° - 12° C until end of October), while Welton (1979) measures temperatures above 10° C in May. This results in the prominent difference between the onset of activity between the simulated and natural populations (Figure 7). However, once these temperature differences are taken into account, the trends of yearly modelled population dynamics fit quite well with the data from Welton (1979). Reproduction finishes around the same period in both the natural and modelled population, i.e. end of October.

Appendix 5.1

Description of the population model of the non-biting midge, *Chironomus riparius*

The model description follows the ODD protocol for describing individual- and agent-based models (Grimm *et al.* 2006). This document describes version 1.4 of the population model (ChD_v1.4).

Overview

Purpose

The main purposes of this model are to simulate the population dynamics of the non-biting midge, *Chironomus riparius*, to evaluate population persistence and recovery after stress in managed landscapes. Both persistence and recovery are assessed in relation to the permeability of the landscape matrix, edge permeability and distance between the aquatic habitat. Dispersal in the landscape is simulated with a separate movement/dispersal model.

State variables and scales

The entities of the model are habitat and female individuals. Habitat is divided into patches (square cells).

The chironomid individuals are characterized by following state variables: age, developmental stage (egg, larval, pupal and adult stages), body size of larvae, reproductive status and fertility of females, dispersal status and their location.

The environment is a 2x200 cell grid, where 400 cells are aquatic habitat. These cells form 2 ditches, each consisting of a string of 200 cells (Figure 1). The state variables of ditch patches are the mortality probability induced by pesticides and by the density of individuals in the patch. Only one ditch is treated with pesticides, while the second one serves as the source of individuals needed for recolonization.

The basic time step in the model is one day. There are 360 days in a year. The simulation runs for 9 years or until there are no surviving individuals left. The first year of simulation is discarded to avoid transitional effects in the output, leaving, thus, eight simulation years for analysis. Processes in the model were executed in a prescribed order, but randomly within the population. All parameters and their distributions are provided in Table 1.

The model is programmed within the NetLogo platform (Wilensky 1999).

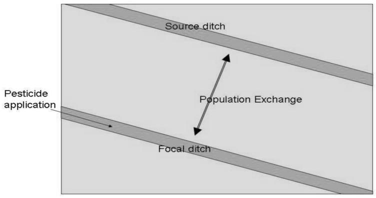

Figure 1. Schematic representation of the modelled chironomid habitat, consisting of two ditches. Only one ditch is treated, while the other one serves as a source of recolonizers. Individuals in both ditches go through, otherwise, identical processes.

Process overview and scheduling

The model includes different processes for different life stages of a chironomid population.

Here we first describe the basic life-history as implemented in the model, followed by the pseudo-code

Only female individuals were modelled. The life-cycle started with the larval stage, which contained an inactive phase, mimicking the egg life stage (five days). Active larvae grew according to a temperature-dependent von Bertalanffy growth curve (von Bertalanffy 1957). Once the larvae reached their maximum size, they pupated and stayed in this stage for two days after which individuals emerged as adults. Based on the dispersal simulation results (thus depending on ditch distance and landscape permeability values, see above), dispersing adults had a probability of staying in the natal ditch, of moving to the other ditch and of dying in the landscape matrix. If an adult female was successful in dispersing (found a suitable aquatic habitat), she deposited a certain number of eggs/inactive larvae; the number of eggs/inactive larvae was drawn from a uniform distribution where the amount was corrected for modelling only females. From here, the life-cycle started from the beginning.

The following pseudo-code gives an overview of the processes and their schedule, which is run each day and, depending on the life stage distribution in the population, is differentially activated.

```
Update age of individuals by one time step

If mortality of juveniles and adults

    Delete from the population

Else hatch from egg – for inactive larval stage

    Grow – for active larval stages

    Pupate - ditto

    Emerge – for pupal stages

    Disperse – for adults that have not yet found the right patch (relevant

                parameters obtained from the dispersal model; see below)

    Oviposit – once they found a suitable patch, females will oviposit
```

Plotting – plots describe the dynamics of the total and of the population in only the treated ditch, averaged growth of individuals, population size distribution, population death rate, temperature dependent growth rate, abundance of adult females.

Changes in state variables caused by the model processes are updated immediately.

Design Concepts

Emergence. Population dynamics and spatial arrangement of individuals emerges from the model rules. Number of generations is not imposed, it is based on individuals' growth and reaching the threshold size for reproduction. Individual growth is dependent on water temperatures with a consequence that higher temperatures lead to more generations (see SA of the model, Appendix 5.2).

Interaction. Individuals do not interact directly with each other; density dependent responses (mortality) are based on the density of larvae in 1 patch of aquatic habitat.

Stochasticity. Some parameter values are drawn from probability distributions obtained from literature data to represent natural variability observed in chironomid populations. All parameter values and distributions are shown in Table 1.

Scheduling. Time is modelled using discrete time steps, each representing a day. The year starts with day 1, at January 1st. Processes in the model are executed in a prescribed order, but randomly within the population.

Observation. For model testing, the behaviour of single individuals and of the whole population was observed.

Details

Initialization. The model is initialized with a given number (10 per patch) of individual larvae. All individuals represent an active larval form (inactive being the egg stage). Individuals are distributed randomly in a ditch. Each initialization starts with the same number of individuals, but with different spatial coordinates and state variable values, e.g. body size (mean 3.5, SD 0.5 mm, based on sizes of overwintering larvae from (Huryn 1990).

The pseudo-code gives an overview of the initialization process

```
to initialize
  initialize global parameters
  initialize landscape [ set carrying capacity
                         set pesticide induced mortality probability …

                        initialize chironomids [ set size
                                                 set age
                                                 set location …]]
end
```

Input. Water temperature is an exogenous process that serves as an input into the model. Temperatures are based on year round data collection from ditches in the Netherlands and form a basis for individual growth (Figure 2). The temperatures in the model change, therefore, in each time step within one simulated year, but no interannual differences are assumed.

