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ABSTRACT

Ecological models are useful tools for evaluating the *ecological significance* of observed or predicted effects of toxic chemicals on individual organisms. Current risk estimation approaches using hazard quotients for individual-level endpoints have limited utility for assessing risks at the population, ecosystem, and landscape levels, which are the most relevant indicators for environmental management. In this paper, we define different types of ecological models, summarize their input and output variables, and present examples of the role of some recommended models in chemical risk assessments.

A variety of population and ecosystem models have been applied successfully to evaluate ecological risks, including population viability of endangered species, habitat fragmentation, and toxic chemical issues. In particular, population models are widely available, and their value in predicting dynamics of natural populations has been demonstrated. Although data are often limited on vital rates and doseresponse functions needed for ecological modeling, accurate prediction of ecological effects may not be needed for all assessments. Often, a comparative assessment of risk (*e.g.*, relative to baseline or reference) is of primary interest. Ecological modeling is currently a valuable approach for addressing many chemical risk assessment issues, including screening-level evaluations.

Key Words: ecological model, risk assessment, population, ecosystem, toxic, chemicals.

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INTRODUCTION

Ecological models may be used in a specific risk assessment to evaluate the *ecological significance*¹ of observed or predicted effects on individual organisms (Barnthouse *et al.* 1986; Bartell *et al.* 1992; Norton *et al.* 1992; Pastorok *et al.* 2002). Essentially, ecological models predict population, ecosystem, and landscape responses to perturbations of individual-level endpoints, such as survivorship or fecundity. For example, the effects of toxic chemicals on population dynamics can be simulated by perturbing the age-specific mortality and fecundity values in a Leslie matrix (life-history) model on the basis of knowledge about changes in these parameters obtained from toxicity test results (*e.g.*, Ferson *et al.* 1996). More complex ecological models, such as IFEM (Integrated Fates and Effects Model; Bartell *et al.* 1988) and AQUATOX (Park *et al.* 1974; Park 1998; USEPA 2000a,b,c), have built-in functions to account for toxic effects, as well as fate and transport of chemicals.

Many ecologists recognize the value of population and ecosystem modeling as applied to risk assessments for toxic chemicals (e.g., Barnthouse et al. 1986; Emlen 1989; Bartell et al. 1992; Ferson et al. 1996; Landis 2000; Suter and Barnthouse 2001; Sample et al. 2001). Ignoring population- or higher-level effects and focusing only on individual-level endpoints can lead to inaccurate risk estimates and possible errors in environmental management decisions. Failure to consider endpoints above the individual-organism level often leads to an overestimation of risk but in some cases may lead to an underestimation of risk (Forbes and Calow 1999). Kammenga et al. (2001) used population matrix models to evaluate the effects of cadmium and pentachlorophenol on soil invertebrates and found that exposure to toxicants could increase the sensitivity of organisms to the effects of other stressors on vital rates different from the ones affected by the toxicants. From their review of laboratory toxicity test data, Forbes and Calow (1999) concluded that the basic population growth parameter, r, integrates potentially complex interactions among life-history traits and thereby provides a more relevant measure of toxicant impacts than individual-level endpoints. Others (e.g., Bartell et al. 1988, 1992, 2000; DeAngelis 1996; DeAngelis et al. 1989) have emphasized the importance of using ecosystem and landscape models to interpret exposure-response data to identify possible population interactions that have effects on community structure and ecological processes above the population level.

In their review of ecological models that are potentially useful for chemical risk assessment, Pastorok *et al.* (2002) scored various models on the basis of evaluation criteria such as scientific support, regulatory acceptance, state of development, and ability to predict relevant assessment endpoints. They addressed population models (Ferson 2002; Carroll 2002; Regan 2002; Akçakaya and Regan 2002), ecosystem

Ecological significance is defined here as importance to population, community, or ecosystem responses, especially those with impacts on ecological structure and function. Norton *et al.* (1992) considered several factors that should be evaluated to determine ecological significance, including the nature and magnitude of effects, the spatial and temporal extent of effects, and the recovery potential under partial or complete removal of a stressor.

models (Bartell 2002; Mackay and Pastorok 2002a), and landscape models (Mackay and Pastorok 2002b) and recommended selected models for further evaluation and testing. They also discussed when ecological modeling would provide the greatest value in a chemical risk assessment, how to select specific models, and needs for training environmental managers and technical personnel (Ginzburg and Akçakaya 2002; Pastorok 2002).

The objectives of this paper are to define different types of ecological models and present examples of the utility of some recommended models in chemical risk assessments. Characteristics of ecological models recommended by Pastorok *et al.* (2002) are also summarized, including their input and output variables. Detailed descriptions of the models and the rationale for the scoring relative to evaluation criteria are provided in Pastorok *et al.* (2002). Bartell *et al.* (1992), Pauwels (2002), Landahl *et al.* (1997), and others give detailed examples of how ecological models provide useful information for risk assessment of toxic chemicals. Crutchfield and Ferson (2000) and Glaser and Connelly (2000) discuss the use of ecological models in assessing recovery from toxic chemical impacts.

TYPES OF ECOLOGICAL MODELS

For our purposes, an *ecological model* is a mathematical expression that can be used to describe or predict endpoints such as population abundance (or density), community species richness, productivity, or distributions of organisms. Ecological models typically deal with endpoints at the population, ecosystem, or landscape level, which are directly relevant to natural resource managers.

Population models describe the dynamics of the abundance or distribution of single species, sometimes with explicit descriptions of endpoints in time and space. *Ecosystem models* describe ecological systems composed of interacting populations. For simplicity, we include food web (*i.e.*, community) models in the category of ecosystem models, even though the former do not include abiotic components (following Pastorok *et al.* 2002). Spatially explicit, multispecies models are defined as *landscape models*, whereas spatially explicit models of single-species populations are defined as *metapopulation models*.

Models that address only toxic chemical transport, fate, and exposure are not considered ecological models in our review. These excluded models include chemical fate and transport models (Mackay and Paterson 1982; Southwood *et al.* 1989; Zacharias and Heatwole 1994), predictive bioaccumulation models (*e.g.*, Thomann *et al.* 1992, Gobas 1993, Traas *et al.* 1996), and food-web *exposure* models (*e.g.*, Fordham and Reagan 1991; Pastorok *et al.* 1996), which do not include functions for describing ecological effects. Nevertheless, such models may be combined with relationships describing toxic chemical effects model (Bartell *et al.* 1988; Koelmans *et al.* 2001). Many ecological models that predict ecosystem and landscape endpoints also include submodels that describe environmental transport, fate, and exposure. We do not address simple community indices such as the Index of Biological Integrity (*e.g.*, Karr 1981), habitat models such as the habitat selection index (USFWS 1981), and toxicity-extrapolation methods such as species sensitivity distributions

(OECD 1992; Aldenberg and Slob 1993), analysis of extrapolation error (Barnthouse *et al.* 1986), and allometric relationships (Mineau *et al.* 1996).

Our focus is on models that can be used to predict population, ecosystem, or landscape effects from endpoints at lower levels of biological organization, especially from effects on individual organisms. To exclude the models and indices listed above in no way indicates that they are not useful in ecological risk assessment. Indeed, biogeochemical, chemical fate, and bioaccumulation models, eutrophication models, and other excluded approaches may form the basis for the exposure analysis (U.S, EPA 1993). Thus, the population and higher-level effects models reviewed here must be linked to them for a comprehensive risk assessment. Such linkages may require that the output of an exposure model be used as input for the exposure-response functions included as components of the ecological models or used to set inputs for effects models. For example, a wildlife exposure model can be used to estimate the ingested dose of a toxic chemical in receptors of interest (*e.g.*, Pastorok et al. 1996). An exposure-response function or a series of such functions for different endpoints would be used to determine the level of effect(s) corresponding to the estimated exposure. This step is already included in some ecological models already (e.g., CASM, AQUATOX). In other cases, the risk assessor implements the linkage between exposure and effects models manually. That is, the exposure-effects functions are separate from the ecological model ultimately used to interpret effects; in this case (which we term *implicit modeling of toxicity*), the risk assessor takes exposure estimates and determines effect levels, such as mortality rates or reductions in reproductive output, from the exposure-response relationships. The magnitude(s) of individual-level effects is then entered as input data to the ecological model (e.g., increases in mortality and reductions in fecundity caused by toxic chemicals would be added to background rates in a Leslie population projection matrix). Few models truly integrate fate and effects (Koelmans et al. 2001), so this is an area of active research.

