Individual-Based Models Applied to Species Abundance Patterns in Benthic Macroinvertebrate Communities in Streams in Response to Pollution

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An Individual-Based Model (IBM) was developed by employing natural and toxic survival rates of individuals to elucidate the community responses of benthic macroinvertebrates to anthropogenic disturbance in the streams. Experimental models (dose-response and relative sensitivity) and mathematical models (power law and negative exponential distribution) were applied to determinate the individual survival rates due to acute toxicity in stressful conditions. A power law was additionally used to present the natural survival rate. Life events, covering movement, exposure to contaminants, death and reproduction, were simulated in the IBM at the individual level in small (1 m) and short (1 week) scales to produce species abundance distributions (SADs) at the community level in large (5 km) and long (1~2 years) scales. Consequently, the SADs, such as geometric series, log-series, and log-normal distribution, were accordingly observed at severely (Biological Monitoring Working Party (BMWP<10), intermediately (BMWP<40) and weakly (BMWP≥50) polluted sites. The results from a power law and negative exponential distribution were suitably fitted to the field data across the different levels of pollution, according to the Kolmogorov-Smirnov test. The IBMs incorporating natural and toxic survival rates in individuals were useful for presenting community responses to disturbances and could be utilized as an integrative tool to elucidate community establishment processes in benthic macroinvertebrates in the streams.

Key words : ecotoxicology, pollution, tolerance, sensitivity model, dose-response model, power law, negative exponential distribution

INTRODUCTION

Understanding biological response to environmental disturbance is a key issue in contemporary ecological science due to the ubiquitousness of disturbances in ecosystems, such as climate change and pollution. Since communities occupy the highest level in biological organization (i.e. accommodating individuals and populations in a hierarchy) in ecosystems and consists of diverse species varying in a characteristic manner, analysis of community composition has garnered special attention in the elucidation of ecological processes re-

sponding to environmental disturbances. Benthic macroinvertebrates are considered to be one of the most representative taxa for examining the ecological states of aquatic ecosystems in response to disturbances (James and Evison, 1979; Resh and Rosenberg, 1984; Hellawell, 1986; Resh *et al.*, 1995). Since benthic macroinvertebrates are characterized by diverse taxa, sedentary habituation, and proper life span for checking continuous environmental effects (i.e., season-year), those have been widely used for ecological water quality assessment (Hellawell, 1986; Rosenberg and Resh, 1993; Wright *et al.*, 2000; Chon *et al.*, 2002; Park *et al.*, 2007; Allan and Castillo, 2007).

Communities with diverse taxa, such as benthic macroinvertebrates, are also suitable in presenting species abundance distribution (SAD). Since Motomura (1932), SAD has been used to reflect the structural changes in communities. Numerous studies have reported on SADs in a wide scope of taxa: terrestrial plants (del Moral, 1999; Begon *et al.*, 2006; Forster and Warton, 2007) and terrestrial animals (Fisher *et al.*, 1943; Syrek *et al.*, 2006; Ford and Lancaster, 2007). Various models were also proposed to present SADs, including geometric series (e.g., Motomura, 1932), log series (e.g., Fisher *et al.*, 1943), log-normal distribution (e.g., Preston, 1948; Sugihara, 1980), and broken stick model (e.g., MacArthur, 1957, 1960). Since 1970s importance of community response to disturbances has drawn attention in forecasting and management of ecosystems, and SADs have been extensively reported, including neutral model (Hubbell 1997, 2001) and niche partitioning (Tokeshi, 1993, 1996), to elucidate community establishment mechanism and to provide alternative interpretations on biodiversity composition (McGill *et al.*, 2007). Extensive reviews on SADs can be found in May (1975), Tokeshi (1993), Marguet *et al.* (2004), Magurran (2004), May *et al.* (2007), McGill *et al.* (2007) and Poulin *et al.* (2008).

SADs, however, have rarely been applied to benthic macroinvertebrates in aquatic conditions, beside reports on marine benthic communities responding to disturbances (Gray, 1981; Hughes, 1984; Magurran and Henderson, 2003). Recently, Qu *et al.* (2008) evaluated SADs of benthic macroinvertebrates in polluted streams and depicted the ecological states of the sampling sites by comparing them with models of SADs, such as geometric series, log-series, and log-normal distribution. Tang *et al.* (2010) investigated chironomid communities in streams and comparatively applied SAD models, reporting that the ecological states of chironomidae pertaining to the sample sites could be reflected by SAD models such as random fraction and dominance decay.

Since communities consist of numerous species varying in a diverse manner, however, the dynamic response of communities to environmental stressors are difficult to illustrate. We utilized Individual-Based Models (IBMs) to present complex ecotoxicological processes by focusing on the integrative relationships between individuals and communities. Pioneering studies using IBMs reported individual uniqueness and variability in late 1970s (Łominicki, 1978; DeAngelis *et al.*, 1980). Since then, IBMs have been implemented in ecology in a broad scope of different scales covering populations, communities, and ecosystems. Reviews of IBMs can be found in DeAngelis and Gross (1992), Grimm (1999), Grimm and Railsback (2005), Grimm *et al.* (2006, 2010), Breckling *et al.* (2005), and Chon *et al.* (2009).

Although IBMs have been applied to forest dynamics (Lett *et al.*, 1999) and food web dynamics (Reuter, 2005), they have been seldom applied to the investigation of SADs at the community level. Dewdney (2000, 2003) constructed an IBM in community development to propose a multispecies logistic system, consequently allowing for a high diversity of species with minimal abundance in the system. Chave *et al.* (2002) applied IBMs to investigate species area relationships and SADs in order to check pattern diversity and trade-offs (i.e., reproduction vs. competition). They reported that the models allowing the nearest neighbor dispersal, in general, produced "S-shaped" curves on the log-linear plots of abundance in relation to species rank. Giacomini *et al.* (2009) explored community assembly through an IBM for suggesting a weak influence of interspecific interactions in a trophic network. In the studies stated above, however, the models mainly examined natural processes, focusing on predator-prey relationships, competition, trade-offs, etc. Effects of anthropogenic effects on community establishment have not been reported extensively in IBMs.

Ecotoxicological effects were mainly reported on population level including the classical probit analysis (Busvine, 1971), and the dose-response based model (e.g., Van den Brink *et al.*, 2007). Anderson (2000) applied mathematical models to illustrate probability of survival according to organis-

m's vitality in response to chemical exposure and reported stressor distribution and survivorship curves in relation with age. Few studies, however, have been conducted on investigating mortality of the whole species. Species sensitivity distribution has been discussed in Posthuma *et al.* (2002) and sensitivity distribution of toxic materials (e.g., copper and zinc) on aquatic invertebrates at the community level was reported by Warren-Hicks *et al.* (2002). Based on mesocosm experiments Van den Brink *et al.* (1995) investigated effects of single application of insecticide (chlorpyrifos) to check overall species composition and analyzed the data with multivariate ordination technique to demonstrate a rapid concentrations-dependent decrease in numbers after insecticide application (direct effect) in certain taxa (i.e., Crustacea and Insecta). Hoekstral *et al.* (1998) checked sensitivity of different species to chemicals and presented skewness and kurtosis of log transformed 50% lethal concentration (LC_{50}) to facilitate comparison of the observed distributions with log-normal and log logistic distribution. Wogram and Liess (2001) and Von der Ohe and Liess (2004) noted importance of exposure of multitude of species to toxicants and proposed the relative sensitivity model of different species using a reference to lethal concentration (LC_{50}) of an indicator species, *Daphnia magna* (Koivisto, 1998).

Communities in severely stressful conditions such as pollution in aquatic systems, however, have not been extensively dealt with IBMs, although IBMs have been applied to populations of a single species in numerous cases, including trout (Madenjian *et al.*, 1993), earthworm (Baveco and De Roos, 1996), waterlouse (Van den Brink *et al.*, 2007), and bass (Van Winkle *et al.*, 1993). Hall *et al.* (2006) applied IBMs to assess population consequences of an anthropogenic contaminant (polychlorinated biphenyl) to bottlenose dolphins to indicate a possibility of depression in population growth. Pastorok *et al.* (2003) outlined ecological modeling in risk assessment, covering chemical effects on populations including IBMs (Regan, 2003) and metapopulation models (Akçakaya and Regan, 2003). Recently, an ecotoxicological IBM was developed to illustrate suitable species establishment in adaptation to toxic response and metabolic efficiency through the gene-individual-population relationships (Cho *et al.*, 2011).

We used simple mathematical and experimental models to present natural and toxic survival rates of individuals in an IBM and investigated responding community structure of benthic macroinvertebrates due to acute toxicity in stressful conditions. The SADs were obtained from the models and were compared with field data collected in streams across different levels of pollution.

MATERIALS AND METHODS

1. The model

1) General framework and purpose

Natural and toxic mortalities at the individual levels were applied to life events including movement, exposure to toxic substances, death, and reproduction in an IBM. SADs of benthic macroinvertebrates were consequently observed across different concentrations of contaminants in streams. A description of the model was arranged in accordance with the IBM protocol (Grimm *et al.*, 2006, 2010) with a slight modification of the components, including system environment, attributes, and design concepts. A summary of the programming and parameters used in the IBM are provided in Tables 1 and 2, respectively.

2) System environment

In this study individuals of benthic macroinvertebrates were exposed to pollutants in streams. System environment was established to provide overall spatial and temporal conditions in virtual space where life events for each individual will be performed according to the rules given in the model. Simulations were performed on a 2D space (5 ×5000 site in size) in order to resemble a segment of stream (Table 1). The length of the stream was determined by taking the investigated river into account (i.e., Suyoung River, the upper stream: 5～7 km) (Table 2). One site was set to represent an area of about 1 m^2, representing a segment of a tributary in the 2nd or 3rd order. In the context of empirical sampling, the size of site was equivalent to the size for one time sampling of benthic macroinvertebrates (Qu *et al.*, 2008; Tang *et al.*, 2010) and to the size presented in other studies, such as gap models (Shugart, 1984). Reflective boundary conditions were assumed upstream and at the left- and right-banks of the stream, while the boundaries of downstream were taken to be absorbing. For simplicity, we mainly examined the longitudinal distribution of communities, assuming variation in toxic effects in the cross section is

Table 1. Components of an IBM employing natural and toxic survival rates of individuals presenting SADs in communities.