Submodels. Submodels include: mortality of aquatic and terrestrial stages, individual growth and dispersal with oviposition.

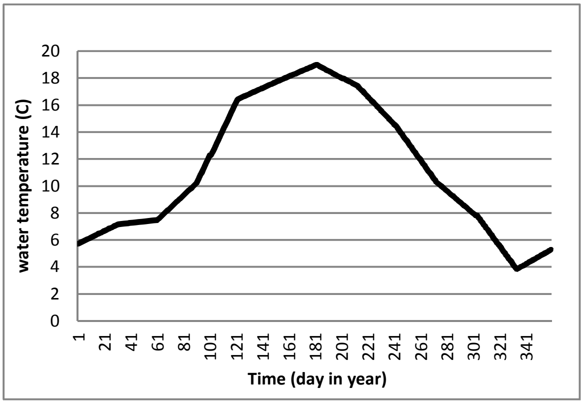

Figure 2. Yearly dynamics of water temperatures measured in the Dutch ditch system.

Mortality of aquatic stages

There are three different mortalities affecting individuals in aquatic part of the life-cycle, background or natural mortality, density-dependent and pesticide-induced mortality. We assume daily mortality rates only for the larval stage (eggs and pupae have 100% survival).

Including density-dependent mortality is an indirect way of modelling resource competition, because we do not model resource dynamics. Even though exact mechanisms of density dependence are not clear, it is known that populations of chironomids are regulated by their densities, although these densities can be very high before any regulation occurs, e.g. (Pery *et al.* 2002)show that animals in beakers with higher numbers of individuals grow slower due to food limitation (beakers used have a surface are of 14 cm^2 and the effects on growth are visible already with 10 individuals in 1 system). With ad libitum feeding conditions, density dependent effects seem to be much less pronounced. Hooper *et al.* (2003)(Hooper *et al.* 2003) also show that at densities of 16 individuals/cm^2, only 1% of individuals eventually emerges.

The realized densities in the model are kept lower than observed in the natural environment, due to speed of computation. Within this model, we follow the mortality based on local densities from Van den Brink *et al.* (2007)

$$\mu_{dd} = \mu_1 \cdot N \qquad \text{eq. 1}$$

where μ_1 is a parameter governing the steepness of the density dependence (m^2/ind*d) and *N* is the local density (ind/m^2). Density-dependent mortality is cell based, so all individuals in one cell have the same probability of dying due to overcrowding.

Eq. 1 is the simplest assumption on effects of density, where each individual has a certain effect on each of its conspecifics within 1 cell. We test the model output with regards to different values of μ_1 (See Appendix 5.2 for details)

An additional mortality implemented in the model is the winter mortality of larvae. It has been observed that only forth instar chironomid larvae survive the winter period (Rasmussen 1984). We, thus, assume that all individuals smaller than 3.5 mm (personal communication M. Marinkovic) do not survive the winter period and are removed from the population.

Mortality of terrestrial stages

In the model, adult females may suffer from dispersal mortality. If they survive the dispersal routine and oviposit in one of the ditches, they may survive for maximum of 4 days.

Individual growth

This species' growth and development are highly dependent on available food and temperature of the surrounding environment. It can be uni- to multivoltine, depending on local environmental conditions (Armitage, Cranston & Pinder 1995; Eggermont & Heiri 2011). In this model, the population has 3 generations in a year, found also in (Learner & Potter 1974) and Eggermont & Heiri (2011).

With an ad libitum feeding regime, isomorphic larvae grow according to von Bertalanffy growth curve (von Bertalanffy 1957)

$$l(a) = l_{\max} \cdot (1 - e^{-\gamma \cdot a}) \qquad \text{eq. 2}$$

where l_{max} is the maximum larval size after which individuals pupate, and γ is the daily growth rate. With the given individual growth rate (Table 1), larvae finish their growth within approximately 12 days.

Differentiating the growth function, we obtain the daily increment in growth

$$\frac{dl}{da} = \gamma \cdot l \cdot (\frac{l_{\max}}{l} - 1) \qquad \text{eq. 3}$$

Growth is dependent on water temperatures, which change on a daily (time step) basis, and is implemented as

$$TD = \frac{1}{10 \cdot e^{-0.1 \cdot externaltemperature}} \qquad \text{eq. 4}$$

This is then multiplied with the daily growth increment

$$increment = \gamma \cdot l \cdot (\frac{l_{\max}}{l} - 1) \cdot \frac{1}{10 \cdot e^{-0.1 \cdot externalTemperature}} \qquad \text{eq. 5}$$

and added to the current size of the individual. The function is set up in such a way that the size increment exponentially increases with rising water temperatures, e.g. with the water temperature of 24° C, the increment added is maximal and eq. 4 reaches a plateau (Eggermont & Heiri 2011). This was also compared with the laboratory data on chironomid growth, where water temperatures are kept at a constant 21° or 25°; when the individuals are kept at 21°, one generation takes approximately 35, whereas in the model it takes ca. 45 days.

Modelled individuals do not grow at all if the temperatures are lower than 8 degrees (adapted from Rasmussen 1984). The maximum value in the water temperature values used in this model is 18.8° C.

Reproduction

Each adult female that survives the dispersal process oviposits a number of eggs; the value is drawn from a uniform distribution (Table 1) and is corrected for modelling only females assuming a 1:1 sex ratio.

Dispersal

Generally, chironomids are relatively weak dispersers that cover bigger distances with the help of wind (Armitage, Cranston & Pinder 1995). Delettre & Morvan (2000) showed that the number of trapped chironomids drop significantly (exponential decrease) with the distance from the nearest water body. Their results also suggest that adults accumulate in nearby hedges for resting, their dispersal is therefore hampered. Furthermore, it seems that dispersal distances can be linked to seasonal foliage cover of trees, where earlier in the year, more organisms can be found further, due to low tree cover and, thus, less barriers. The limited lateral dispersal is corroborated also by the findings of, amongst many others, (Petersen 2004) who find the majority of adult mayflies and caddisflies no further than 7 – 11 m from the stream they emerged from. (Smith, Alexander & Lamp 2009) review the dispersal of aquatic insects in the context of restoration efforts, and find the preference of adults for vegetated areas. Chironomid dispersal usually includes 3 types of movement: initial dispersal after emergence to the resting site, swarming behaviour and ovipositing flight of females (Oliver 1971). (Briggs & Latto 2000) show that a species of gall-forming midge disperses from the point of release on average only about 1.7 m.