ECOLOGICAL MODELING IN CHEMICAL RISK ASSESSMENT

Ecological risk assessments should be based on the definition of clear assessment endpoints and measures of effect. *Assessment endpoints* are defined as environmental characteristics or values that are to be protected (*e.g.*, deer population abundance, bird species diversity, or wetland ecosystem productivity) (USEPA 1998). *Measures of effect* (formerly termed *measurement endpoints* by EPA) are quantitative expressions of an observed or measured biological response, such as the effects of a toxic chemical on survivorship or fecundity, related to the valued environmental characteristic chosen as the assessment endpoint. The primary measures of effect for a chemical risk assessment are related to the survival, growth, and reproduction of exposed organisms because these processes are related to population abundance and dynamics (USEPA 1998).

In some cases, the measure of effect is the same as the assessment endpoint (*e.g.*, when benthic macroinvertebrate communities are surveyed directly in a stream to assess species richness). If not, an ecological model can be used to extrapolate a measure of effect to an assessment endpoint. The mathematical model is used to precisely define the relationship as well as assumptions and uncertainties in the

extrapolation between endpoints. Many ecological models incorporate mechanistic functions to describe natural processes, such as nutrient and energy flows, organism growth, life stage transitions, dispersal, competition, predation, and interactions between organisms and the environment. The output of an ecological model will typically correspond to one or more assessment endpoints. The model may also provide probabilistic risk estimates derived from simulation of multiple scenarios (*e.g.*, Monte Carlo, first order error analysis, or probability bounds analysis). Regan *et al.* (this issue) discuss ways of expressing risk from the output of a population model.

Jørgensen *et al.* (2000) concluded that ecological models could be applied to assess risks associated with new chemicals and their uses, impacts associated with past uses of chemicals, and remedial actions or restoration options for cleanup of contaminated sites. In the first type of application, a generic ecological model would be used to support notification and registration activities for chemicals (*e.g.*, pesticides). In this case, the model must be flexible enough to accept alternative parameterizations to represent the characteristics of the different kinds of habitats, receptors, and chemical release scenarios expected. The second and third applications involve derivation of clean-up criteria for soil, water, sediment, and air, as well as evaluation of options for reducing risk (*e.g.*, under the U.S. Environmental Protection Agency (USEPA) Superfund program). Applications at specific contaminated sites require models precisely specified for the conditions at the site (*e.g.*, chemicals, habitats, and receptors of interest).

Ecological models could be used to develop environmental criteria. In the past, only toxicity-extrapolation models (Klaine et al. 1996; Solomon et al. 1996; Posthuma et al. 2002) and exposure models have been used to develop generic environmental criteria (Stephan et al. 1985; OECD 1992; van Leeuwen 1990). For example, a species sensitivity distribution may be used to determine the environmental concentration considered protective of a specified percentage of species in the community (typically 95% of the species as in development of EPA ambient water quality criteria). Because the species sensitivity distribution is derived from toxicity thresholds (e.g., EC50s or LC50s) for individual-level endpoints, the actual population- and community-level effects of toxic chemicals may not be adequately represented. Using ecological models to develop generic environmental criteria directly may prove difficult because of the numerous species, habitats, and environmental conditions that such criteria must cover. Nevertheless, use of a population model, for example, in interpreting the results of toxicity testing could be valuable in guiding the choice of protection levels even if the population-level endpoints are not directly included in the criteria algorithms.

Pastorok *et al.* (2002) discussed the use of ecological models in various phases of an ecological risk assessment. For example, food-web modeling may provide information about the keystone species in a community, which could be critical for selecting receptors and endpoints during the problem formulation phase. Population modeling can help in interpreting observed population dynamics to determine the extent of natural variability in abundance and the possible sources of the fluctuations (*e.g.*, effects on birth rate vs. effects on death rate). After a baseline risk assessment and remediation, ecological models may aid in assessing natural recov-

ery (Glaser and Connelly 2000), in planning restoration strategies, or in developing monitoring programs (*e.g.*, Urban 2000).

Ecological modeling would not always benefit a risk assessment (Pastorok *et al.* 2002). For example, when a worst-case analysis using individual-level endpoints shows that the risk is negligible, application of population and higher-level models would not be warranted. In such analyses, endpoints should be carefully chosen to include potential sublethal effects, and risk estimates conservatively interpreted. A proper worst-case analysis should minimize the chance of missing cases where individual-level effects have impacts on the population or higher levels. Conversely, suppose quantitative field evidence indicates severe effects on the abundance of target species from chemical contaminants. In this case, application of ecological models may not be necessary during the baseline risk assessment. Such models may still prove useful for evaluating the mechanisms of population-level effects (*i.e.*, which vital rate is affected or if indirect effects mediated through trophic interactions are likely), which would aid in designing remedial actions.

Description of Models

Recommended ecological model types are described below according to categories defined by Pastorok *et al.* (2002):

- Population Models
 - Scalar abundance
 - Life history
 - Individual-based
 - Metapopulation
- Ecosystem Models
 - Food webs
 - Aquatic
 - Terrestrial
- Landscape Models
 - Aquatic
 - Terrestrial

Because the recommended ecological models have already been described in detail (Pastorok *et al.* 2002 and references therein), only summaries of the characteristics and variables of selected models are provided here.

Two of the model categories listed above (*i.e.*, individual-based population models and terrestrial ecosystem models) are not addressed because of their limited potential for use in chemical risk assessments in the near future. Individual-based population models are very specific to the species and sites for which they were developed (*e.g.*, snail kite, great blue heron, and other species in the Florida Everglades for ATLSS), and extrapolating them to other ecological risk assessments is not generally practical (Regan 2002). Spatially aggregated ecosystem models are described below only for aquatic systems, not for terrestrial ecosystems. Mackay and Pastorok (2002a,b) concluded that spatially explicit (*i.e.*, landscape) models should generally be applied to ecological risk assessments for terrestrial ecosystems because of the high degree of heterogeneity in the habitat structure of these systems. In contrast, certain aquatic systems, such as well-mixed lakes, can be modeled effectively with spatially aggregated models.

Characteristics of Ecological Models

General characteristics of the various types of ecological models are summarized in Tables 1 to 3. Tables 4 to 6 list community, population, environmental, and disturbance variables included in the models recommended by Pastorok *et al.* (2002). The choice of a specific model for addressing an ecological risk assessment problem depends on the balance between model complexity and the availability of data, the degree of site-specificity of available models, and the issue, ecosystem, endpoints, and chemicals of interest (Pastorok 2002). The models summarized here are not the only models that would be useful for ecological risk assessments in the near future. Nevertheless, they illustrate classes of such models and their characteristics.

Because ecological models vary greatly in their complexity and ease of use, some are more appropriate for screening-level ecological risk assessments, whereas others are best reserved for detailed assessments. For example, stochastic scalar abundance models (either discrete or continuous time) and deterministic life-history matrix models are most appropriate for screening-level ecological risk assessments. Ecosystem and landscape models are generally used only for comprehensive ecological risk assessments because of the extensive effort and expense involved in applying these models. Stochastic life-history matrix models and metapopulation models (*e.g.*, RAMAS GIS and VORTEX) are recommended for detailed assessments where modeling of food webs is not required.