Components	Sub-components	Description
System		
Domain	Space Time (t)	Imaginary 2-D ($5 \times 5{,}000$ units) Imaginary time step (i.e., week)
Constraint	Boundary Termination	Absorbing (downstream) and reflection (upstream and side) t=50-100
Environment	Pollutant	Lognormal distribution from the source
Attributes and states		
Individual	Position Age No. of offspring	x, y coordinate in 2D Life stage (young/intermediate/old larva and adult) 5
Population	Size (different species)	Number of individuals
Community	Size	SAD
Sites	Occupied state	Empty, or occupied by individuals
Events and interaction		
	NSR	Power law
	TSR	Dose-response based model, Sensitivity model, Power law, Negative exponential
Movement	Random walk Escaping	Neighbor sites ESR
Reproduction		Constant (5)
Competition		Density dependence; controlled by local carrying capacity
Initial condition		
Species		100 species; random determination
Individuals		Random between 0~50 individuals per species; random distribution
Pollutant		Lognormal distribution from the source
Output		
Population		Change in population size
Community		SAD

negligible in this study. We neither took into consideration for the physical environments of the stream, for example, variations of depth, velocity, and width of the stream. The depth was considered to be constant at 1 meter.

Each iteration was equivalent to one week in simulation. Observations were made after community dynamics were stabilized, usually taken 50~100 iterations (i.e., approximately equivalent to 1~2 years) (Table 2). An IBM was constructed using MATLAB (The Mathworks Inc. 2012).

3) Attributes and states

The community at iteration t was composed of N individuals in total, and each individual belonged to one of the given S species {1, 2, 3, ⋯, S}. In this study species of general benthic macroinvertebrates were considered, since theoretical analysis (e.g., community structure) and practical application (e.g., water quality indices) are based on entire species (Hellawell, 1986), and whole taxa are usually collected through field surveys (Qu *et al.*, 2008; Tang *et al.*, 2010). We assumed mortalities due to either natural death or intoxication. For simplicity of calculation we defined survival rates as the reverse of mortalities. Two types of survival rates were used: Natural Survival Rate (NSR), presenting survival rate in natural conditions (i.e., reverse of natural mortality), and Toxic Survival Rate (TSR), presenting survival by overcoming

Table 2. The parameter values of an IBM employing natural and toxic survival rates of individuals presenting SADs in communities.

Parameter (Unit)	Symbol	Description (Equation)	Source*
Total river width (m)		4	[1],[2]
Total river length (m)	n	$5000 \sim 7000$	[1],[2]
Number of species	S	100	[1],[2]
Movement range (sites)		$1 \sim 5$	[3]
No. offspring (individuals)		5	
Life stage		(young, intermediate and old larvae, and adult)	[1],[2]
Pollutant concentration (lognormal distribution)	C	$0 \sim 1$ Eqn.6	[4]
Mean		1	
Variance		1	
Carrying capacity (Local)	K	10000	[1],[2]
Natural mortality			
Power law	α, μ	0.95, 0.2 (Eqn.5)	Assumed
Toxic mortality			
Relative sensitivity	δ, d	0.01, 1.0 (Eqn.1)	[5]
Dose-response	b, ξ	1.0, 0.03 (Eqn.2)	[6]
Exponential	a, β	1.0, 1.5 (Eqn.3)	Assumed
Power law	α', μ'	0.95, 4.5 (Eqn.4)	Assumed

*[1] Qu *et al.* 2008, [2] Tang *et al.* 2009, [3] Englund and Hambak 2004, [4] Al-Khallidi 2002, [5] Van den Brink *et al.* 2007, [6] Von der Ohe and Liess 2004

toxic effects (i.e., reverse of toxic mortality). TSR is assumed as the minimum survival rate corresponding to the maximal level of contaminants at the source. The values of NSR and TSR were determined by the proposed models which will be described later (see equations $1 \sim 5$ in the section of "5) Design concepts and submodels"). We additionally defined Effective Survival Rate (ESR) of individuals at the current site where the contaminants were diluted from the source. Survival or death of individuals was determined by ESR in response to concentration of contaminants (see "(2) Criteria for survival" and "(4) Effective Survival Rate (ESR)" in "5) Design concepts and submodels").

Species assignment for each individual was performed according to the levels in two criteria, NSR and TSR (Fig. 1). We considered these two survival rates as the traits for determining species. Each criterion was divided into 10 ranks. The 10 levels of TSR and NSR were then combined (i.e., two dimensions) to assign species. Random numbers were run two times for each individual to determine the ranks for NSR and TSR. Consequently one hundred species were produced for simulation (Fig. 1).

After generation of individuals, attributes such as location and life stage were assigned to each individual in addition to NSR and TSR. Since

Fig. 1. Species assignment of individuals according to the rank of natural (NSR) and toxic (TSR) survival rates (normalized between $1 \sim 10$).

NSR and TSR were fixed at 10 levels per species, the same values of NSR and TSR were assigned for all individuals belonging to the same rank in the same species. But a low level of noise was added to the NSR and ESR values (see "(6) Stochasticity" in "5) Design concepts and submodels").

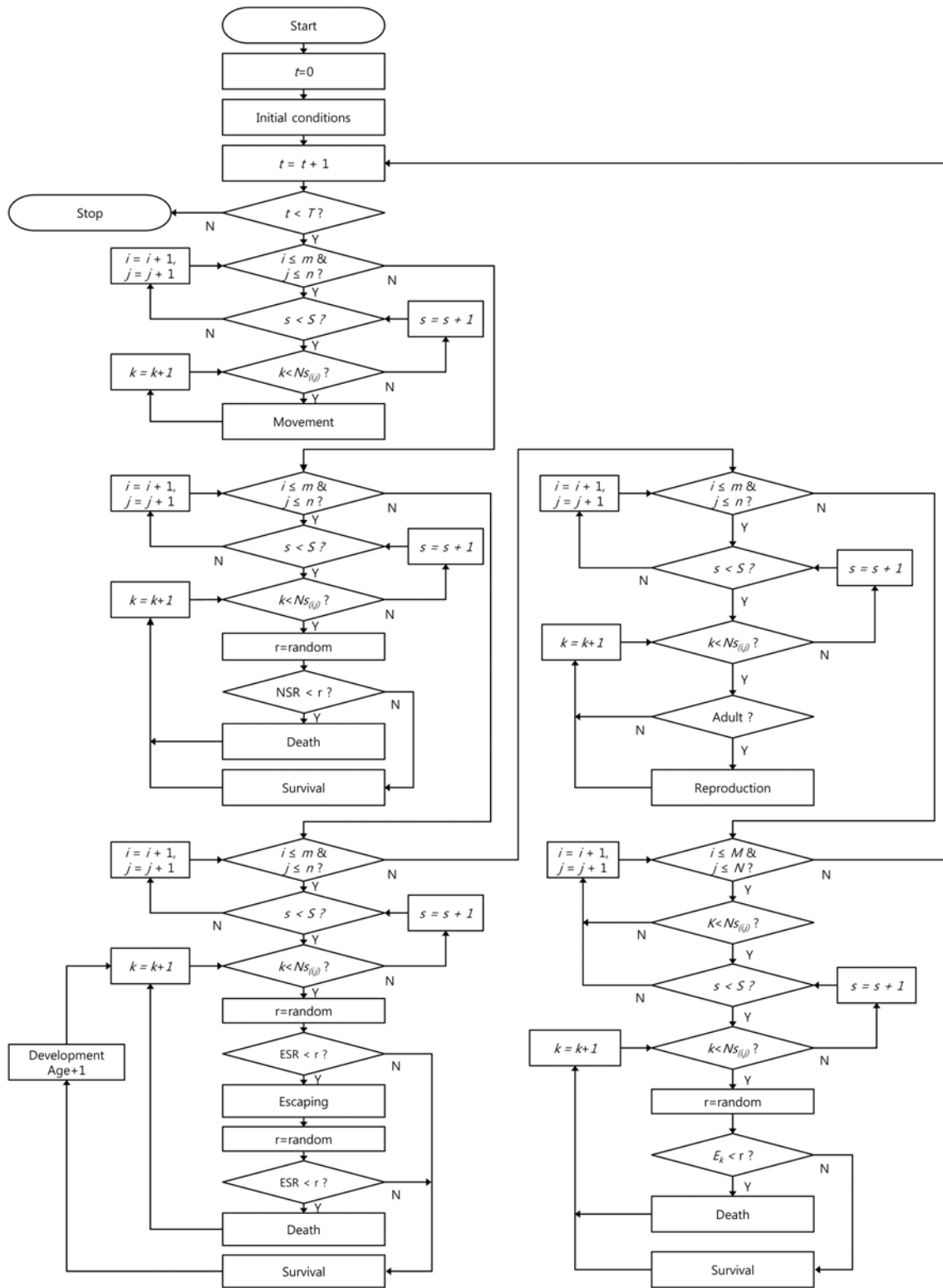Life stage composed of young, intermediate and old larva, and adult. We assumed that all adults

Fig. 2. Flowchart of an IBM employing natural and toxic survival rates of individual in presenting SADs in communities (*t*: time, T: total iteration, *i*, *j*: site coordinate, *m*, *n*: system size, *S*: number of species, *s*: species index, N_s (*i*, *j*): number of individuals in species *s* at site *i* and *j*, *k*: index of individual, *K'*: local carrying capacity, ESR: effective survival rate, NSR: natural survival rate, E_k: density dependent survival rate).

were females that laid 5 offspring each.