In a separate dispersal model, where we simulate large numbers of individuals dispersing in landscapes, three main factors are alternated: landscape permeability, distance between two ditches and type of movement individuals perform. Movement types include random walk, correlated random walk and Levy walk.

In this version of the population model, we consider only individuals performing the correlated random walk (CRW).

Here we provide a description of assumptions and processes in the dispersal model.

Dispersal model

In the dispersal model, we assume a single movement pattern to apply to all phases (as described by Oliver 1971). Correlated random walks (CRW) (Barton *et al.* 2009; Hawkes 2009) combine a non-uniform distribution of turning angles with an exponentially decaying distribution of step lengths. Here we used the von Mises angular distribution (Best & Fisher 1979), i.e. a normal distribution on a circle, in which we vary the degree of angular correlation by altering the shape parameter, κ, which is the measure of concentration for this distribution and is analogous to $\frac{1}{\sigma^2}$ of a normal distribution. Smaller values of κ diffuse the distribution, while it becomes a uniform distribution at value 0, resulting in Brownian motion (also random walk). Larger values of κ result in the distribution centring more on the mean, which means that the movement will be more directed. Here we set the mean value to 0 and the value of κ to 6 (fairly correlated movement). Every time step, each adult individual was assigned a turning angle and a step from respective distributions (see Table 1 for details). Given the tiny size of our model organisms, we assumed one minute as a simulated time step, and a total dispersal period of 16 hours (960 minutes). Adult individuals were thus assumed to disperse only for one day.

The simulated landscape consisted of aquatic habitat, i.e. ditches, separated by the terrestrial (non-)habitat, in the following referred to as the landscape matrix (Figure 3). A large number (10000) of movement paths was generated, all starting from the centre of one ditch (natal ditch in Figure 3). The landscape impacted movement through edge and matrix permeability. Edge permeability refers to the probability of crossing the border between the natal ditch and landscape matrix, for a movement path that ‘hits’ this edge from the inside of the ditch. Note that the probability of crossing this edge in the opposite direction is set to 1. Matrix permeability refers to the extent to which the landscape facilitates movement (the reciprocal of ‘resistance’), and is represented by a scaling factor on realized step size (or velocity, see above).

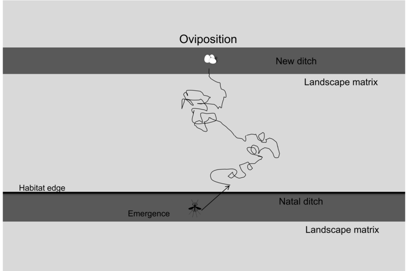

Figure 3. Schematic overview of the simulated landscape in the dispersal model.

Movement continued for the full dispersal period, unless water (a ditch) was encountered. In that case, movement halted, but only outside the period of ‘obligatory’ movement, the swarming period. Dispersers that did not encounter any water at all were assumed to perish in the landscape matrix (dispersal mortality). Note that dispersers that encountered another than the natal ditch were always allowed to settle, even within the swarming period. We simulated movement for the following landscape configurations and landscape-dependent movement coefficients. The duration of the swarming period was set to 240, 480, 720 and 960 time steps. Distance between ditches amounted to 10, 20 and 30 m. Edge permeability values were 0.001, 0.005, 0.01, 0.05 and 0.1, while matrix permeability values amounted to 0.2, 0.4, 0.6, 0.8 and 1.0. Our definition of matrix permeability allowed us to combine matrix permeability and distance between ditches in one metric, effective distance (= distance / matrix permeability).

Each dispersal simulation produced three probabilities for use in the population model when run for the same spatial settings: 1) probability of staying in (or returning to) the natal ditch, 2) probability of encountering the other ditch (functional connectivity), and 3) probability of dying during the dispersal process (not encountering the aquatic habitat). In addition, for dispersers ending up in one of the ditches, from their x-coordinates one-dimensional dispersal kernels were estimated, defining the probability of covering a certain distance within a ditch. These results refer to an ‘infinite’ landscape, where each ditch will have another neighbouring ditch on both sides.

Table 1. Table with all parameter distributions and values (with references where existing)

Submodel	Parameter	Distribution	Value	Unit	Reference
Mortality	background larval mortality probability	constant	0.0007	/day	Calibration estimate; also expert opinion
	adult lifespan	constant	4	days	Adapted from Downe 1973 and Charles et al. 2004
	μ_1 - density-dependent mortality factor	constant	0.005		Based on Van den Brink et al. 2007
Growth	gamma	constant	0.095	/ day	Calibration estimate; based on ca 15 days that it takes to reach maximum size of larvae before pupation
	female max size	constant	13.72	mm	Pery et al. 2002
	initial larval size	normal	mean 0.002, SD 0.0001	mm	Adapted from Pery et al. 2002
Duration of different stages	egg stage	constant	5	days	Expert opinion; adapted from Charles et al. 2004, Oliver 1971
	pupal stage	constant	2	days	Expert opinion; adapted from Charles et al. 2004
Reproduction	fecundity	uniform	50-150	eggs	Adapted from Pery et al. 2002 and Ducrot et al. 2004 ; corrected for modelling only females, assuming 1:1 sex ratio
Dispersal	turning angles	von Mises	mean 0, κ 6	°	Own estimation
	step length	exponential	mean 24	cm	Own estimation

Appendix 5.2

Sensitivity analysis of the *Chironomus riparius* population model

We tested the output of the population model to changes in parameters. Here we focused on the impact temperature dependent growth, adult mortality and density-dependent mortality have on population abundance.