Example Applications of Ecological Models

In addition to evaluating selected ecological models, Pastorok *et al.* (2002) tabulated applications of various types of ecological models used to assess effects of toxic chemicals and physical habitat disturbance. Below, we discuss selected applications of ecological models recommended by Pastorok *et al.* (2002) for use in ecological risk assessment:

• Scalar model of Japanese crucian carp: A stochastic differential scalar abundance model was applied to local populations of Japanese crucian carp (*Carassiun auratus* subsp.) using data from Lake Biwa, Japan (Hakoyama and Iwasa 1998, 2000; Hakoyama *et al.* 2000).

Table 1. Characteristics of population models.^a

Model Type	Characteristics	Examples
Scalar Abundance Models		
Malthusian Growth	Exponential growth or decay	Models of colonizing species
Density-Dependent Growth	Growth rate decreases as a function of increased population abundance	Logistic (sigmoidal) Growth
	4	Stock-Recruitment (e.g., Ricker function, Beverton- Holt model)
		Ceiling model (growth rate is zero above specified threshold)
Stochastic Differential Equation and Discrete-Time Models	Natural variability modeled either as random noise or as noise with autocorrelation structures (<i>e.g.</i> , positive exponentially declining autocorrelation to simulate realistic environmental noise).	Calculation of probability of population decline (or recovery) to a given level within a specified time horizon
Equilibrium Exposure Models	Models birth and death rates as explicit functions of the toxicant concentration. Deterministic differential equations whose underlying biology is logistic population growth.	Hallam's model
Bioaccumulation and Population Growth Models	Consider chemical kinetics and bioaccumulation as well as population dynamics	RAMAS Ecotoxicology (includes options to specify function for density dependence)
		Ecotox simulator (bioenergetics model)
Life-History Models		
Deterministic Age- or Stage-Based Matrix Models	Survival rate and fecundity depend on the age-class or stage to which an organism belongs. Density- dependence may be included.	Leslie matrix (density-independent)
		RAMAS Age, Stage, Metapop, or Ecotoxicology
Stochastic Age- or Stage-Based Matrix Models	As above, but also incorporate environmental or demographic stochasticity or both in the estimates of survival probabilities and fecundities.	Caswell's models
Individual-Based Models		
	Track individuals defined in terms of their behaviors (procedural rules) and characteristics. Often spatially explicit.	SIMPDEL (Spatially explicit Individual-based simulation Model of Florida Panthers and white-tailed Deer in the Everglades and Big Cypress Landscapes)
		CompMech, which models compensatory mechanisms in fish populations
		CIFSS (California Individual-based Fish Simulation System)
		PATCH (Program to Assist in Tracking Critical Habitat)
Metapopulation Models		
Occupancy (Presence-Absence) Models	Models for determining the occupancy status or transitions in status of habitat patches	Incidence Function Models
		State Transition Models
Spatially Structured Demographic Models	Spatially explicit models incorporating population dynamics	RAMAS Metapop and RAMAS GIS
		Vortex

* References for models listed in this table can be found in Pastorok et al. (2002).

	<u></u>
Table 2.	Characteristics of ecosystem models. ^a

Model Type	Characteristics	Examples
Food-Web Models		
Predator-Prey Models	Two species models, with differential or discrete difference equations representing the population dynamics of a predator and its prey	Lotka-Volterra model
		Predator functional response models
and and a second of the second		Others
Population-Dynamic Food-Chain Models	Multiple predator-prey models (in differential equation form) coupled to form food-chain models with equations for the dynamics of a toxic chemical	Mussel (Mytilus edulis) model
Complex Food-Web Models	Predator-prey, food-chain, or food-	RAMAS Ecosystem, a multispecies population
	web models	dynamics modeling with toxic chemical effects
		Populus, a multispecies model without toxic chemical effects
ter - 1 - 1976		Ecotox, a bioenergetics and toxic chemical effects model
Aquatic Ecosystem Models		
Process-Based Models of Aquatic Ecosystems	Differential (or difference) equation models of organism bioenergetics, growth, and population dynamics with species interactions. Spatially aggregated, although some may be applied in a modular fashion to mimic landscape models. Some (e.g., IFEM) include detailed chemical fate models.	AQUATOX, a lake or river model
		LERAM (Littoral Ecosystem Risk Assessment Model)
		CASM (Comprehensive Aquatic System Model), a lake or river model
		SIMPLE (Sustainability of Intensively Managed Populations in Lake Ecosystems), the Lake Ontario fisheries model
n an		FLEX/MIMIC, a hierarchical lotic ecosystem model IFEM (Integrated Fates and Effects Model), a
		chemical fate and risk model
Fitness-based Model	Includes fitness as an explicit term and optimizes population distribution among habitats	INTASS (INTeraction ASSessment model), a general model applicable to aquatic and terrestrial ecosystems
Terrestrial Ecosystem Models		
Process-based Models of Terrestrial Ecosystems	Differential (or difference) equations of organism bioenergetics, growth, and population dynamics with species interactions. Spatially aggregated, although some may be applied in a modular fashion to mimic landscape models. Generally without functions for toxic chemical fate and effects.	Desert Competition Model, a model of two competing mouse species
		Forest gap models, which project forest development through time; e.g., FVS (Forest Vegetation Simulator), FORCLIM (FORest CLImate Model), FORSKA
Model Type	Characteristics	Examples
		Grassland ecosystem models; e.g., Energy Flow for Short Grass Prairie Model, SAGE (System Analysis of

Model Type	Characteristics	Examples
		Grassland ecosystem models; e.g., Energy Flow for Short Grass Prairie Model, SAGE (System Analysis of Grassland Ecosystems), SWARD, and SPUR (Simulating Production and Utilization of Rangeland)
Species Turnover Models	Model for evaluating community species composition	Island biogeography models; <i>e.g.</i> , Multitimescale Community Dynamics Model, a model of species turnover in bird communities
Nestedness Models	Patterns of ecosystem structure quantified based on variance from that expected under random conditions	Nested Species Subset Analysis, a model for analyzing patterns of nestedness for subsets of species
Fitness-Based Model	See above, equatic ecosystem model	INTASS (INTeraction ASSessment model), a general model applicable to aquatic and terrestrial ecosystems

^a References for models listed in this table can be found in Pastorok et al. (2002).

Table 3. Characteristics of landscape models.^a

Model Type	Characteristics	Examples
Landscape Models		
One-Dimensional Spatially Segmented Models	Spatially explicit models with only one dimension of segmentation, typically for rivers	Delaware River Basin Model
Paratlel Process-Based Models of Aquatic, Terrestrial, and Wetland Systems	Spatially explicit models consisting of multiple subcomponents typically organized within a matrix. Parameterization of the subcomponents is a function of its location and is often relative to the states of other defined subcomponents.	ERSEM (European Regional Seas Ecosystem Model), a model of marine benthic systems
		Patuxent River Watershed Model, a whole watershed model comprising ecological and economic systems Disturbance to Wetland Vascular Plants Model, a
		model of wetland plant communities Forest landscape models:
		LANDIS (LANdscape DIsturbance and Succession)
		FORMOSAIC (FORest MOSAIC) Model
		FORMIX (FORest MIXed) Model
		ZELIG
		JABOWA
		Regional Landscape Model, a model of ozone effects on a forest and associated water bodies
		Spatial Dynamics of Species Richness Model, a model for evaluating the effects of habitat fragmentation
		Grassland models:
		STEPPE, a gap-dynamic model of grassland productivity
		Wildlife-Urban Interface Model, a model to predict the effects of human activities on wildlife
Island Biogeography Models	Models describing the distribution of species among habitat patches based on immigration and emigration rates	SLOSS (Single Large or Several Small), a model of distribution of species assemblages in habitat patches
	and sometimes considering the probability of mortality or reproduction in a patch based on habitat factors	Island Disturbance Biogeographic Model, a model of species distributions within linked island habitats
Coupled LaGrangian and Eulerian Model	Coupled chemical fate and ecosystem model for lakes and rivers based on a combination of mathematical approaches	CEL HYBRID (Coupled Eulerian LaGrangian HYBRID)

Model Type	Characteristics	Examples
Markovian/Probability Occupancy Models	Markovian transition matrix that permits the simultaneous consideration of land-cover categories within each individual grid cell	Multi-scale Landscape Model, a model of landscape structure based on probability of species occurrences
Modular Modeling Systems	Multitrophic level modeling system with different mathematical representations for various trophic levels: process-based models for lower levels; matrix life-history models for mid levels, and individual-based models for higher levels. Coupled to comprehensive abiotic model (e.g., hydrology).	ATLSS (Across-Trophic-Level System Simulation), a landscape model of the Everglades

^a References for models listed in this table can be found in Pastorok et al. (2002).