4) Process overview and scheduling

A flowchart describing the overall process of IBM is given in Fig. 2, covering movement, development, exposure to toxic substances, escaping, death, and reproduction. The simulation started with the old larval stage, since macroinvertebrates spend as larval stage in winter and the life stage generally starts with the old larva in spring in temperate zones. The individuals moved in two phases under natural and stressful conditions. Individuals moved under natural conditions first. Afterwards the individuals were exposed to contaminants at new site. Depending on ESR at the site the larva will either move (i.e., escape) again or remain at the current site. After escaping, death will be subsequently determined according to ESR at new site (see "(1) Movement" and "(5) Effective Survival Rate (ESR)" in "5) Design concepts and submodels").

Each stage was processed per iteration; 4 iterations were equivalent to one generation. The offsprings produced by the females were considered to be young larvae. The newly produced larvae repeated the life events as the time step progressed (Fig. 2).

5) Design concepts and submodels

(1) Movement

Movement occurred under natural and stressful conditions as stated above. Intermediate and old larvae moved at random within the neighbor sites (7×7) under natural conditions. Young larvae, however, moved according to the Gaussian distribution along the longitudinal axis. The mean values were the previous positions of the adults and standard deviation was 5 sites. Escaping or remaining was determined according to ESR at new site. A random number was generated. If the value was lower than ESR, the individual will remain at this site. Otherwise the individual will search for the site with the lowest concentration of contaminants in the neighborhood sites, which was defined as the 5 downstream sites from the target site. After escaping to new site, another random number was generated for determination of survival due to toxic effect. If the number was higher than ESR at new site, the individual died. Otherwise the individual survived. The same movement rules were applied to all larval stage under stressful conditions. The long distance movements

(e.g., flooding effect) were not considered in the model.

(2) Criteria for survival

NSRs and TSRs were used to determine survival or death of individuals in natural and stressful conditions, respectively. We mainly considered acute toxic effects in determining mortalities in stressful conditions in this study. In presenting toxic effects on communities, the important is the physiological sensitivity to the contaminants presented in the acute toxicity test (Wongram and Liess, 2001). The stress from the acute toxicity (e.g., oxygen depletion) is prevalent in streams (Hellawell, 1986). Only a few species in the tolerant groups to oxygen depletion, such as chironomids and tubificids, will be selectively abundant in severely polluted conditions in freshwater ecosystems while the abundance of other species will decrease rapidly (Hellawell, 1986; Rosenberg and Resh, 1993; Wright *et al.*, 2000; Chon *et al.*, 2002; Park *et al.*, 2007). This type of rank abundance pattern (i.e., hollow curve for emphasizing a few dominant species) in communities could be also observed in natural conditions, although the degree of slope may be less sharp (Odum and Barrett, 2005).

In order to employ this type of sharp decrease in survival at the individual level, 4 models were considered: two experimental models, dose-response model (Van den Brink *et al.*, 2007) and relative sensitivity (Van der Ohe and Liess, 2004), and two mathematical models, power law and negative exponential distribution. Relative sensitivity (S) (Van der Ohe and Liess, 2004) is expressed as $S=\log(L_D/L_S)$ where L_D is LC$_{50}$ (lethal concentration) of *Daphnia magna*, and L_s is LC$_{50}$ of species s. We assumed that the survival rate and lethal concentration measured at the population level could be applied to the individual level ($S \rightarrow S_i$, $L_S \rightarrow L_i$) for individual i. TSR for individual i, v_i, can be expressed as the reverse of S_i as $v_i = 1 - S_i = 1 - \log L_D + \log L_i$. We considered that the degree of L_i changes according to the rank of species (T_i) to which individual, i, belongs to. We further assumed that, L_i and T_i are equivalent, and the term "1-log L_D" is a constant. The first case for individual survival rate based on relative sensitivity could be expressed as:

$$v_i = e^{\delta C} T_i + d, \tag{1}$$

where C is concentration of contaminants, δ and d

are constants.

The second is the dose-response based model according to Van den Brink (2007). The model was used for determination of population mortality based on lethal concentration, $S=[1+e^{-b(D-a)}]^{-1}$, where S is survival rate, b is a slope, a is natural logarithm of effective concentration 50% ($\ln(EC_{50})$), and D is natural logarithm of predicted environmental condition. We assumed a varied in accordance with the species rank T_i of individual i, and D was concentration of contaminants at the site. The second case based on dose-response was:

$$v_i=[1+e^{-b(C-\xi T_i)}]^{-1}, \tag{2}$$

where ξ and b are constants.

The third and fourth cases were mathematical models. The third was the case of negative exponential function as shown

$$v_i=\alpha e^{-\beta C T_i}, \tag{3}$$

And the last case was power law given by

$$v_i=a' T_i^{-\mu' C}, \tag{4}$$

where α, β, a', and μ' are the constants and other symbols are the same as above.

Fig. 3 compares the curves for the four models after normalization of values on x (rank) and y (0.0 -1.0) axes with the parameters: $\delta=0.01$; $d=1$ (sensitivity model), $b=1$; $\xi=0.03$ (dose-response based model), $\alpha=1$; $\beta=1.5$ (negative exponential distribution), and $a'=0.95$; $\mu'=5.0$ (power law). Survival rates decreased along with decrease in the ranks (i.e., higher values T_i) on the x-axis. The slopes presenting the experimental models appeared to be less decreasing (i.e., less sharp) compared with the mathematical models. The dose-response based model decreased most slowly, while the relative sensitivity model showed linear decrease. The negative exponential distribution, in contrast, appeared to decrease most rapidly (Fig. 3). In species assignment, the values were divided into 10 ranks as stated above (see "3) Attributes and states").

We additionally used the power law to present NSR in natural conditions. NSR for each individual was defined to be the reverse of natural morality and was given for individual i as:

$$p_i=aT_i^{-\mu}, \tag{5}$$

where T_i is the species rank to which individual i belongs, and a and μ are the constants. The survival of individuals was determined on a stochastic basis according to p_i and v_i in natural and
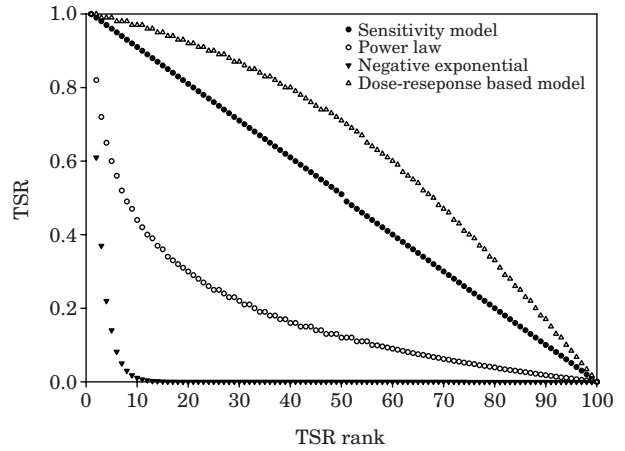

Fig. 3. Comparison of TSRs across different ranks in different models (see text for parameter values).

stressful conditions, respectively.

(3) Pollutant concentration

We used the log-normal distribution model in determining the concentration of pollutants along with the distance, x, in stream (Al-Khallidi, 2002):

$$p(x)=f_x(x,\,\lambda,\,\sigma)=\frac{1}{x\sigma\sqrt{2\pi}}\,e^{-\frac{(\ln x-\lambda)^2}{2\sigma^2}},\,x>0, \tag{6}$$

where x is mean and equal to $\log_{10}(n/10)$, n is system size, and $\sigma=1$ is standard deviation. We assumed that the concentration levels of pollutant over the space were stabilized before the initiation of simulation. We considered the water current to be slow, and that shear force and turbulence were not produced during simulation. Velocity differences were assumed not existing over cross sections of the stream, and thus that longitudinal dispersal coefficient (Boeker and van Grondelle, 1995) was negligible. We considered that the source of pollution was evenly distributed across cross sections of the stream. Subsequently, concentrations of pollutants continuously diffused evenly along with the longitudinal axis from upstream.

(4) Effective Survival Rate (ESR)