As the result of different parameter sets, the abundance of control populations and population dynamics are presented. Daily abundances of the total population (from both simulated ditches) were averaged over the 9 years of simulation and presented in boxplots, with denoted median and interquartile ranges.

From the dispersal model simulations, we obtained 3 main parameters (see ODD in Appendix 5.1) that were used in the population model, namely the probability to stay in the natal ditch, the probability to colonize the new ditch and the probability to die in the landscape matrix between the ditches. Here, we keep the effects of dispersal constant and assume, for the purposes of this analysis, the dispersal mortality of 0.1, and equal probability to colonize a new ditch and stay in the native one.

This sensitivity analysis relates to the version 1.4 of the *Chironomus riparius* population model, implemented in the NetLogo platform (Wilensky 1999).

1) Temperature-dependent larval growth

This species' growth and development is highly dependent on available food and temperature of the surrounding environment. Its populations can be uni- to multivoltine, depending on local environmental conditions (Armitage, Cranston & Pinder 1995). In this model, the population has 3 generations in a year, reported also by Learner & Potter (1974). The function is set up in such a way that the size increment exponentially increases with rising water temperatures, e.g. with the water temperature of 24° C, the increment added is maximal. This was also tuned to laboratory data on chironomid growth, where water temperatures are kept at a constant 21° or 25°; when the individuals are kept at 21°, one generation takes approximately 35 days, whereas it takes ca. 45 days in the population model (if the temperature is kept constant).

Modelled individuals do not grow at all if the temperatures are lower than 8°. The water temperature values used in the model are based on measurements from the Dutch ditch system (pers.comm. A. Veraart) and vary on a daily basis. The maximum value of the water temperature used in this model is 18.8°. We, therefore, assume yearly temperature dynamics, but do not account for possible interannual variability in temperatures, i.e. the same temperature set is used with each new simulation year.

Here we analyse the impact of increasing temperatures on voltinism (Figure 1) and total population abundance (Figure 2).

Increase in temperatures enhances the growth of larvae, resulting in shorter generation duration periods, when compared to the default parameter set (see Appendix 5.1 for details on the growth submodel). Ultimately, this yields increase in the number of generations (Figure 1); note that only the third year of the simulation is shown. Here we plotted the default temperature set with the one where all daily temperatures were increased by 2° and by 6° C. With the temperature increase, new generations form, that are initially relatively small in size, but also grow as the temperatures increase even further.

Increase in the number of generations per year also increases the total population abundance (Figure 2). The overall increase in abundance does not exceed one magnitude (note the log scale on y-axis) as the realized densities are mainly governed by the density-dependent mortality.

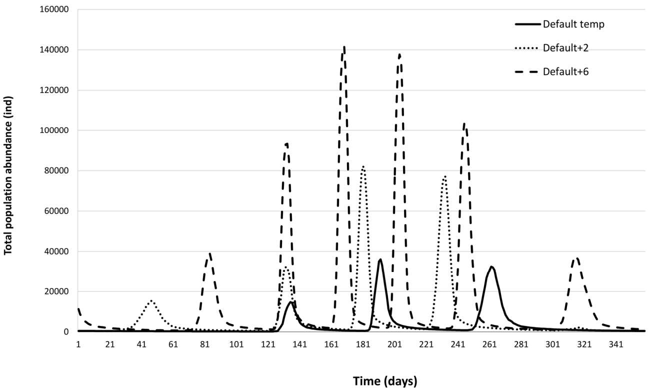

Figure 1. Effects of increasing water temperatures (deltaT = 2) on the number of generations in the modelled population. The number of generations (voltinism) increases.

Increase in temperature causes faster larval growth and emergence and consequently, species in lower latitudes typically experience more generations in one year than species in higher latitudes (Eggermont and Heiri, 2011, and references therein). However, chironomids are also sensitive to microclimatic temperature conditions resulting in the same species exhibiting different number of generations in the same system (Eggermont and Heiri, 2011).

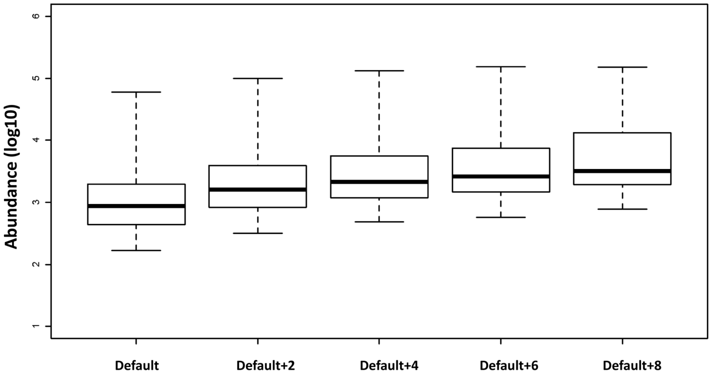

Figure 2. Total population abundance (log10) as a result of increasing water temperatures. The difference between the median abundance as a result of the default parameter set and the maximum increase in temperature (8° C) is less than one order of magnitude.

2) **Effects of adult mortality**

Integration of the dispersal model with the population model revealed that population persistence is very sensitive to dispersal (adult) survival, as it affects the population reproductive output. Therefore, we tested a range of mortalities and plotted only the total population abundance of one year (Figure 3, first year of simulation is discarded). Populations that lose 45% and more adults in each generation go extinct within 6 years from the start of the simulation.