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Table 4. Summary of community and population variables in selected ecological models.

		Populati	Pepulation Models		Ec	Ecosystem Models			Landsca	Landscape Models	
	Scalar	Life History Matrix	Food Web	Metapopulation - RAMAS-GIS							Island
Variable [°]	Abundance (crucian carp)	(fathcad minnow)	(red-tailed hawk)	(California gnatcatcher)	AQUATOX	CASM	IFEM	ATLSS	LANDIS	LANDIS JABOWA	Biogeographic Model
Community Characteristics											
Number of species	one	one	two	one	multiple	multiple	multiple	multiple	multiple	multiple	multiple
Typical species	any	Age- or	any	Spatially	phytoplankton,	phytoplankton,	zooplankton,	aquatic	tree	tree	non-specific
	,	structured	`	structured	zooplankton, benthic infauna,	zooplankton, benthic infauna,	benthic invertebrates,	vegetation, fish, seed-	species	species	ı
					fish	fish	fish	eating birds, piscivorous birds, deer			
Type of trophic interactions ^b	ON	NO	FC	NO	FC	FC	PC	FC	NO	NO	ON
Relative abundances in immigrant population										х	x
Individual Population Characteristics											
Abundance or biomass in native population	x	×	×	x	х	x	×	х	х	х	×
Age- or stage-specific abundance or biomass				х	X°			xª		Х	
Carrying capacity	х		x	x							×
Density dependence		×	×	х							
Maximum age	х		x				×		×	x	×
Population growth rate	x	×	×	x							
Overall montality rate		х	×	x	x	×	×				×
Age- or stage-specific mortality rate		х	х	х	x			×	X*	x	
Age of first reproduction		x	X	х				Xª	×		
Overall frequency of reproduction	х	x	×	х							x
Overall fecundity (offspring per reproduction)		x	×	x	х	x	x	х			×
Age- or stage-specific fecundity			×	x				X ⁴			
Home range size			×	x							
Periodicity (seasonality) of presence in home range	nge							х			
Offspring dispersal distance				×					X²		х
Immigration or emigration probability or rate				x						x	x
Habitat suitability coefficients (by habitat type)				×				×	×	×	

Role of Ecological Modeling in Risk Assessment

Table 4. (continued)

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		 	tole	tolerance, tolerance	rance	
				fire		
	-		tol	crance		
Spatially Explicit Population Data						
Locations inhabited	x		x	х	x	x
Abundances	×		x		X	
Distribution of competitors					X	
Distribution of predators			x			

^b None (NO), food chain or food web (FC), producer-consumer (PC)
^e Two cohorts for fish species
^d Age-structured models are used only for aquatic species
^e For 0-age individuals only, representing sprouting ability
^f Specified as a range
⁸ Both effective and maximum seed dispersal distance

		Popula	Population Models		Ecos	Ecosystem Models	ls		Lands	Landscape Models	
	Scalar	Life History	Food Web	Metapopulation -							Tsland
	(crucian	(fathead	(red-tailed	(California							Biogeographic
Variable [*]	carp)	minnow)	hawk)	gnatcatcher)	AQUATOX	CASM	IFEM	ATLSS	LANDIS	JABOWA	Model
Environmental media, variables, and species categories modeled	tegories modele	q									
Soil								×		×	
Surface water					х	x	Х	х			
Sediment					х		х				
Suspended particulates							х				
Soil biota											
Sediment infauna					x	х	х				
Terrestrial vegetation										х	
Aquatic vegetation					х		×	Х			
Plankton					x	х	х	х			
Fish	x	х			х	х	х	Х			
Small mammals											
Birds			x	x				х			
Spatially explicit site data											
Location of immigrant population source				х							x
Distribution of habitat types or land types				x				×	×	×	
Distribution of food, water, nesting sites, etc.				x		·		x	×		
Chemical toxicity or other disturbance data											
Types of disturbances or stressors	Chemical, habitat	Chemical (Mirex)	Chemical (Fenthion)	Cold, wet winters; fire	Chemical	Chemical	Chemical (PAH)	Low water levels	Fire, wind damage	Mortality (e.g., logeine)	Non-specific mortality
Contaminant mass balance modeled	*******				х	X	Yes		No		No
Soil contamination modeled											
Surface water contamination modeled					х	Х	х				
Sediment contamination modeled					x		х				
Terrestrial vegetation contamination modeled											
Aquatic vegetation contamination modeled							×				
Bioaccumulation					х	x	X				
Growth rates/effects	х					×	×				
Mortality rates/effects	×	х	×		×			×	×		×
Reproductive effects		Х			_						

Table 5. Summary of environmental variables in selected ecological models.

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Table 5. (continued)

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		Populat	Population Models		Ecos	Ecosystem Models	s		Lands	andscape Models	
	Scalar	Life History		Metapopulation -							
	Abundance	Matrix	Food Web	RAMAS-GIS							Island
	(crucian	(fathead	(red-tailed	(California							Biogeographic
Variable [*]	carp)	minnow)	hawk)		AQUATOX CASM	CASM	IFEM	ATLSS	LANDIS	ATLSS LANDIS JABOWA	Model
Other effects	Risk of	Risk of	Risk of Probability	Dispersal of	Population Population	Population				Community	
	extinction	population	population of abundance	juveniles,	size (biomass)	size				composition,	
		decline	and biomass	subpopulation		(biomass)				species range	
			decline	characteristics,						and density	
				spatial correlations							
Exposure indicators											
Spatial location of disturbance									х		х
Spatial extent of disturbance									х		х
Time scale of disturbance ^b	c	c	υ		c	ບ		Р	I		Ι

^a A blank cell indicates that the variable is not applicable to the model.

^b Continuous (C), periodic (P), irregular or any pattern (I)

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Table 6. Summary of chemical toxicity and other disturbance variables in selected ecological models.

Variable Matrix Abundance (athtab) List Matrix (califormise) Metric Matrix (califormise) Metric Matrix (califormise) Metric Matrix (califormise)			Populat	Population Models		Ecos	Ecosystem Models	sl		Lands	Landscape Models	
		5	Life History	T1 W/-L	Metapopulation -							Laland
		Abundance	fathcad	rood web (red-tailed	(California)		,				-	Island Biogeographic
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	Types of disturbances or stressors	Chemical,	Chemical	Chemical	Cold, wet	Chemical	Chemical	Chemical	Low	Fire,	Mortality	Non-specific
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ation modelediii<	Terrestrial vegetation contamination modeled											
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Aquatic vegetation contamination modeled							x				
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c c c c c c c c c c c c c c c c c c c				decline	characteristics, spatial		(comion)				and density	
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	Spatial location of distribution									~ ~		< >
										; '		
	Time scale of disturbance ^b	ပ	v	ပ		C	c					Ι

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Role of Ecological Modeling in Risk Assessment

- Life-history model of fathead minnow: Spencer and Ferson (1998) used RAMAS Ecotoxicology to apply Waller *et al.*'s (1971) life-history model to the fathead minnow (*Pimephales promelas*) data.
- **Metapopulation model of California gnatcatcher:** Akçakaya and Atwood (1997) used RAMAS GIS to develop a habitat-based metapopulation model of the threatened California gnatcatcher (*Polioptila c. californica*).
- Food-chain model for red-tailed hawk: Long *et al.* (1997) used RAMAS Ecosystem to construct a food-chain model for red-tailed hawk (*Buteo jamaicensis*) feeding on fenthion-exposed songbirds.
- Aquatic ecosystem model for experimental ponds: Bartell *et al.* (1992) applied SWACOM (Standard Water Column Model) to evaluate the effects of phenolic compounds on aquatic systems.
- Aquatic landscape model for the Everglades: DeAngelis (1996) and others (<u>www.atlss.org</u>) are developing a comprehensive modeling framework for the Everglades that includes different kinds of models for various trophic levels.
- **Terrestrial landscape models:** LANDIS (Mladenoff *et al.* 1996; Mladenoff and He 1999), JABOWA (Botkin 1993a,b), and the Island Disturbance Biogeographic Model (Villa *et al.* 1992) were developed mainly for predicting the effects of physical disturbance on forests or associated fauna.