Concentration of pollutants was diluted according to the distance from the source as stated above (Eqn. 6). ESRs for the individuals at the site were obtained by the product of Equation 6 and TSR in different models (Eqns. 1-4). In Fig. 4 the ESR values were illustrated according to species rank and distance from source of contaminants in dif-
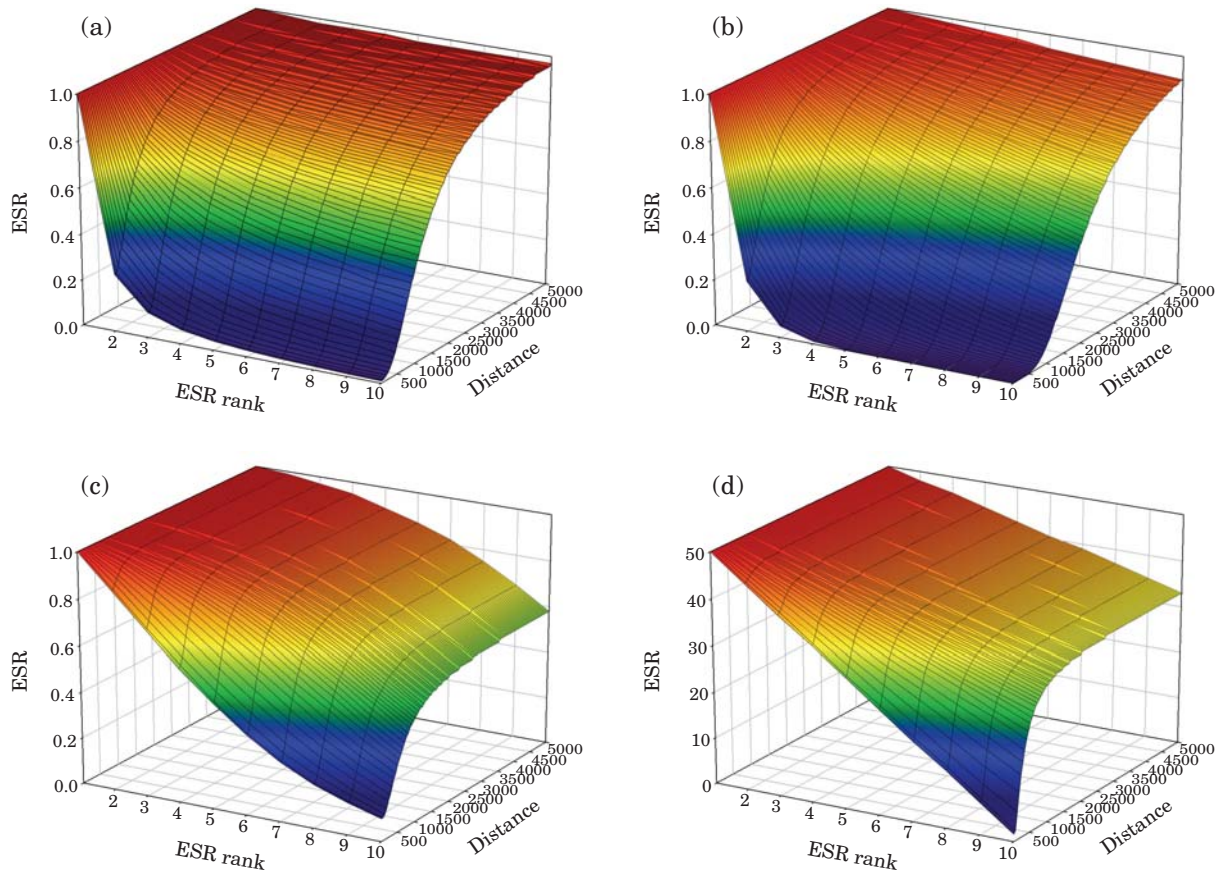
Fig. 4. Comparison of ESRs across different ranks and distance from pollutant source in different models (see text for parameter values). (a) Power law, (b) Negative exponential distribution, (c) Dose-response based model, and (d) Sensitivity model.

ferent models. ESRs consequently increased along with decrease in contaminant concentration. Different patterns in ESR were also observed in different models. The surfaces of ESR (Fig. 4) reflected the corresponding patterns of TSR (Fig. 3) at the individual level. The ESR surfaces for the dose-response based model, for example, appeared to be flatter first, reflecting slow decrease in the high ESR rank, and sharply declined in the low levels of the ESR rank near the source area (Fig. 4). The experimental models, dose-response and relative sensitivity, showed somewhat flatter surfaces of ESR compared with the mathematical models (Fig. 4).

Death of individuals was determined according to ESR at the site on a stochastic basis. By generating a random number between 0~1, the individual died if the number was higher than ESR at the current site.

(5) Competition

Density dependent effect due to competition was also considered in the model. Local carrying capacity, K', was set to 10000 individuals per lattice (Table 2). This value was the approximate maximum density of first-rank species in abundance observed in field conditions (Qu *et al.*, 2008; Tang *et al.*, 2010). When the population size at a site was over K', an oversize term was applied to reduce the number of survived individuals at the site. The survival rate for individuals, $E_k(t)$, at site k in iteration t was determined as follows:

$$E_k(t) = \begin{cases} 1 + \left(\dfrac{K' - N_k(t)}{K'} \right) & : \text{if } N_k(t) > K', \\ 1 & : \text{otherwise,} \end{cases} \quad (7)$$

where $N_k(t)$ is local density at site k in iteration t. In the case that the local population density was 11000 at a site, for instance, the survival rate con-

sidering density effect ($E_k(t)$=0.9) was used to determine survival of individuals according to the probability of 0.9.

(6) Stochasticity

As stated several times above, life events were determined based on probability. The probability of uniform distribution was used for the following events: species assignment, the initial number of individuals per species, location of individuals, and determination of dead individuals. Movements were determined by the use of a Gaussian distribution (young larvae) or random walk (intermediate and old larvae). NSR and ESR were added with noise by multiplying Gaussian random numbers: means were the values obtained from the concentration at the current site (Fig. 4) and standard deviation was 0.1.

6) Parameters

The parameter values used for simulation are listed in Table 2. Basic information such as the total river length and width, total number of species, and local carrying capacity were based on field data collected in streams in Korea (Qu *et al.*, 2008; Tang *et al.*, 2010). Movement ranges of aquatic macroinvertebrates in one week ($1 \sim 5$ m) were based on data presented by Englund and Hambak (2004). The number of offspring by females of benthic macroinvertebrates is in the range of $40 \sim 4000$ individuals in field conditions (Merritt and Cummins, 2008). Due to limit of computation resource (i.e., exponential growth of population), however, a small number of offspring was used for simulation. We checked the offspring ranging $2 \sim 20$ individuals per female in preliminary tests while local carrying capacity was set to a constant, K'=10000. General trends in community establishment appeared to be similar over the different range of offspring, while the time of community stabilization seemed dependent upon the number of offspring (i.e., early stabilization with a high number of offspring). Considering both simplicity in modeling in one side and ensuring variability in presenting the model results (i.e., SADs) in the other side, 5 offspring per female were used for simulation in our study.

Distribution of pollutant concentration was determined according to Al-Khallidi (2002) (Table 2). The parameters in the dose-response based model and relative sensitivity were obtained according to Von der Ohe and Liess (2004) and Van den Brink *et al.* (2007), respectively. Considering that the
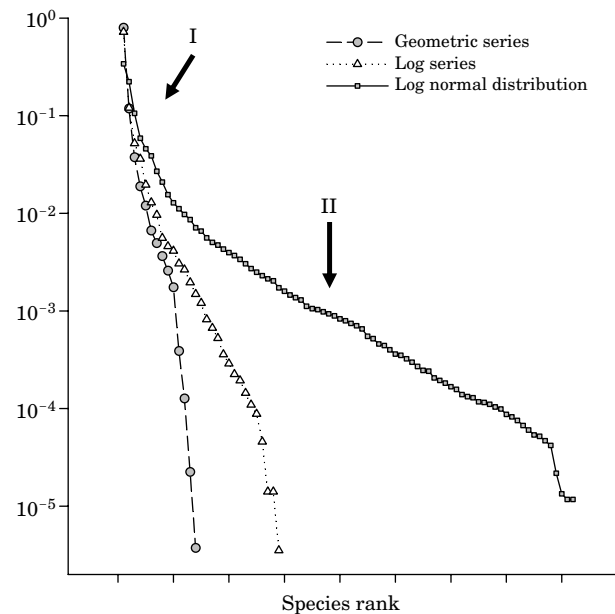

Fig. 5. SADs produced from geometric series, log series, and log-normal distribution in relation to species rank (post-determined) (see text for parameter values) from IBM.

power law and negative exponential distribution were used *de novo* for determining mortalities of entire species in communities, the parameters for the models were adjusted to fit the models in SADs (i.e., geometric series, log series and log-normal distribution). Two parameters were used in each model for controlling the variables (Table 2).

7) Output

The population sizes of all species were recorded as the iteration proceeded and were combined to produce a SAD according to the rank of abundance. In this study, the term "rank" was distinguished in two meanings. The first case was the rank of abundance in SADs and was post-determined after simulation. In this type of SADs, identification of each species is not necessary. Only overall configurations of the rank-order relationships are considered in defining different patterns in SADs (Magurran, 2004; McGill *et al.*, 2007). The second case was the ranks determined by TSR and NSR, which were pre-determined at the time of species assignment (Fig. 1) (see "3) Attributes and states"). We discussed about species abundance patterns based on both ranks in community response (first case; Fig. 5, second case; Figs. $6 \sim 7$).

The model results presenting SADs were stati-

stically compared with field data and with SADs based on theoretical distribution by using the Kolmogorov-Smirnov test (two samples). The results were averages of 20 replications for each set of simulation condition.

8) Initialization

In each site, individuals belonging to 100 species were generated with the ranks defined by TSR (and NSR) in species assignment (see "3) Attributes and states"). The number of individuals for each species at a site was uniformly determined between 1 and 50. Pollution sources were provided at one end of cross section of the stream, and the concentrations of pollutant at different sites were determined using the log-normal distribution (Eqn. 6), as described above.

2. Field data

Benthic macroinvertebrates were collected monthly with a Surber sampler from streams in Korea with different levels of pollution from 1992 to 2007. Sampling sites were chosen from reports by Qu *et al.* (2008) and Tang *et al.* (2010). Six sampling sites from 4 streams (Banae, Suyoung, Soktae and Yangjae Streams) represented severely, intermediately, and weakly polluted states. In total 18 orders, 68 families, and 187 species were collected at 175 sample sites during the survey period. The sketch of the sampling sites with environmental and community data is listed in Table 3. The Suyong and Soktae Streams are trajectories of the Suyoung River, which passes through the Busan Metropolitan area. The Soktae stream has been exposed to pollution sources, including domestic and industrial pollutants. Three sample sites were selected from this stream, a severely polluted site, THP (Biochemical Oxygen Demand (BOD); 42.23 ±17.35, Biological Monitoring Working Party (BMWP); 3 (range; 0~6)), intermediately polluted site, TKC (BOD; 6.94±5.61, BMWP; 17 (range; 5~36)), and weakly polluted site, TSD (BOD; 4.87 ±4.21, BMWP; 46 (range; 3~105)). Species richness was in the maximal range at the less polluted site, TSD (90), and in the minimal range at the severely polluted site, THP (18) (Table 3).

An extra site was chosen for each level of pollution. One site from the Baenae stream in the tributary of the Nakdong River Basin, BCN (BOD; 1.15±0.80, BMWP; 121 (range; 68~157)), was selected to present a less polluted state. One site from the Suyoung Stream in the Suyoung river in

the

Table 3. Environmental factors (mean±SD), community data, and biological indices at different sample sites.