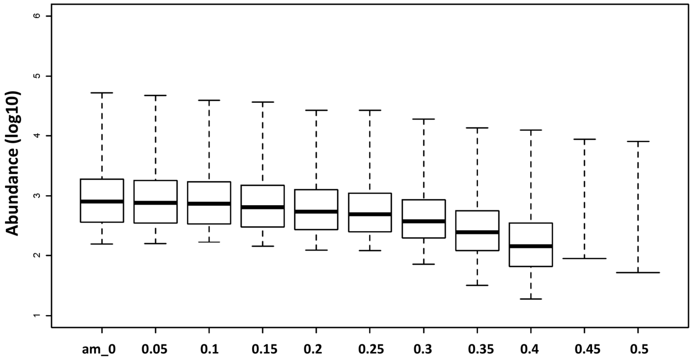

Figure 3. Total population abundance (log10) dependent on increasing adult mortality.

The first effects on total abundance start occurring after 20% of the adult population is lost.

3) **Density-dependent mortality**

In the population model, we include three different mortalities affecting individuals in the aquatic part of the life-cycle, background or natural mortality, density-dependent and pesticide-induced mortality. We assume daily mortality rates only for the larval stage (eggs and pupae have 100% survival).

Including density-dependent mortality is an indirect way of modelling resource competition, because we do not model resource dynamics. Even though exact mechanisms of density dependence are not clear, it is known that populations of chironomids are regulated by their densities, although these densities can be very high before any regulation occurs, e.g. Pery *et al.* (2002) show that animals in beakers with higher numbers of individuals grow slower due to food limitation (beakers used have a surface are of 14 cm^2 and the effects on growth are visible already with 10 individuals in 1 system). With ad libitum feeding conditions, density dependent effects seem to be much less pronounced. Hooper *et al.* (2003) also show that at densities of 16 individuals/cm^2, only 1% of individuals eventually emerges.

The realized densities in the model are much lower than observed, due to computational reasons. The default value of 0.005 /ind per patch, results in the probability of dying of 1.0 if the density within the cell reaches 200 individuals. Consequently, the densities of local populations (in a cell) are regulated.

Here we test the model output, i.e. total population abundance, while changing the strength of this parameter. Relaxing the strength of density-dependence results in very high abundances (and very long simulation time) (Figure 4, first year of simulation is discarded). On the other hand, strengthening the density-dependent factor yields very low abundances, and hampers populations' survival over winter (Figure 4, density-dependent mortality factor of 0.007 and 0.008). These populations became extinct within 5 years.

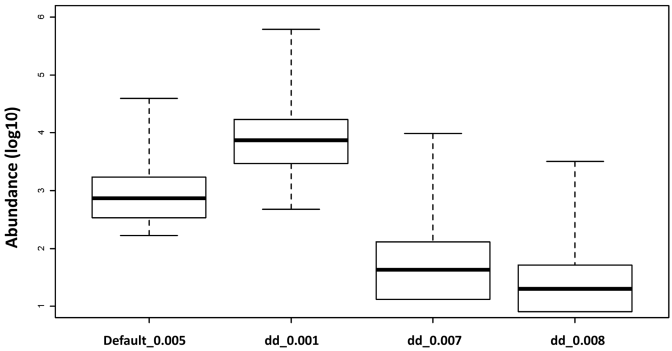

Figure 4. Effects of the density-dependent factor on total population abundances (log10 scale).

Consequently, the default value was chosen in such a way that the population abundances were computationally manageable, and that population densities were high enough so that they are not subject to demographic or environmental stochasticity.

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Summary

Ecosystems provide various services that are beneficial to humans. The main function of the agroecosystem, has, traditionally, been providing food for the human population. However, agroecosystems also provide other service, such as nutrient cycling, pollination, soil structure and quality, but also aesthetical and recreational services, the sustainability of which has to be ensured. As the activities of the growing human population pose increasing pressures to all ecosystems, the question how to assess a system's recovery potential is becoming more prominent. Many of ecosystem services are provided by single species and communities, recoveries of which are mainly dependent on their life-history traits, stressor specific characteristics, but also on features in the landscape.

The main hypothesis of this thesis is that the combination of these three factors governs the recovery potential and time to accomplish recovery of populations. Furthermore, a sub-hypothesis of this thesis is that ecological models are the only tools that can combine all relevant factors and assess recovery, and other endpoints, in alternative scenarios. Therefore when (small) impacts of stressors are acceptable, the use of models to assess recovery potential and times is indispensable for their risk assessment.

In **Chapter 2** we assess whether existing, published ecological modelling studies have addressed or have the potential to address the protection aims and requirements of the chemical directives of the European Union. The current chemical risk assessment (RA) schemes within the EU focus mainly on toxicity and bioaccumulation of chemicals in individual organisms, but most protection goals aim at preserving populations of non-target organisms, rather than individuals. Ecological models are tools rarely recommended in official technical documents on RA of chemicals, but are widely used by researchers to assess risks to populations, communities and ecosystems. In this chapter, we review 148 publications, evaluate and summarise them in a database according to defined criteria. Published models are also classified in terms of five areas where their application would be most useful for chemical RA. These areas include: extrapolation of effects to the population level, extrapolation of exposure regimes, extrapolation of population recovery, assessment of indirect effects and bioaccumulation. Most reviewed models were developed to estimate population-level responses on the basis of

individual effects, followed by assessment of the recovery process, both in individuals and at the level of metapopulations. The lack of clarity about protection goals in legislative documents makes it impossible to establish a direct link between modelling studies and protection goals. We, however, conclude that there is great potential for a variety of ecological models in the published literature to be used for chemical RA.

Various organisms in agroecosystems may regularly be exposed to stressors, such as pesticides. As a species' sensitivity to stress depends on its life-history, the toxicity of the stressor and on landscape structure, in **Chapter 3**, we describe an individual-based model of an isopod, *Asellus aquaticus,* the water louse, that was developed to explore how timing of stress events affects population dynamics in a seasonal environment. We also test the relevance of habitat connectivity and spatial distribution of stress for the recovery of a local and total population. The simulation results indicate that population recovery is mainly driven by the reproductive periods of the water louse. Furthermore, even though high habitat connectivity leads to faster recovery both for the local and the total populations, the effects of landscape structure disappear for homogeneously stressed populations, where local survivors increase the recovery rate. Overall, local populations recover faster, implying that assessing recovery in the field needs careful consideration of spatial scale for sampling. In conclusion, we emphasize the need for a coherent definition of recovery in order to provide more relevant information for ecosystem risk assessment and management.