The models listed above are examples of the kinds of models we have confidence in for use in supporting environmental management decisions. Although the value of using ecological models in risk assessment and management should be apparent based on the discussion of each model, more details on the use of the models can be found in the original references. Other authors (*e.g.*, Barnthouse *et al.* 1986; Barnthouse 1998; Bartell *et al.* 1992; 2000; Ferson *et al.* 1996; Urban 2000) also provide examples of how ecological models can inform decision-making in the context of risk assessment and management. Pastorok *et al.* (2002) present information on the cost and effort needed to apply various kinds of ecological models.

Stochastic Scalar Population Model of Japanese Crucian Carp

A stochastic differential scalar abundance model was applied to local populations of Japanese crucian carp (*Carassiun auratus* subsp.) using data from Lake Biwa, Japan (Hakoyama and Iwasa 1998, 2000; Hakoyama *et al.* 2000). The model is:

$$dN/dt = rN(1 - N/K) + \sigma\xi_e(t)N + \xi_d(t)\sqrt{N}$$

where

dN/dt = the rate of change in population growth N = population abundance r = the instantaneous rate of intrinsic increase

- *K* = the carrying capacity (*i.e.*, maximum population size that the environment will sustain)
- σ = the magnitude of environmental stochasticity
- ξ_e = white noise for environmental stochasticity, and
- ξ_d = white noise for demographic stochasticity

Estimates of *r*, *K*, σ , and the parameters for stochasticity are necessary to apply the model to field populations. The population abundance, growth rate, and environmental stochasticity were estimated from 40 years worth of data on catch per unit effort (CPUE) of Japanese crucian carp with an assumed generation time of 4 years. Forty years of population data is a substantial amount of data, which would be available only for well-studied ecosystems and species. Confidence limits were calculated for the appropriate maximum likelihood of each of these estimates using Monte Carlo analyses. The carrying capacity of Lake Biwa was estimated as >10⁶.

The effects of toxic chemicals on the carp population were incorporated into the model through both a decline in the rate of survivorship and a reduced carrying capacity. A logistic regression formula was used to estimate the survivorship decline rate in relation to concentrations of copper (Hakoyama *et al.* 2000). A decrease in the logarithm of the carrying capacity was used to simulate a reduction in habitat size.

The effects of toxic chemicals were modeled implicitly rather than explicitly. The effect of copper on the intrinsic rate of population increase for crucian carp was modeled according to the function observed for *Daphnia* by Tanaka and Nakanishi (1998):

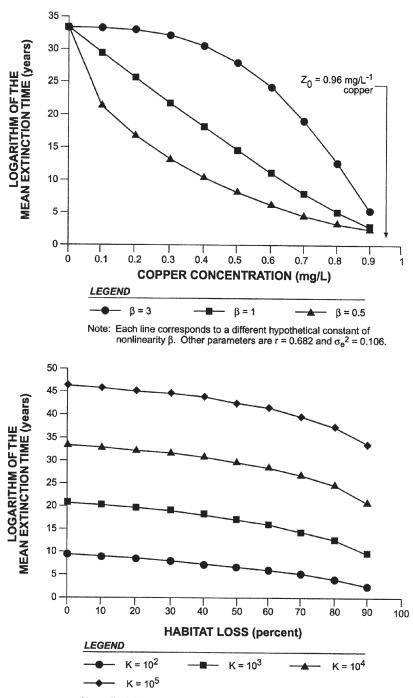
$$r(z) = r_{\max}\left[1 - \left(\frac{z}{z_0}\right)^{\beta}\right]$$

where

r	=	intrinsic population growth rate
z	=	chemical concentration
z_0	=	chemical concentration when $r = 0$
r_{max}	=	maximum intrinsic population growth rate
β	=	nonlinearity parameter

The mean time to extinction was calculated for both toxic chemical effects and habitat loss (Figure 1). The magnitude of habitat loss that induces extinction risk comparable with the effects of toxic chemicals was calculated. It was shown that the relative importance of habitat loss and toxic chemical exposures varies with the carrying capacity. The stochastic differential scalar abundance model applied to the Japanese crucian carp data can be used to evaluate the magnitude of threat to a wide range of species caused by a variety of risk factors. These impacts might include habitat size reduction, chemical contamination, habitat fragmentation, harvest or hunting, recurrent spread of epidemics, invasion of competitors, or

Pastorok et al.



Note: Each line corresponds to a different hypothetical carrying capacity. Source: Hakoyama et al. (2000). With permission.

Figure 1. Logarithms of the mean extinction times of a carp population for (top) different doses of copper and (bottom) different degrees of habitat loss.

genetic deterioration. The model is very flexible and easy to implement given some data on population growth or component parameters, data or assumptions about the magnitude of environmental and demographic stochasticity, and corresponding data on the effects of the stressor of interest on the population parameters.

Life-History Model of Fathead Minnow

Spencer and Ferson (1998, pp 29 to 35) used RAMAS Ecotoxicology to apply Waller *et al.*'s (1971) life-history model to the fathead minnow (*Pimephales promelas*) data. The Waller *et al.* (1971) model took the form of a Ricker density dependence model:

$$N_{t+1} = e^{\varepsilon} \alpha N_t e^{-\beta N_t}$$

where

N_{t+1}	=	the number of females at time <i>t</i> +1
N_t	=	the number of females at time t
ε	=	a dimensionless error term representing environmental variability
α	=	the maximum population growth rate (dimensionless), and
β	=	a measure of the strength of density dependence (females ⁻¹).

The study of Mirex effects on fathead minnow (Waller *et al.* 1971; Spencer and Ferson 1998) includes extensive data on the number of eggs per female, hatching success, juvenile survival, adult survival, and density dependence. These laboratory test data were used to calculate the best estimate and standard deviation of β , and a best estimate and 95% confidence interval for α . Both parameters were estimated from regression models constructed from the fecundity, survival, and test population density data in Waller *et al.* (1971). e^{ε} was defined as a lognormal distribution with a mean and standard deviation estimated from the data. α and e^{ε} were then combined into a single fecundity value.

Life-cycle toxicity data for the effects of the organochloride insecticide Mirex on egg production, juvenile mortality, and adult mortality for fathead minnow were selected from Barnthouse *et al.* (1986) for five Mirex concentrations. These data were used because of their apparent reliability and the relatively large number and wide range of concentrations tested. Because only a single stage was included in the population model, the number of eggs per female, hatching success, juvenile survival, and adult survival acted multiplicatively as components of the maximum population growth rate α , and the maximum population growth rate was calculated as a proportion of the control maximum growth rate estimated from the natural system. Thus, for any concentration of Mirex, the maximum population growth rate was calculated as:

$$\alpha_x = \alpha \frac{E_x H_x J_x S_x}{E_c H_c J_c S_c}$$

where

- α_x = the maximum population growth rate at concentration x (μ g/L)
- α = the maximum population growth rate in an unaffected population
- E = the number of eggs per female
- H = hatching success
- J = juvenile survival, and
- S = adult survival.