Streams	Sites	BOD (mg L⁻¹)	Turbidity (NTU)	Conductivity (μs cm⁻¹)	BMWP*	Species richness	Shannon diversity	Pollution level	1st dominant species / 2nd dominant species	Dominance	No. of samples
Baenae	BCN	1.15±0.80	0.84±0.95	23.86±6.66	121 (68-157)	93	3.33	Low	Heterotanytarsus nudivers / Ecdyonurus kibunesis Imanish	0.15 / 0.11	12
	TSD	4.87±4.21	11.15±8.50	192.70±73.31	46 (3-105)	90	3.14	Low	Eukiefferiella sp.1 / Cheumatopsyche Kua	0.22 / 0.08	35
Soktae	TKC	6.94±5.61	6.12±13.24	335.40±97.61	17 (5-36)	65	2.75	Intermediate	Eukiefferiella sp.1 / Physa acuta Drapamaud	0.15 / 0.14	35
	THP	43.23±17.35	25.51±15.25	571.20±151.91	3 (0-6)	18	0.81	High	Chironomus flaviplumus / Psychoda sp.	0.75 / 0.19	35
Suyong	YSC	3.72±4.46	7.51±11.70	325.10±156.47	23 (2-40)	74	2.50	Intermediate	Orthocladius yugashimaensis Sasa / Cricotopus triannulatus	0.31 / 0.16	22
Yanjae	JHH	4.67±1.50	9.06±4.54	413.58±68.58	6 (1-17)	26	1.11	High	Chironomus flaviplumus / Cricotopus bicinctus	0.72 / 0.11	36

*median (range)

Busan area, YSC (BOD 3.72 ± 4.46, BMWP; 23 $(2 \sim 40)$), was chosen to show an intermediately polluted state. One site from the Yangjae Stream, which is a tributary of the Han River Basin in the Seoul Metropolitan area, JHH (Yangjae stream, BOD 4.67 ± 1.50, BMWP; 6 $(1 \sim 17)$), was selected to present a severely polluted state. Species richness was also accordingly maximal at the less polluted site, BCN (93), and was minimal at severely polluted site, JHH (26) (Table 3). Dominant species covered the species in Plecoptera, Trichoptera and Ephemeroptera at the less polluted sites, while species in Tubifidae (Oligochaeta) and Chironomidae (Diptera) were extremely abundant at the severely polluted sites. More detailed information can be found in Chon and Kwon (1991), Chon *et al.* (2000), Park *et al.* (2004), Kwak *et al.* (2002), Kwon and Chon (1991, 1993), Song *et al.* (2006), Qu *et al.* (2008), and Tang *et al.* (2010).

3. Community analysis

Three conventional SAD models, geometric series (Motomura, 1932), log series (Fisher *et al.*, 1943), and log-normal distribution (Preston, 1948; Magurran, 2004), were selected to compare with the SADs produced from simulations. In the geometric series, species abundance, ranked from most to least abundant, is expressed as (Motomura, 1932; May, 1975; Magurran, 1988):

$$n_i = NC_k(1-k)^{i-1} \tag{8}$$

where n_i is the number of individuals in the ith species, k is the proportion of the available resource that each species utilizes, N is the total number of individuals, and C_k is a constant (see Magurran, 2004).

The log series, originally proposed by Fisher *et al.* (1943), is presented as:

$$\alpha x, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3}, \dots, \frac{\alpha x^n}{n}, \tag{9}$$

where α is the index of diversity, n is species sequence from minimum to maximum, and x is estimated from the iterative solution of $S/N=(1-x)/x$ $[-\ln(1-x)]$ (S; the total number of species, and N; the total number of individuals).

The log-normal distribution (Preston, 1948; May, 1975) illustrates that the frequency of species arranged on the logarithmic scale of species abundance follows the normal distribution as:

$$S(R) = S_0 \exp(-a^2 R^2), \tag{10}$$

where $S(R)$ is the number of species in the Rth octave (i.e. class) in abundance to the right and left of the symmetrical curve and S_0 is the number of species in the modal octave. In this study, the truncated log-normal distribution was used to fit to the community data based on Magurran (2004).

RESULTS

Initially, simulation was conducted with an IBM based on NSR according to a power law (Eqn. 5) to produce SADs in natural conditions. The well-known "S shape" curves for the rank abundance relationships in SADs were obtained from simulation, including a sharp decrease in abundance for species with the highest ranks (post-determined rank) ("I" in Fig. 5) and a flat slope for species with the medium ranks ("II" in Fig. 5). The parameters for NSR in the power law were fixed at $\alpha=0.95$. The different SAD patterns were accordingly produced by increasing the parameter, μ. The value of parameter was 0.1 at the minimally and 0.5 at intermediately decreasing slopes, respectively. For the most decreasing slope, μ was increased to 1.0 (i.e., sharp slope). The patterns of SADs were in accord with the theoretical models (Magurran, 2004) (Fig. 5). With increase in parameter, the SAD curves matched in the order of log-normal series (less disturbed), log series (intermediately disturbed), and geometric series (severely disturbed) (Magurran, 2004; May *et al.*, 2007). The total number of species also accordingly decreased (Fig. 5).

TSRs in different models (Eqns. 1-4) were additionally employed in the IBM to present toxic effects in stressful conditions. In this case, power law for presenting NSR in natural conditions was commonly applied to the models at a low level with parameter $\mu=0.2$ with $\alpha=0.95$. The IBMs employing TSRs from different models were also able to generate the three types of SAD models. The SADs were clearly presented by two theoretical models, power law (Eqn. 4) and negative exponential distribution (Eqn. 3) (Fig. 6a and 6b). According to the negative exponential distribution (Fig. 6b), the slopes (especially in the intermediate range of ranks) tended to be sharper in general compared with those based on the power law (Fig. 6a). The models according to the experimental
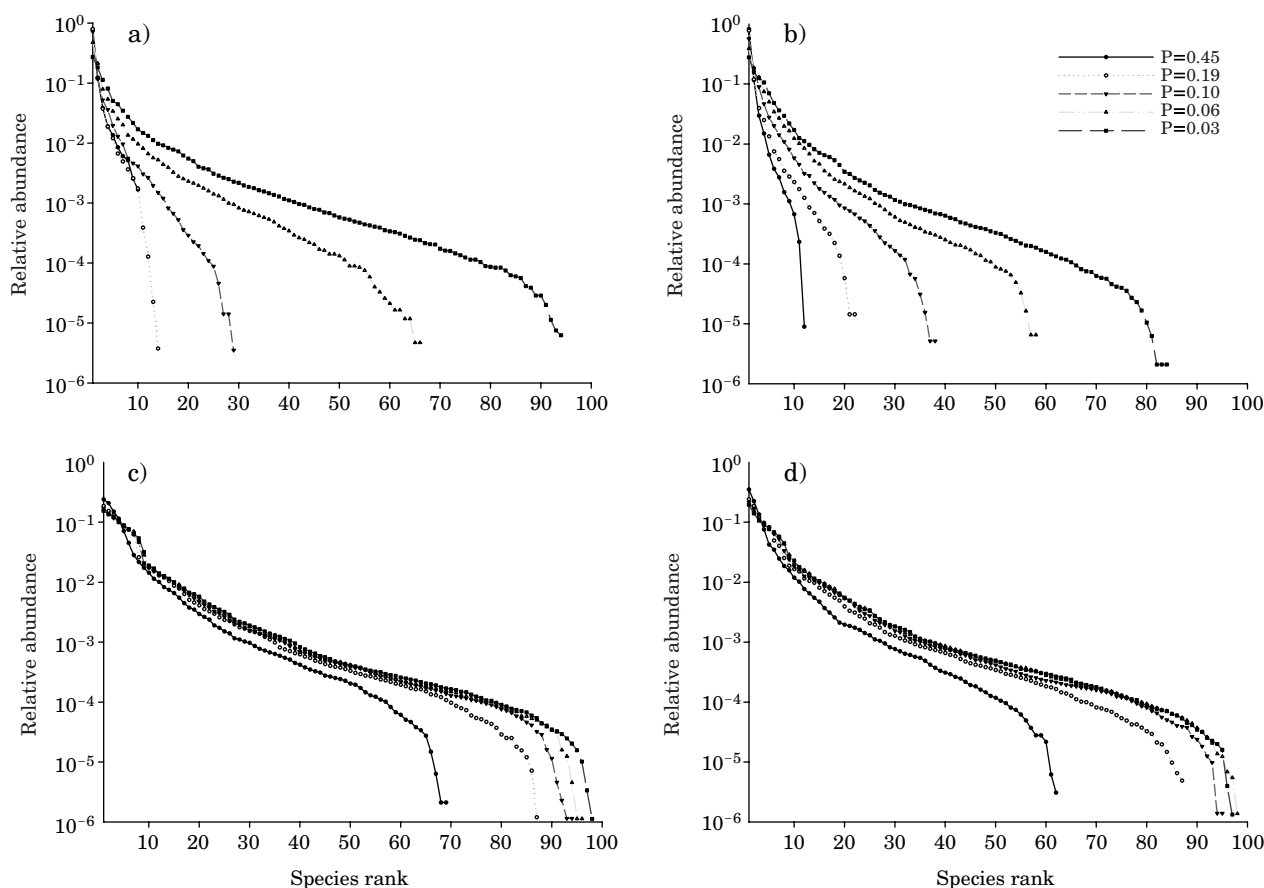
Fig. 6. SADs produced from (a) Power law, (b) Negative exponential distribution, (c) Dose-response based model, and (d) Sensitivity model (P indicating pollution levels; see text for explanation).

models (Fig. 6c and 6d), however, appeared to be difficult in producing the different SAD patterns, beside the log-normal distribution. We tested a wide range of parameter in two models but obtained the similar ranges as shown in Fig. 6c and 6d for both models.