In **Chapter 4**, we investigate the effects of different pesticides with different modes of action (i.e. diazinon, chlorpyrifos, carbaryl and pentachlorophenol), on the individual survival and population recovery of the freshwater amphipod, *Gammarus pulex*. Standard ecological risk assessment practices develop dose-response relationships, by fitting dose-response models on the results of standard laboratory toxicity tests, in order to evaluate the magnitude of effects across different exposure concentrations. Such tests are performed at fixed concentrations and duration, where delayed effects, i.e. those occurring beyond the exposure period, are not included. Detailed processes of toxicokinetics and toxicodynamics that can take delayed toxicity into account are combined in TKTD models, e.g. the threshold damage model (TDM). Effects on amphipod survival were calculated using dose-response relationships and the TDM. We also develop an individual-based model of *Gammarus pulex* in order to assess the potential for population recovery after exposure in different scenarios. Our results demonstrate that delayed effects calculated by the TDM have a significant impact on both individual survival probability as well as subsequent population recovery times. Furthermore, we evaluate the assessment of effects after short-term exposures with the standardly used dose-response relationship and the TDM. We show that the practice of using a 96 h dose-response model is sufficiently protective for all pesticides when exposure is shorter than 12 hours. Population recovery times estimated with the individual-based model follow the trends as observed in the decreased survival, i.e. the larger the decrease, the longer it took the population to reach the control abundances. This study emphasizes the need to reconsider standard tests, especially for pesticides with specific modes of action, to allow for quantification of possible delayed effects.

In **Chapter 5**, we evaluate the effects of landscape permeability, i.e. of riparian vegetation (edge permeability) and other vegetation (landscape matrix permeability), and distance between waterbodies on the colonization and recovery potential of weakly flying insects. We chose the non-biting midges, *Chironomus riparius*, as our model organisms, due to their importance in energy transfers in aquatic and terrestrial food webs, their global distribution and low flying capabilities. To investigate the interplay between landscape permeability, distance between water bodies, and re-colonization and population recovery after a stress event, we developed two models. With a movement model we predict the outcome of dispersal in a landscape with several linear water bodies (ditches) under different assumptions regarding landscape-dependent movement. The outcome of the movement model, in particular the probabilities of encountering another ditch (functional connectivity) and of staying in the native ditch or perishing in the landscape matrix, is used in a second model.

With this individual-based population model we assess the implications for population persistence (taking abundance as a proxy for viability) and in particular for recovery potential (i.e. time to recovery) after an extreme stress event. We show that low values of edge permeability hamper colonization, but also minimize dispersal mortality, while in more permeable landscapes the colonization probability increases. High effective distances in the landscape result in high mortality probability that was directly related to population abundance in the population model, with populations in many dispersal scenarios becoming extinct. Furthermore, in a large part of landscape parameters space, i.e. combinations of edge permeability and effective distance, no recovery was accomplished. We discuss these findings with regards to landscape management and seasonal environments.

Current ecological risk assessment (ERA) practices incorporate very little ecology and base their risk estimates on the results of standard tests performed with several standard species. The main obstacles for a more ecologically relevant ERA are the lack of clear protection goals and the inherent complexity of ecosystems that is hard to approach empirically. In **Chapter 6**, we argue that the ecosystem services framework offers an opportunity to define clear and ecologically relevant protection goals. At the same time, ecological models provide the tools to address ecological complexity to the degree needed to link measurement endpoints and ecosystem services, and to quantify service provision and possible adverse effects from human activities. The challenges of the ecosystem services approach are discussed as well as the limitations of ecological models in the context of ERA. However, we argue that both fields are advancing quickly and can prove very valuable in achieving more ecologically relevant ERA.

In **Chapter 7**, I discuss the findings of this thesis in a broader context. I aim to identify the shortcomings of current ERA practices, focussing specifically on definitions of recovery and acceptable time to accomplish recovery, and propose ways forward.

Samenvatting

Doordat de groeiende wereldbevolking een steeds grotere druk op natuurlijke ecosystemen legt, wordt de vraag naar een goede methode voor het beoordelen van de mogelijkheid tot herstel van een systeem steeds groter. Dit is vooral relevant voor agrarische ecosystemen welke traditioneel als functie hebben om voedsel voor de menselijke populatie te produceren. Agrarische ecosystemen leveren echter ook andere ecosysteemdiensten zoals omzettingen van nutriënten, bestuiving, het op peil houden van een bepaalde bodemkwaliteit en structuur, maar ook esthetische en recreatieve diensten, waarvan de duurzaamheid moet worden gewaarborgd.

Soms worden veel van deze diensten echter geleverd door één bepaalde levensgemeenschap of zelfs soort. Het herstel van deze gemeenschap of soort na een blootstelling aan een stress factor hangt vooral af van de specifieke *life-history* karakteristieken, de toxiciteit van de stressor, maar ook van het ruimtelijke landschap waarin de gemeenschap of soort zich bevindt.

De voornaamste hypothese van dit proefschrift is dat de combinatie van deze drie factoren de potentie voor herstel en de hersteltijd van populaties bepaalt. Daarnaast suggereert een sub-premisse van dit proefschrift dat ecologische modellen de enige technieken zijn die alle relevante factoren kunnen combineren om herstel en andere parameters te beoordelen in meer dan één scenario. Om die reden is het gebruik van modellen onmisbaar voor risicobeoordeling wanneer een (geringe) impact van stressoren toelaatbaar is en hierdoor voor een populatie of gemeenschap aangetoond moet worden welke blootstelling aan een stressor, welk gevolg in ruimte en tijd heeft.