The subscript c indicates control parameters, and the subscript x indicates parameters at contaminant concentration x. The coefficient of variation in the fecundity was kept the same at different toxicant concentrations.

In this model also, the effects of toxic chemicals are modeled implicitly rather than explicitly. In this case the effect of a toxic chemical on the population growth parameter was estimated directly from available life-cycle toxicity data for the species of interest. Changes in the population growth rate were therefore calculated only for the specific chemical concentrations used for the life-cycle toxicity tests of Barnthouse *et al.* (1986). Estimation of population effects at other chemical concentrations would require a modified approach (*e.g.*, determination of dose-response relationships for egg production, hatching success, and survival).

The model applied to the fathead minnow data was used to predict and compare the risk of population decline at each of five Mirex concentrations (Figure 2). A wide range of uncertainty in α had marked effects on the dynamics of the model. Results of the model indicate that concentrations greater than 3 µg/L give risks of decline that the authors considered unacceptably high. The authors conclude that more experimental data are required to separate the effects of toxicity and uncontrolled variation and to improve the estimate of control group fecundity from field data. Given the importance of the density-dependence term in this model, the most cost-effective applications will be for those populations where data on density dependence is already available or it can be readily obtained (*e.g.*, aquatic organisms and small-bodied terrestrial species that can be manipulated in field or laboratory experiments).

Metapopulation Model of California Gnatcatcher

Akçakaya and Atwood (1997) used RAMAS GIS to develop a habitat-based metapopulation model of the threatened California gnatcatcher (*Polioptila c. californica*) in Orange County. The study started with a compilation of detailed habitat data on vegetation and topography and with demographic data on survival, reproduction, and dispersal of this species. The habitat data included raster maps of habitat variables. These data were organized by a geographic information system and combined with locations where gnatcatchers were observed.

These data were then used in a stepwise logistic regression in which the gnatcatcher observations were the dependent variable and values from habitat maps were independent variables. The predicted habitat suitability was a function of the variables coastal sage scrub (CSS), elevation (ELV), distance from trees (DTR), and distance from grassland (DGR) and the interactions $CSS \leftrightarrow ELV$, $CSS \leftrightarrow DTR$, and



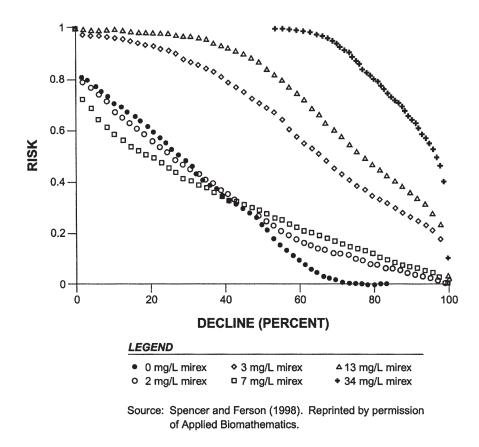


Figure 2. Risk of a given percentage decline in a fathead minnow population during the simulation interval as a result of exposure to the pesticide Mirex.

ELV↔DTR (see Table 1 in Akçakaya and Atwood 1997). The habitat function that was predicted by the regression was then used to calculate a habitat suitability (HS) value (between 0 and 1) for each cell in a raster map. The value gave the probability of finding a gnatcatcher pair at that location and thus reflected the suitability of the habitat.

The resulting habitat suitability map was then validated by estimating the regression function from the northern half the landscape and using this function to predict the habitat suitability for known locations in the southern half. Because the observations used to estimate the function were not the same as those used to test it, the result showed the predictive ability, and hence the validity of the function rather than simply its goodness-of-fit. The validated habitat suitability map was analyzed to calculate the spatial structure of the species' metapopulation (*i.e.*, the number, size, carrying capacity, and location of its subpopulations) based on the distribution and quality of the habitat.

At the population level, the model for the California gnatcatcher incorporated demographic data on survival, reproduction, and environmental variability for each population inhabiting a habitat patch. Demographic data collected in banding

studies were used to parameterize a stage-structured, stochastic matrix model with two stages (juveniles and adults). The stage matrix, which assumes a "birth-pulse" population and a post-reproductive census, is:

$$\begin{bmatrix} P_{JB}M & S_aM \\ S_j & S_a \end{bmatrix}$$

where

 S_a = survival rate of adults

 S_i = survival rate of juveniles

 P_{IB} = proportion of last year's juveniles that are breeders this year, and

M = maternity or fertility (number of fledglings per breeder).

Because the demographic data were collected for several years, both the average values and the temporal variability of the matrix elements could be calculated. The temporal variabilities were used to model environmental stochasticity (random, year-to-year fluctuations in vital rates). In addition, the model included two types of catastrophes: cold/wet winters that affect vital rates and fires that affect carrying capacities.

At the regional (metapopulation) level, the model incorporated data on spatial factors that are important determinants of the risk of decline, including dispersal among patches (based on sightings of banded juveniles), catastrophes, and spatial correlation of environmental fluctuations among the patches. The model was used to perform a risk assessment that incorporated the effects of natural variability as well as the uncertainties in model structure and parameters associated with lack of knowledge and measurement errors (see Akçakaya and Atwood 1997). This model did not incorporate any estimation of effects caused by toxic chemicals. To use this model to estimate impacts of toxic chemicals, their effects on demographic parameters or habitat suitability would have to be estimated independently and those revised parameters then substituted into this model.

Food-Chain Model for Red-Tailed Hawk

Long *et al.* (1997) used RAMAS Ecosystem (Spencer and Ferson 1997) to construct a food-chain model with red-tailed hawk feeding on fenthion-exposed pest birds. The goal was to examine the population-level consequences of the secondary poisoning by fenthion. RAMAS Ecosystem was used to link the toxicant uptake in the prey (mainly starlings, sparrows, and grackles for the purpose of this study), population growth, and predator-prey interactions. The model used estimates of raptor biomass, birth and mortality rates, and carrying capacity from the red-tailed hawk data. The hawk population was assumed to be stable and at or very near carrying capacity and closed to immigration and emigration. Toxicity test data for the raptors were used to estimate LC50 concentrations with 95% confidence intervals and a Weibull dose-response function (Long *et al.* 1997). Raptor exposure was assumed to be a function of the percentage of pest bird biomass poisoned and the

960

area affected. Pest birds were assumed to be the sole source of toxicant contamination to the raptors, and approximately 10,000 contaminated prey birds were estimated to survive and disperse each month. Killed pest birds were assumed to be replaced daily by freshly poisoned birds from an unlimited supply. The total area affected was estimated to lie within a 20-mile radius, and fenthion treatment of pest birds was assumed to occur during 2 months of the year for 5 days at a time.

The model was used to calculate the probability of abundance and biomass decline of the red-tailed hawk population. Model results indicated that under these conditions the long-term population-level effects on the hawk population were likely to be minimal. Because fenthion treatment of pest bird populations is often conducted during winter months, the compounding impact of a decrease in temperature on the red-tailed hawk population was also investigated. Long *et al.* (1997) found that if cold temperatures increased the toxicity by 20%, the model predicted a substantial decrease in hawk biomass over time, and the risk of a decline of 50% or more became significant. Results of the model suggested that limiting pest bird control programs to one or two years during the warmer seasons would greatly reduce the risk of decline of hawk populations that prey on the pest species.