We matched concentration of contaminants, C, in the model to the values of water quality index, BMWP, from field data (Qu *et al.*, 2008; Tang *et al.*, 2010). Severely polluted site with $C > 0.19$ matched BMWP < 10 (THP, JHH in field data (Table 3)), while less polluted sites with $C \leq 0.03$ were in accord with BMWP ≥ 40 (BCN, TSD in field data (Table 3)). Intermediately polluted site with $0.03 < C \leq 0.19$ showed the range of BMWP in $10 \sim 40$ (YSC, TKC in field data (Table 3)).

The model results were superposed with the field data to check fitness across different levels of pollution (Fig. 7). Since the SAD curves based on the experimental models were obviously not in accord with the field data in the whole range of

concentrations, we only presented the curves from the power law and negative exponential distribution on the figures. Across different concentrations of pollution, the curves from the IBMs were similar to those from the field data (Fig. 7). The total number of species, however, was slightly different between the field and calculated data.

Statistical significance was further checked with the Kolmogorov-Smirnov test between the field and model data (Table 4). The number of acceptance of was higher for the model results based on the power law and negative exponential distribution. At the highest range in pollution, geometric series was fit to the model results. The SADs were also in accordance with log series and log-normal distribution at intermediately and less polluted sites respectively. The power law appeared to be more accepted in a wide range in less polluted sites compared with the negative exponential. The model results based on the dose-response based model and sensitivity model, however, were most-

Table 4. Statistical values (D_{max}) of Kolmogorov-Smirnov test for goodness of fit (two samples) between field and simulation data in benthic macroinvertebrate communities in streams based on the models employing TSR across different levels of pollution (Parameters $\delta=0.01$, $d=1$, $b=1$, $\xi=0.03$, $\alpha=1$, $\beta=1.5$, $a'=0.95$, and $\mu'=5.0$) (P10; C>0.45, P9; C>0.19, P8; C>0.10, P7; C>0.06, P6; C>0.03, P5; C>0.02, P4; C>0.0018, P3; C>0.0013, P2; C>0.01, P1; C>0)[†] (Gray shade indicating acceptance of model results).

Power law

Site	Pollution level									
	P10	P9	P8	P7	P6	P5	P4	P3	P2	P1
BCN	0.83**	0.81**	0.64**	0.35**	0.23**	0.17	0.19*	0.22*	0.24**	0.22*
TSD	0.81**	0.79**	0.62**	0.3**	0.16	0.17	0.13	0.16	0.17	0.17
TKC	0.56**	0.54**	0.39**	0.14	0.34**	0.37**	0.34**	0.28**	0.27**	0.33**
YSC	0.65**	0.62**	0.45**	0.12	0.25**	0.34**	0.3**	0.23**	0.19*	0.24**
JHH	0.06	0.07	0.25**	0.68**	0.88**	0.91**	0.88**	0.82**	0.81**	0.87**
THP	0.09	0.07	0.18	0.61**	0.81**	0.81**	0.81**	0.75**	0.74**	0.8**

Negative exponential

Site										
BCN	0.82**	0.74**	0.62**	0.46**	0.34**	0.3**	0.28**	0.27**	0.26**	0.27**
TSD	0.8**	0.72**	0.59**	0.44**	0.27**	0.22*	0.2*	0.2*	0.18	0.18
TKC	0.55**	0.48**	0.36**	0.21*	0.18	0.31**	0.33**	0.34**	0.34**	0.34**
YSC	0.64**	0.56**	0.43**	0.26**	0.09	0.22*	0.24**	0.25**	0.25**	0.25**
JHH	0.06	0.11	0.26**	0.46**	0.72**	0.85**	0.87**	0.88**	0.88**	0.88**
THP	0.09	0.03	0.19*	0.39**	0.65**	0.78**	0.8**	0.81**	0.81**	0.81**

Dose-response based model

Site										
BCN	0.39**	0.33**	0.31**	0.31**	0.3**	0.29**	0.29**	0.3**	0.3**	0.28**
TSD	0.36**	0.23**	0.23**	0.21*	0.21*	0.21*	0.21*	0.19*	0.2*	0.19*
TKC	0.14	0.21*	0.28**	0.3**	0.32**	0.31**	0.33**	0.33**	0.32**	0.34**
YSC	0.18	0.12	0.19*	0.21*	0.23**	0.22*	0.24**	0.24**	0.23**	0.25**
JHH	0.57**	0.75**	0.82**	0.84**	0.86**	0.85**	0.87**	0.87**	0.86**	0.88**
THP	0.5**	0.68**	0.75**	0.77**	0.79**	0.78**	0.8**	0.8**	0.79**	0.81**

Sensitivity model

Site										
BCN	0.44**	0.33**	0.3**	0.29**	0.28**	0.28**	0.28**	0.28**	0.28**	0.27**
TSD	0.41**	0.26**	0.23**	0.22*	0.21*	0.21*	0.21*	0.22*	0.22*	0.2*
TKC	0.19*	0.21*	0.29**	0.32**	0.31**	0.31**	0.33**	0.32**	0.32**	0.34**
YSC	0.23**	0.12	0.2*	0.23**	0.22*	0.22*	0.24**	0.23**	0.23**	0.25**
JHH	0.5**	0.75**	0.83**	0.86**	0.85**	0.85**	0.87**	0.86**	0.86**	0.88**
THP	0.43**	0.68**	0.76**	0.79**	0.78**	0.78**	0.8**	0.79**	0.79**	0.81**

*Significant p<0.05
**Highly significant p<0.01
[†]Pollution level corresponding to biological index from field data (C>0.19; BMWP<10, C>0.03; BMWP<40, C≤0.03; BMWP≥40) (Qu *et al.* 2008, Tang *et al.* 2009)

ly not fitted to field data (Table 4).

We also tested fitness of model results with the data obtained from the theoretical distribution of SAD models: geometric series, log series, and log-normal distribution (Table 5). Acceptance of model results was observed correspondingly with increase in contaminant concentrations. Geometric series was acceptable in the highest range. Log series matched the next following range in contaminant concentrations and log-normal distribution was widely acceptable in a broad range (2750~5000 m) far from the pollutant source at low concen-

trations. The overall fitness appeared to be higher in the power law compared with the negative exponential distribution. In less polluted areas the geometric distribution was also accepted in a wide range in addition to log-normal distribution according to model results from the negative exponential distribution (Table 5).

The certainty of model fitness was checked by varying parameter values. The parameter $\mu=5$ showed the most reliable results in the power law and the model results were generally acceptable in the range of 4.0~6.0 in fitting the data. In the

Table 5. Number of acceptance ($\alpha < 0.05$) for fitting SADs from IBMs to SADs from theoretical distributions based on the Kolmogorov-Smirnov goodness of fit (continuous data) when 20 replications were observed across the different levels of distance from the pollution source.

Distance from source (m)	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000	3250	3500	3750	4000	4250	4500	4750	5000
Power law																				
Geometric series	7	5	5	5	0	0	0	0	0	0	0	3	8	4	4	3	2	2	2	0
Log series	0	0	0	12	13	15	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Lognormal	2	0	0	0	5	0	0	0	0	20	20	20	20	20	20	20	20	20	20	20
Negative exponential																				
Geometric series	15	9	4	0	0	0	0	0	0	0	2	4	8	15	17	15	20	15	17	11
Log series	7	10	15	13	3	10	7	0	0	0	0	0	0	0	0	0	0	0	0	0
Lognormal	0	0	0	0	0	0	0	0	0	0	0	4	10	19	20	20	20	20	20	20

intermediately polluted sites (C=0.2), however, the μ values showed a narrower acceptance range in 4.7~6.0 (with C=0.1, and α=0.95). The parameter β in the negative exponential distribution was generally acceptable in the range of 1.0~2.0 across different levels of pollution. The parameter was most probable at β=1.5 (with C=0.1, and a=1) while model results outside of β=1.2-1.8 were not fitted to field data.

The abundance distribution was additionally arranged according to the predetermined TSR rank as stated above (see "3) Attributes and states") (Fig. 9a). In the maximal range of concentration (i.e., nearest to pollution source) abundance of species with the highest TSR ranks was maximal. However, abundance decreased rapidly as the TSR rank decreased. At the areas far away from the pollution source, the reverse was observed. Abundance for species with the lowest TSR ranks were higher while abundance of the species with the highest TSR ranks were lower, indicating that species with the lowest TSR ranks better adapted to polluted sites in the minimal range of contamination (Fig. 9a). This was due to escaping by the species of the low TSR ranks and will be discussed later (see "Discussion"). Fig. 9b shows the abundance of species according to the NSR rank. As expected, abundance was lower as the NSR rank decreased. This trend was consistently observed across different levels of distance from the source, although abundance gradually increased in averages along with increase in distance from the pollution source (Fig. 9b). The abundance according to the negative exponential distribution showed the similar trends (Fig. 9c and 9d). However, the reverse in abundance between the high and low rank, as shown in the case of the power law at the far side of pollutant source (Fig. 9a), was not observed in the case of the negative exponential distribution (Fig. 9c). Abundance according to the NSR ranks (Fig 9d) was similar to the case of the power law (Fig. 9b).