In **Hoofdstuk 2** onderzoeken we of bestaande, gepubliceerde modelstudies zich hebben gericht op (of de potentie hebben zicht te richten op) de beschermingsdoelen en vereisten van de chemische richtlijnen van de Europese Unie. De huidige chemische risicobeoordelingsschemas binnen de EU richten zich voornamelijk op toxiciteit en bio-accumulatie van chemicaliën in individuele organismen, terwijl de meeste beschermingsdoelen juist gericht zijn op populaties van zogenaamde niet-doelwit soorten in plaats van individuen. Het gebruik van ecologische modellen wordt nauwelijks aanbevolen in officiële technische risicobeoordelingsdocumenten van chemicaliën, maar worden door onderzoekers veelvuldig gebruikt om de risico's op populaties, levensgemeenschappen en ecosystemen te beoordelen. In dit hoofdstuk beoordelen we 148 publicaties, vatten deze samen en evalueren ze in een database volgens vooraf gedefinieerde criteria. Tevens worden gepubliceerde modellen geclassificeerd op basis van vijf gebieden waar hun toepassing het meest bruikbaar is voor chemische risicobeoordeling. De meeste modellen die bestudeerd zijn, waren ontwikkeld om effecten op het individu te extrapoleren naar de effecten op het populatie niveau, gevolgd door beoordeling van het herstelproces van zowel individuen als de (meta)populatie. Het gebrek aan duidelijkheid aangaande de precieze beschermingsdoelen in wetgevende documenten maakt het onmogelijk om een direct verband te leggen tussen modelleerstudies en beschermingsdoelen. Wij concluderen echter dat er in de diverse ecologische modellen die in de literatuur beschikbaar zijn, veel potentie is voor gebruik in de risicobeoordeling van chemicaliën.

Diverse organismen in agrarische ecosystemen kunnen regelmatig blootgesteld worden aan stressoren zoals pesticiden. Omdat de stress-gevoeligheid van een soort afhangt van haar *life-history*, de toxiciteit van de stressor en de landschapsstructuur, beschrijven we in **Hoofdstuk 3** een individu-gebaseerd model van een waterpissebed, *Asselus aquaticus* (orde: Isopoda), ook wel waterluis genoemd, welke ontwikkeld was om te onderzoeken hoe de timing van stress-gebeurtenissen de populatiedynamica binnen een seizoen beïnvloed. We testen ook de relevantie van habitat-connectiviteit en de ruimtelijke verdeling van de stressor voor het herstel van een lokale en totale populatie. De resultaten van de modelsimulatie wijzen erop dat vooral de perioden waarin de waterpissebed zich voortplant van belang zijn voor het herstel van de populatie. Daarnaast verdwijnen de effecten van landschapsstructuur voor (ruimtelijk) homogeen gestreste populaties. Hoewel een hoge mate van connectiviteit tussen habitats tot sneller herstel van zowel lokale als totale populaties leidt, zijn het in dit geval vooral lokaal overlevende individuen die hier de herstelsnelheid verhogen. . Over het algemeen herstellen lokale populaties sneller dan totale populaties, wat impliceert dat het beoordelen van herstel in veldsituaties een zorgvuldige overweging van de juiste ruimtelijke bemonsteringsschaal behoeft. Hiermee benadrukken we de noodzaak voor een concretere definitie van herstel, zodat de informatie gegenereerd door ecologische modellen een hogere relevantie krijgt voor risicobeoordeling en management van ecosystemen.

In **Hoofdstuk 4** onderzoeken we de effecten van verschillende stressoren, d.w.z. pesticiden met verschillende werkingsmechanismen (chlorpyrifos, diazinon, carbaryl en pentachlorophenol), op overleving van individuen en herstel van populaties van de zoetwater vlokreeft *Gammarus pulex* (orde: Amphipoda). Standaard ecologische risicobeoordeling ontwikkelt dosis-respons relaties door op de resultaten van standaard toxiciteitstesten dosis-respons modellen te fitten, om zo de grootte van het effect van verschillende blootstellingsconcentraties in te schatten. Zulke tests worden uitgevoerd voor vastgestelde concentraties en blootstellingsduur, vertraagde effecten, die bijvoorbeeld pas optreden na de blootstellingsduur worden over het algemeen niet meegenomen. Echteredetailleerde processen zoals toxicokinetica (TK) en toxicodynamica (TD) waarbij wel vertraagde toxiciteit wordt beschouwd, worden wel gecombineerd in zogenaamde TKTD modellen, zoals bijvoorbeeld het drempelwaarde-schade-model (Threshold Damage Model,TDM). Zo werden middels ‘traditionele’ dosis-response relaties en het TDM-model effecten van een stressor op vlokreeft-overleving werden berekend m.b.v. dosis-respons relaties en het TDM-model. Ook werd er een individu-gebaseerd model voor *Gammarus pulex* ontwikkeld om zo de mogelijkheid voor populatieherstel na blootstelling aan pesticiden te testen voor verschillende scenario’s. Onze resultaten laten zien dat vertraagde effecten berekend door het TDM-model een significante impact hebben op zowel individuele herstelkans als op de bijbehorende populatie hersteltijden. Verder evalueren we de beoordeling van effecten na kortdurende blootstelling met de standaard gebruikte dosis-respons relatie en de TDM. We laten zien dat voor een blootstellingsduur korter dan 12 uur het gebruik van een 96 uur dosis-respons model afdoende beschermend is voor alle geteste pesticiden. Populatie hersteltijden geschat met het individu-gebaseerde model volgen de trends zoals eerder geobserveerd werden als verlaagde overleving: hoe groter de afname in overleving, hoe langer het duurt voordat populaties de controle abundanties behalen. Dit onderzoek benadrukt de noodzaak om de standaardtesten opnieuw te beoordelen, vooral voor pesticiden met specifieke werkingsmechanismen, om zo ook mogelijke vertraagde effecten te kunnen kwantificeren.