Aquatic Ecosystem Model for Experimental Ponds

One of the few examples where an ecosystem model has been truly validated is the use of SWACOM (Standard Water Column Model) to evaluate the effects of phenolic compounds on aquatic systems (Bartell *et al.* 1992). SWACOM is a precursor of CASM (Comprehensive Aquatic System Model) and does not have the ability to model multiple populations of littoral and benthic species (DeAngelis *et al.* 1989; Bartell *et al.* 1992, 1999). CASM also includes multiple nutrients and can simulate time-varying concentrations of toxic chemicals. In both models, the impacts (or risks) posed by toxic chemicals can be evaluated at the population, community, or ecosystem level. Both models can be used to predict time-varying states of phytoplankton, zooplankton, and various categories of fish. The application of SWACOM is discussed here because of the value of the validation results. Applications of CASM include aquatic risk assessments for pentachlorophenol, copper, and diquat dibromide (herbicide) (Bartell *et al.* 1999). A recent application of CASM is also discussed below (see *Comparative Application of Ecological Models*).

Bartell *et al.* (1992) applied SWACOM to experimental ponds (mesocosms) and compared model predictions of species abundances with measurements made in the ponds as well as with the estimated effects thresholds from single-species toxicity tests performed in the laboratory on representative pond taxa. The original version of SWACOM, which includes 19 population types, was simplified to apply to the ponds. Piscivorous fish and two of the three planktivorous fish groups were removed from the model so the model food web resembled the web found in the ponds. A simulation lasting 56 days was used for the comparison of predicted and measured results because that duration encompassed the period in which most ecological effects were observed in the ponds. Only two experimental ponds were used per treatment so the measured data display relatively high variance.

The comparison of SWACOM predictions with the experimental pond data (Figure 3) showed that the model reproduced relative changes in pond ammonia concen-

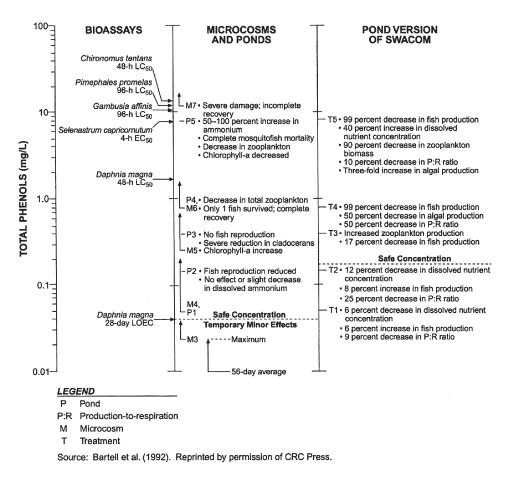


Figure 3. Validation of SWACOM aquatic ecosystem model using observations of the effects of phenols in laboratory microcosms and outdoor experimental ponds.

trations, phytoplankton productivity, zooplankton population size, fish population size, and production: respiration ratios. Most model predictions were within an order of magnitude of the observations. Despite the model's ability to predict relative changes well, many of the predictions were inaccurate (off by greater than a factor of 10), especially for the intermediate exposure treatments. Bartell et al. (1992) summarized the qualitative comparisons of the SWACOM results with toxicity test data and the experimental pond measurements (Figure 3). Generally, the model results agreed with the measured effects in the ponds, although effects were slightly underestimated at low exposures (e.g., the safe concentration in the model results was approximately double that determined from the pond experiments) (Figure 3). Interestingly, the 28day LOEC measured for effects of phenols on the cladoceran Daphnia magna in laboratory experiments was a good predictor of the safe concentration estimated from the pond experiments. LC50 and EC50 values from the laboratory experiments were generally poor predictors of ecological effects because substantial effects were observed in the ponds below these toxicity thresholds for representative species (Figure 3). Bartell et al. (1992) concluded that ecological modeling provides useful information

for decision-making by facilitating the extrapolation of toxicity test results to predict population and higher-level consequences.

Aquatic Landscape Model for the Everglades

ATLSS is a multicomponent modeling framework for the Florida Everglades that simulates responses of species or biotic groups in all trophic levels across spatial and temporal scales that are ecologically relevant to a large wetland system (DeAngelis 1996; www.atlss.org). ATLSS uses different modeling approaches tailored to each trophic level, including differential equations for process models of lower levels and age-structured and individual-based models for higher levels that include animal energetics, behavior, and movement. At present, ATLSS is being developed only for the Everglades, but the modeling concepts could be applied to other systems. The model endpoints include species abundances and biomass, species richness, and organism distributions. The current version of ATLSS focuses on the ecological effects of variations in the hydrologic system. Although it does not presently consider the effects of toxic chemicals, it is being modified to account for the effect of mercury on receptors at high trophic levels. The ATLSS web site (www.atlss.org) and Pastorok *et al.* (2002) provide additional information on components of ATLSS.

Water flow is the major factor controlling the trophic dynamics of the Everglades and Big Cypress Swamp of South Florida. Thus, a key objective of ATLSS modeling studies is to compare the effects of alternative hydrologic scenarios on selected species or biotic groups. Results from applying ATLSS are being used as input to a planning process for ecosystem restoration, including development of appropriate monitoring and adaptive management approaches. Initial applications of ATLSS have included the following models:

- Hydrologic model (high-resolution at 500 m or finer)
- Hydroperiods associated with vegetation types
- Breeding potential models
 - Cape Sable seaside sparrow (SIMSPAR)
 - Wading birds
 - White-tailed deer (SIMPDEL)
 - Snail kite
 - Alligator
- Landscape fish model (ALFISH)
- Individual-based models
 - Cape Sable seaside sparrow (SIMSPAR)

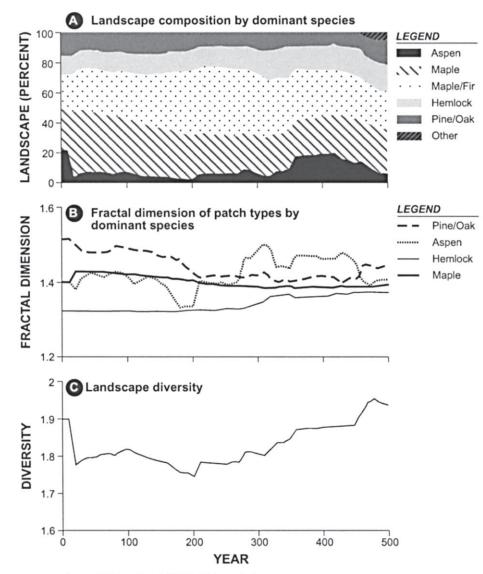
Covering the entire freshwater landscape of this system, ATLSS is linked to various GIS maps and addresses spatial scales of resolution as small as 28 m. The spatial segmentation of the system within the ATLSS project considers both physical and administrative boundaries. For each of the population models in ATLSS, estimates of abundance are presented as graphs that show the projected changes in population size over a 31-year time period. ATLSS includes spatially explicit species index models that compare the relative potential for breeding and foraging of selected species across the landscape based on the spatially explicit, within-year hydrodynamics of the wetland system. These species index models have been applied to the Cape Sable seaside sparrow, the snail kite, short- and long-legged wading birds, white-tailed deer, and alligators. The fish model (ALFISH) considers the size distribution of large and small fishes relative to foraging requirements of wading birds. The individual-based models for the Cape Sable seaside sparrow, the snail kite, the white-tailed deer, the Florida panther, and various wading bird species link each individual animal to specific environmental conditions (e.g., water depth, food availability) on the landscape. The population dynamics and spatial distribution of these species is determined by changes in these conditions. Overall, the kinds of data and models included in ATLSS represent state-of-the-art use of ecological modeling in environmental management. The success of the ATLSS efforts and the value of results for management decision-making will depend on ongoing data collection efforts and the ability to integrate models and results within this innovative framework.

Terrestrial Landscape Models

The terrestrial landscape models, Landscape Disturbance and Succession (LANDIS) (Mladenoff and He 1999; Mladenoff *et al.* 1996), JABOWA (Botkin 1993a,b), and the Island Disturbance Biogeographic Model (Villa *et al.* 1992), were developed mainly to predict the effects of various kinds of disturbance on forests. With the exception of an application of JABOWA to study the effect of acid rain on forests of Long Island, New York (Botkin 2000, personal communication), none of these models has been applied to toxic chemical effects analysis.