DISCUSSION

1. Individual tolerance

Through IBMs, NSRs and TSRs were locally applied to individuals in small (1 m) and short (1 week) scales and were efficiently integrated to produce community responses in large (5 km) and long (1~2 years) scales. The models reflecting the
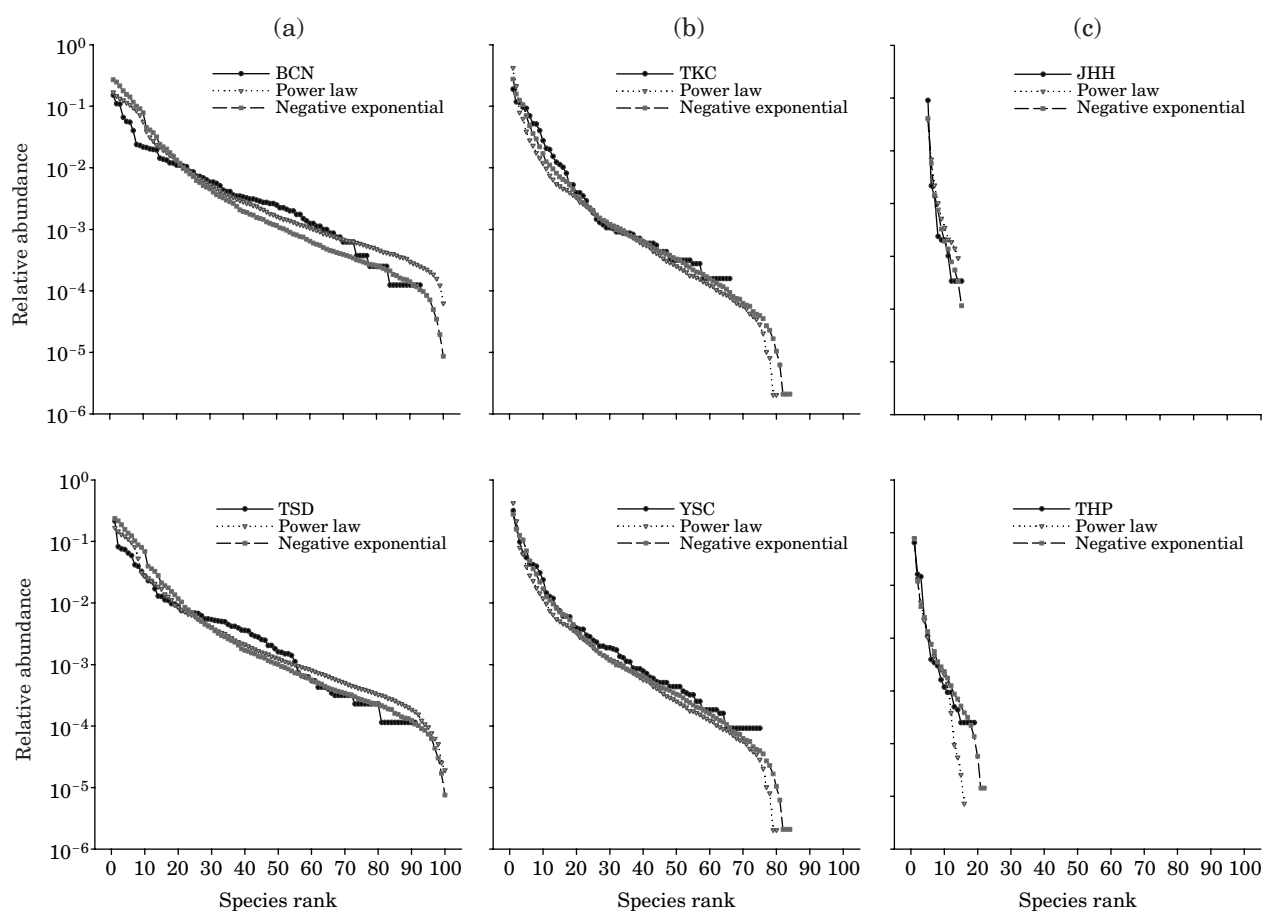
Fig. 7. Comparison of SADs in field and model-derived data (see text for parameter values). (a) weakly polluted (BCN and TSD), (b) intermediately polluted (TKC and YSC), and (c) severely polluted (JHH and THP).

strong selection advantage for a few species, such as the power law and negative exponential function (Figs. 3, 4a, 4b), appeared to be suitable in presenting SADs observed in field conditions (i.e., geometric series, log series and log-normal distributions) across different levels of pollution (Figs. 5-7).

In an environment gradient analysis, Whittaker (1965, 1979) was able to produce different types of SAD models according to the level of productivity (e.g., a geometric SAD for low productivity, a log-normal SAD for high productivity). This study confirmed that the different patterns of SADs could also be produced by an IBM when incorporating the functions related to natural and toxic survival rates at the individual level. Considering that mortality data would not be readily available for entire species in communities, the models would be useful for inferring community responses and

elucidating complex ecotoxicological processes in the individual-community relationships in stressful conditions.

The generality of the power law was demonstrated in presenting community response in this study. The model with NSR was able to illustrate all different types of models in SADs (Fig. 5). The power law has been used for determining species-area relationships (MacArthur and Wilson, 1967). Recently, Pueyo (2006) proposed using a power model to relate the log abundance and log species richness contained in the bins of abundance. Qu *et al.* (2008) indicated that the parameter in the power law in rank-abundance relationships could be useful for indicating changes in water quality if community data are compared at the same site in different times. In this study, we demonstrated that employment of the power law in addressing tolerance at individual level was also possible to illus-
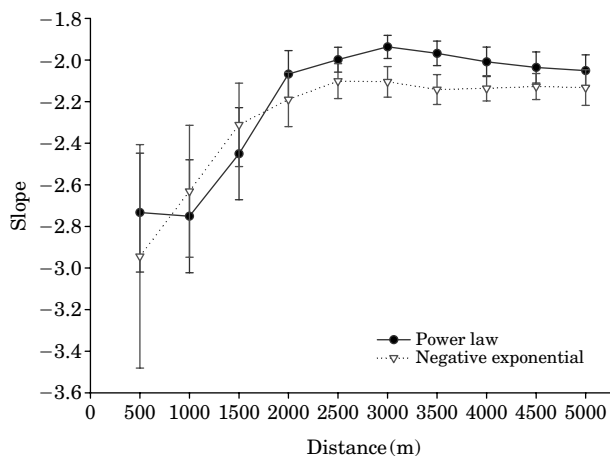
Fig. 8. Changes in the slopes of SAD (log-log transformed) across distance from the pollutant source (vertical bar indicating standard deviation).

trate SADs in different species at the community level.

The parameters in the models appeared to be suitable in controlling degree of community response. Increase in the parameters (μ in the power law and β in the negative exponential distribution) accordingly increased sharpness of the slopes in SADs (Figs. 5-7). This indicated that the slopes may serve as an indicator to present degree of disturbances (Fig. 8). The possibility of using the parameter in the power law as an indicator in community response in rank-abundance relationships was reported in Harte *et al.* (1999), Pueyo (2006a, 2006b) and Qu *et al.* (2008).

Lack of fitting by the empirical models (Fig. 6, Table 4), the dose-response based model and the relative sensitivity model, was understandable. Since the observed mortality data (e.g., LC_{50}) used
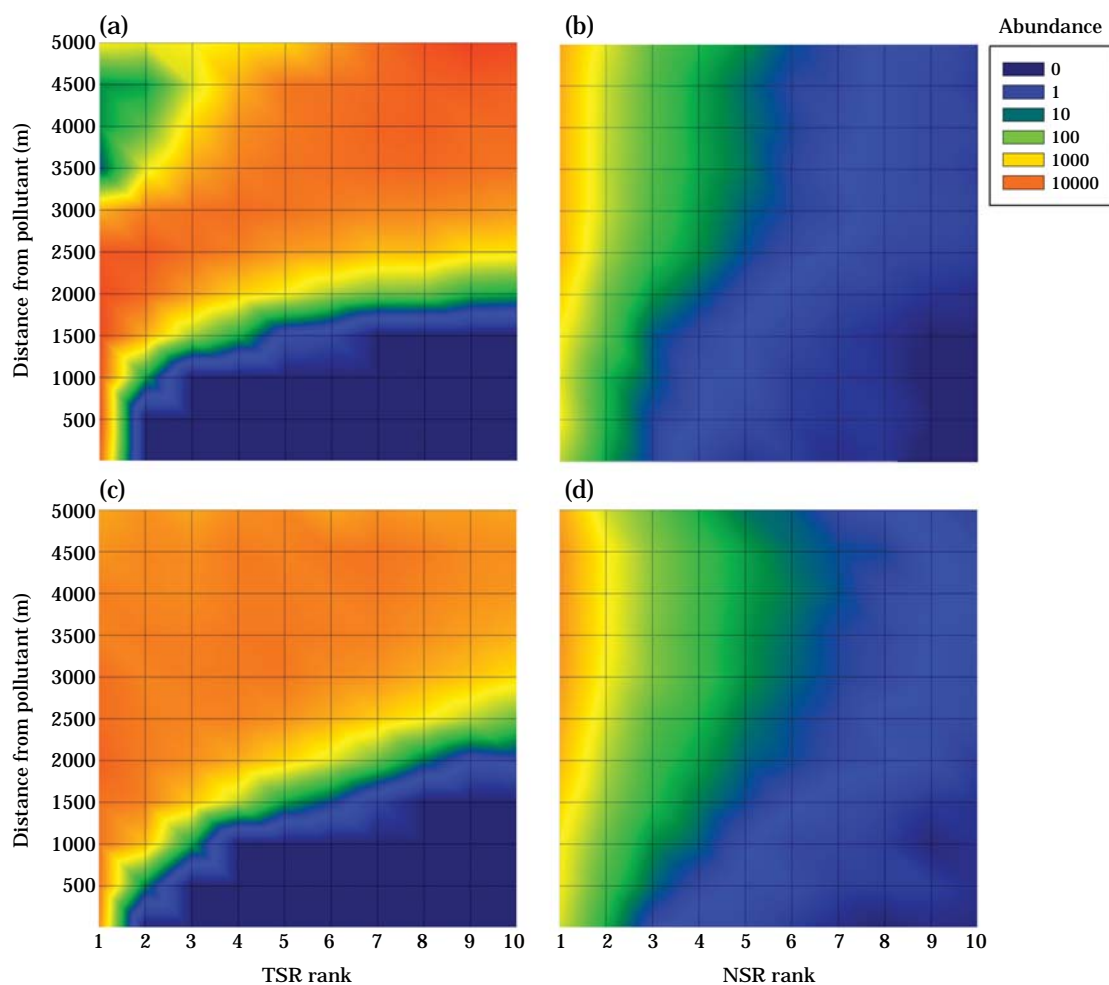

Fig. 9. Abundance profile in relation to TSR (and NSR) ranks (pre-determined) across distance from pollution source. (a) TSR rank with Power law, (b) NSR rank with Power law, (c) TSR rank with Negative exponential, and (d) NSR rank with Negative exponential.

for defining the models were based on populations, not individuals, the data were not able to directly represent instantaneous death of individuals. The averaging effects on life events (e.g., individual death, individual movement distance) appeared to be included in the data, and sharp decrease in survival for less tolerant species was not observed in TSRs and NSRs for the empirical models (Figs. 3 and 4). Due to slow decrease in survival rates, the sharp drop in slopes was not observed in the SADs in the empirical models (Fig. 6).