In **Hoofdstuk 5** evalueren we de effecten van landschapspermeabiliteit, zoals oevervegetatie (rand-permeabiliteit) en andere vegetatie (landschapsmatrix–permeabiliteit) en afstand tussen waterlichamen op kolonisatie door en herstel van insecten met een potentieel matige vliegcapaciteit. We kozen voor dansmuggen *Chironomus riparius,* als ons modelorganisme. Dit omdat ze een belangrijke (voedsel)component zijn in zowel aquatische en terrestrische voedselwebben, hun wereldwijde verspreiding en hun matige vliegcapaciteiten. Om het samenspel tussen landschapspermeabiliteit, afstand tussen waterlichamen en rekolonisatie en populatieherstel na een stress-gebeurtenis te onderzoeken, hebben we twee modellen ontwikkeld. Met een bewegingsmodel voorspellen we dispersie in een landschap met een aantal lijnvormige wateren (sloten) onder verschillende aannames over landschapsafhankelijke beweging. De uitkomsten van het bewegingsmodel, vooral de kans om een andere sloot tegen te komen (functionele connectiviteit), of juist in de thuissloot te blijven, of te sneuvelen in de landschapsmatrix, is gebruikt in een tweede model. Met dit individu-gebaseerde populatie model testen we de implicaties voor de weerbaarheid van populaties (waarbij we abundantie als benadering voor levensvatbaarheid gebruiken) en in het bijzonder de mogelijkheid tot herstel (hersteltijd) na een extreme stress gebeurtenis. We laten zien dat lage randpermeabiliteit de kolonisatie remt, maar tegelijkertijd ook de sterfte door verspreiding minimaliseert, terwijl in meer permeabele landschappen de kans op kolonisatie toeneemt. Grote effectieve afstanden in het landschap resulteren in een hoge sterftekans, die direct gerelateerd was aan de abundantie van de populatie in het populatie model, waarbij populaties voor veel verspreidingsscenario’s uitsterven. Daarnaast werd voor een groot deel van de parameter ruimte, d.w.z. combinaties van randpermeabiliteit en effectieve afstand, geen herstel bereikt. We bespreken deze bevindingen in relatie tot landschapsmanagement en seizoen.

De huidige ecologische risicobeoordeling bevat in de praktijk maar weinig ecologie, de risicoanalyses zijn vooral gebaseerd op standaardtests uitgevoerd met een aantal standaard soorten. De grootste obstakels voor een meer ecologisch relevante ecologische risicobeoordeling zijn het gebrek aan duidelijke beschermingsdoelen en de inherente complexiteit van ecosystemen die zich lastig empirisch laat duiden. In **Hoofdstuk 6**, stellen wij dat het ecosysteemdiensten-concept een goede mogelijkheid biedt om duidelijke en ecologisch relevante beschermingsdoelen te definiëren. Tegelijkertijd leveren ecologische modellen de handvatten om ecologische complexiteit te benaderen op het niveau dat nodig is om eindpunten uit metingen aan ecosysteemdiensten te koppelen en de hoeveelheid geleverde diensten en mogelijke nadelige effecten van menselijke activiteiten te kwantificeren. De uitdagingen van de ecosysteemdiensten aanpak worden bediscussieerd evenals de limitaties van ecologische modellen in de context van ecologische risicobeoordeling. Echter, we stellen dat beide onderzoeksgebieden snel vooruitgaan en erg waardevol kunnen zijn in het bereiken van een meer ecologisch relevante risicobeoordeling.

In **Hoofdstuk 7**, bespreek ik de bevindingen van dit proefschrift in een bredere context. Ik streef ernaar om de tekortkomingen van huidige ecologische risicobeoordeling te identificeren, me daarbij vooral richtend op definities van herstel en acceptable tijd om herstel te bereiken, en stel mogelijke verbeteringen voor.

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Curriculum vitae

Nika Galic was born (1979) and raised in Zagreb, Croatia. From her early age she was fascinated with the natural world, and especially its faunal part. Due to a humanistic orientation of her parents, she obtained her primary and secondary education with a strong emphasis on classic and other languages. When the time came to choose a university, she broke free and focused on her primary interests and enrolled in the Faculty of Natural Sciences at University of Zagreb to pursue a degree in biology with a specialization in ecology. She obtained her diploma in 2002 on the topic of use of ecoducts (bridges across roads that allow movement of animals) in Croatia.

After exploring the life of accountants and financial consultants, she continued her academic education by enrolling in a master's programme in Ecology - ecological and evolutionary dynamics, at University of Amsterdam. Here, a world of theoretical ecology and ecological modelling opened up. For her first project, she looked (with her supervisor Chris Klok) into consequences of polluted soils in the Netherlands for the earthworm-godwit trophic chain. For her thesis she chose to work with horses. Instead of riding them, Nika investigated whether a population in the Oostvaardersplassen, a Dutch nature reserve, might crash during especially long winters. For this, she developed (with her supervisor Andre de Roos) her first individual-based model that included horse energy budgets. She found out that horse populations in the Netherlands are safe from any crashing and several months later she graduated with distinction. Once back in Croatia, she worked for the NGO Green action where she performed a biodiversity assessment of the river Lika basin. She then spent several months working as an environmentalist in a company that produced plastic polymers.

In September 2007, she started her PhD project in the Aquatic Ecology and Water Quality Management group at Wageningen University and the Environmental Risk Assessment team in Alterra, under the supervision of Paul van den Brink and Hans Baveco. This thesis is the product of more than 4.5 years' worth of research on recovery of stressed aquatic arthropod populations. Nika will continue doing research on human impacts on global ecosystems and hopes to develop mitigation and management actions that ensure the sustainability of natural resources.

Her free time is usually spent on walks and playing with her canines (her dogs, not her teeth), watching movies with her husband, travelling, baking and reading. She is no stranger to an occasional indulgence in a variety of beers the Netherlands has to offer and is an avid apprentice to the world of beverage distillation.

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