LANDIS is a stochastic, spatially explicit model of forest landscape succession that includes interacting windthrow and fire disturbance elements, as well as harvesting effects. Species life-history parameters that drive the model include longevity, age of sexual maturity, shade tolerance class, fire tolerance class, windthrow tolerance class, effective and maximum seed dispersal distance, vegetative reproductive probability, maximum sprouting, and seed establishment coefficient by land cover type. The model has an associated spatial analysis package (APACK) that calculates landscape indices and summary results (Figure 4). LANDIS is now being expanded to look at the effects of physical disturbance on landscape pattern and associated effects on forest birds and wolf recolonization.

JABOWA is a generalized model of the reproduction, growth, and death of trees in mixed-species forests in response to environmental conditions. JABOWA has been widely used to evaluate the effects of global warming, acid rain, and commercial forest harvesting practices (Botkin 1993a,b; 2000 personal communication). The user determines the kind and number of tree species for up to 45 species and



Source: Mladenoff et al. (1996). With permission.

Figure 4. Example of selected analytical and landscape index output from APACK module of LANDIS plotted through the 500-year simulation. (A) landscape composition by dominant species; (B) fractal dimension of patch types by dominant species; (C) landscape diversity

assigns each tree a series of state variables that determine the shape of the tree, growth, and mortality. The model includes algorithms to account for the effects of key variables on growth and reproduction: light, soil moisture, soil depth, soil waterholding capacity, soil nitrogen, percentage of rocks in the soil, latitude, and snow melt rate. Ecologically relevant endpoints from output of JABOWA include tree biomass, forest productivity, and species richness. Many types of forests have been modeled over a wide range of environmental conditions in North America, in Siberia, in Eastern Europe, and in Costa Rica.

The Island Disturbance Biogeographic Model is used to evaluate the effects of immigration and perturbations on the distribution of species in island habitats. Because the model deals specifically with the effects of disturbance on community composition and distribution, it could be useful for ecological risk assessments of toxic chemicals. For example, a chemically contaminated site could be considered as a "habitat island" or series of islands embedded within the surrounding landscape, and the subpopulations of various species exposed to the site could be considered as a focal modeled component. Toxic chemical effects could be modeled implicitly by varying reproductive and mortality parameters or perhaps by modifying the model to include dose-response functions. However, this model has been applied mainly for developing ecological theory and has not been applied to specific cases. It could be most useful as a tool for exploring general effects of chemicals and generating hypotheses rather than for making individual site-specific risk assessments.

Comparative Applications of Ecological Models

Bartell *et al.* (2000) compared three different approaches to modeling of ecological risks using a case study for the pesticide diquat dibromide applied to a lake or pond. These authors applied an individual-oriented model (Hallam *et al.* 1990) for the cladoceran *Daphnia*, a life-history (modified Leslie matrix) model for bluegill (*Lepomis macrochirus*) (Ferson 1993; Bartell *et al.* 2000), and the aquatic ecosystem model CASM (DeAngelis *et al.* 1989). Each of these approaches goes beyond the simple hazard quotient method for comparing an estimated exposure and an effects threshold and attempts to represent the physical, chemical, biological, and ecological processes that mechanistically determine particular adverse effects as a result of chemical exposures.

The individual-oriented model of *Daphnia* is based on the energetics of an individual female *Daphnia* followed through a stage-structured life history from egg to juvenile to adult. The bioenergetics model of individual growth was embedded in a system of McKendrick–von Foerster partial differential equations to describe the growth dynamics of a population (Hallam *et al.* 1990). Bartell *et al.* (2000) coupled the *Daphnia* model with an exposure model, the Food and Gill Exchange of Toxic Substances Model (Barber *et al.* 1988). Pesticide effects were evaluated using a NOEC, an EC50 for *Daphnia* growth, and an LC50.

The bluegill demographic model was based on a Leslie matrix (Ferson 1993), which describes the fecundity and survivorship values for specific size classes of individual fish. The matrix is used with an initial size-class vector of abundance values to project the total population size and age structure at the next time interval. Successive iterations of the model yield a trajectory of population abundance over time. Bartell *et al.* (2000) modified the Leslie matrix to incorporate seasonal spawn-

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ing of the fish, the proportion of individuals growing from one stage to the next, and density-dependence. Pesticide effects were expressed as decreases in the fecundity, survivorship, and growth parameters.

CASM is a modification of the SWACOM model described above (see Aquatic Ecosystem Model for Experimental Ponds). CASM consists of a graphic user interface coupled with a biological and ecological modeling framework that describes the growth of populations of aquatic plants and animals in surface water and sediments of rivers, lakes, and reservoirs. CASM extends the capabilities of SWACOM by including multiple populations of aquatic organisms characteristic of the littoral and benthic communities. Like many other aquatic ecosystem models, CASM calculates the biomass of primary producers by using equations describing physiological processes such as photosynthesis, grazing, nonpredatory death, respiration, and so on. For consumer populations, consumption, egestion, nonpredatory death, respiration, and other processes are considered. The impacts (risks) posed by toxic chemicals can be measured at the population, community, or ecosystem level in CASM. A statistical distribution of an effects factor derived from an exposureresponse relationship is used within CASM to estimate sublethal effects on individual organisms. Bartell et al. (2000) implemented CASM in a Monte Carlo mode to estimate risks of diquat dibromide expressed as the probability of observing various magnitudes of effects (e.g., 10, 20, 30, ...100% reductions in production).

Bartell *et al.* (2000) found that the results of these different types of ecological models were consistent in predicting that the expected pesticide concentrations resulting from recommended application rates of diquat dibromide would pose a minimal ecological risk. The authors suggested that each of the modeling approaches could provide a useful perspective as part of a comprehensive method for assessing the ecological risks of pesticides or other toxic chemicals. The selection of one or more approaches would depend on the specification and importance of differently scaled (*i.e.*, individual-based, population, or ecosystem) endpoints deemed appropriate for a particular risk assessment.

CONCLUSION

Ecological models are used to translate the results of risk characterization for individual organism endpoints into estimates of effects on population, ecosystem, and landscape endpoints. Population and ecosystem models have been applied successfully in past ecological risk assessments, including those that address toxic chemical issues. These models provide valuable perspective on the ecological significance of risk estimates calculated for individual organism endpoints such as survival, growth, or reproductive measures. In particular, population models are widely available, and their value in predicting dynamics of natural populations has been demonstrated. Although data are often limited on vital rates and dose-response functions needed for all assessments. Often, a comparative assessment of risk (*e.g.*, relative to baseline or reference) is of primary interest. Thus, population modeling is currently a cost-effective approach for addressing most chemical risk assessment issues, including screening-level evaluations. Without some kind of ecological modeling as part of the risk assessment, reliance on hazard quotients for individual-

organism endpoints and qualitative predictions of population or higher-level effects can lead to serious misjudgment of ecological risks.

Modeling approaches can be tailored to the issues and level of detail that need to be addressed in a risk assessment. For example, stochastic scalar abundance models and deterministic life-history matrix models are most appropriate for screening-level ecological risk assessments. Stochastic life-history matrix models and metapopulation models (*e.g.*, RAMAS GIS and VORTEX), as well as aquatic ecosystem models like AQUATOX, CASM, and IFEM, are suitable for detailed ecological risk assessments. Applying population models to chemical risk assessments is more cost-effective than using ecosystem and landscape models. Nevertheless, landscape modeling approaches like the Everglades modeling system ATLSS and the terrestrial-landscape models LANDIS and JABOWA should be developed further and evaluated for use in chemical risk assessment. These models are promising tools for assessing potential impacts on systems resulting from multiple causes and complex interactions among populations.

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