Warren-Hicks *et al.* (2002) reported effects of both acute and chronic toxicity based on sigmoidal response function. The response patterns in communities were diversified from the geometric series in severely polluted conditions, allowing more species across different level of pollution with a higher number of species. In this study, however, we mainly considered acute toxicity (i.e., oxygen depletion due to organic pollution) on benthic macroinvertebrates in aquatic ecosystems in a short time period. Considering both acute and chronic effects are commonly observed in the field condition, IBMs will be further developed to accommodate both acute and chronic (e.g., bioaccumulation) effects with a longer simulation period in the future.

Considering that the number of eggs produced by a female is in a wide range of $40 \sim 4000$ in aquatic invertebrates (Merritt and Cummins, 2008), we need assumptions to simplify the number of offspring for simulation. We considered three criteria for simplification: 1) securing high level of population size to provide sufficient variability in presenting SADs, and 2) realistic computation time, and 3) using field data such as local carrying capacity and densities for modeling. Considering that a huge number of eggs are produced but only a small fraction of individuals survive to adults in benthic macroinvertebrates (Merritt and Cummins, 2008), difficulties would arise if extremely high fecundity and high mortality are allowed at the same time in simulation. Fluctuation of population size would be inevitable in a great degree.

Density dependence effects will also additionally contribute to fluctuation in population size (i.e., higher excess population size, higher reduction in feedback). According to field observations, 10000 individuals per 1 m^2 was the maximal number of individuals observed in field conditions in streams (Qu *et al.*, 2008; Tang *et al.*, 2010). By considering this value as the local carrying capacity (K), simu-

lation with a high number of offspring per female (say $100 \sim 1000$ offsprings per female) would be prone to abrupt decrease and fluctuation in population size due to extremely strong feedbacks (i.e., environmental resistance). Sudden drops or ups in population size were observed as the number of offspring was close to 10 individuals per female in this study. Densities observed mostly in field conditions were in the range of $10 \sim 1000$ individuals per m^2 per species in streams (Park *et al.*, 2007; Qu *et al.*, 2008; Tang *et al.*, 2010). We assumed that these values were effective densities to simulate with. By allowing two to five offspring per females, the IBMs could produce a similar range of densities observed in field conditions.

2. Biological factors and consequence

A neutral model was also able to generate the different SAD models (Hubbell, 1997). The neutral model is generally focused on natural communities and is based on the assumption that each species (and each individual) has an equal probability of survival (Hubbell, 1997). In this study, however, equal probability of survival was somewhat difficult to observe in especially stressful conditions. Once the communities were exposed to a strong environmental stressor such as organic pollutant, there was an obvious selection pressure against species with low tolerance to oxygen depletion. Consequently, only a few tolerant species would be selectively abundant while other species with low tolerance would quickly become extinct as a result of hypoxia (James and Evison, 1979; Hellawell, 1986). The selective advantage of high tolerance (as shown in high TSRs (Fig. 3)) played a major role in determining community patterns under stressful conditions in this study. This was also in accord with field observations: a few species selectively tolerant to pollution (e.g., tubificids and chironomids) were strongly dominant in polluted streams (Hellawell, 1986; Qu *et al.*, 2008; Tang *et al.*, 2010). However, the model results were obtained under the limited conditions and would not be useful for evaluating generality of the neutral model.

In our study the tolerance were fixed for species and the models were run under continuously stressful conditions in a shorter time period ($1 \sim 2$ years). Consequently the tolerant species (i.e., with high TSR rank) would have the pre-determined advantage over the less tolerant species. We nei-

ther considered diversity and flow rates in simulation in this study. If the traits were not fixed and were allowed to evolve in a long time period, establishment of the tolerant species may be determined randomly based on the probability equally given to all individuals in all species. The IBM may be further extended in this regard to check neutrality in dynamic processes in community response in ecotoxicology in the future.

The range of contaminant concentration appeared to be uneven in presenting water quality. In a narrow range of concentration (i.e., $C=0.05\sim0.2$), the SADs at intermediately and less polluted sites occurred closely together, while the SADs from the severely polluted sites were presented in a broad range $C=0.2\sim1.0$ (Figs. 6, 7, and Table 4). This indicated that community structure may be sensitive at low and narrow ranges of contaminant concentrations in stressful conditions.

We considered escaping behavior of individuals against contamination in the model (Fig. 2; see "(1) Movement" in "5) Design concepts and submodels"). Considering that benthic macroinvertebrates have various locomotive means (e.g., crawling, swimming, drifting), escaping (or avoiding) against contaminants would be one of the main consequences of response behaviors after exposure to contaminants. Drifting, for instance, was reported to occur as a means of escaping in response to toxic chemicals (Lauridsen and Friberg, 2005; Heckmann and Friberg, 2005). Effects of escaping on population size were observed in the model. If the power law was applied to the TSR ranks, abundance of species with the high TSR ranks appeared to be low at the far distance from the pollution source (i.e., concentration in the minimal range), while abundance of species of the low TSR ranks was high at the same area (Fig. 9a). This could be explained from escaping. Species with the low TSR ranks may more readily escape to less contaminated areas since there is a higher probability of escaping due to the movement rule (Fig. 4a) (see "(1) Movement" in "5) Design concepts and submodels"). Consequently there would be a higher chance of entering individuals from upstream to downstream for the species with the low TSR ranks. For species with the high TSR ranks, in contrast, individuals would not be able to readily escape due to the high levels in ESR in this area (Fig. 4) (see "(1) Movement" and "(5) Effective Survival Rate (ESR)" in "5) Design concepts and submodels"). Consequently, the downstream

area would mainly consist of residents for species with the high TSR ranks (i.e., lower density). For the species with the low TSR ranks, however, populations would consist of the residents plus the entering individuals (i.e., higher density) (Fig. 9a). This implied a trade-off between tolerance and movement. The detailed processes could be further discussed in the future by closely revealing different movement types and toxic impacts.

The tendency of not escaping by tolerant species could be indirectly supported by field data. When an insecticide (Lambda-Cyhalothrin) was treated with pulse exposure in mesocosms, the tolerant taxa such as Chironomidae and Oligochaeta showed either similar or higher level of densities at the same place compared with densities before the treatments. A majority of less tolerant species such as *Gammarus pulex* and *Lectura* sp, however, decreased substantially at the same place after the treatments (Heckmann and Friberg, 2005). More detailed research, however, may be required in the future regarding distance and speed caused by different movement behaviors as stated above. For the case of the negative exponential distribution, however, this type of trade-off was not observed. This may be due to the lower range in ESR values for the species with the low TSR ranks at the far side from the pollutant source (Fig. 4b) compared with the case of the power law (Fig. 4a). The low survival rates appeared to contribute to decrease in population size, compensating the increase by entering individuals from upstream for the case of negative exponential distribution.

We did not include chronic effects in this study. One reason to select only acute toxicity was its importance in determining abundance of entire species in experimental conditions at the community level. Changes in whole aquatic communities have been investigated in mesocosms, and the most important physiological sensitivity to the contaminants was the acute toxicity test (Wogram and Liess, 2001). Acute toxicity is considered critical in causing rapid extinction of multi-species in field conditions. Hypoxia due to organic pollution, as an example, contributes to mass mortality of organisms in streams in a relatively short time (Jørgensen, 1980; Stachowitsch, 1984; Gaston, 1985; Sagasti *et al.*, 2001).

Chronic toxicity, however, is regarded also important in revealing ecotoxicological processes in aquatic communities (Van den Brink *et al.*, 1995; Winter *et al.*, 1996; Hickey and Clements, 1998;

Schulz and Liess, 2001). Effects of mortality caused by chronic toxin (e.g., pesticide) to population growth rate of invertebrate population (e.g., *Daphnia pulex*) were reported (Wennergren and Stark, 2000; Stark and Walthall, 2003). The chronic toxic effects would change physiological, behavioral and ecological responses during the course of organisms' life processes in a long period. In order to elucidate chronic effects, however, more extensive field and laboratory data may be required for entire species (not only one) within communities. Ecotoxicological data obtainment, however, is a difficult task (Von der Ohe and Liess, 2004), although data for chronic effects are necessary in revealing ecotoxicological processes. After acquisition of biological and toxicity data in a sufficient amount from laboratory experiments and field surveys, a model combining the acute and chronic effects could be developed in the future.

3. Simplicity in environmental factors

For simplicity of modeling, we neither considered temperature effects in this model, considering that chronic effects (e.g., delay in development speed) were not included in this study and immediate toxic responses in communities mainly focused in a short period. Benthic macroinvertebrates, however, are poikilothermic and their physiological states would be influenced by temperature change in many aspects. Temperature variations will be a form of stress and will cause changes mediated by hormonal interactions (Hodgson and Levi, 1997). An IBM could be further developed to accommodate temperature effects regarding both biological (e.g., development, disease sensitivity) and environmental (e.g., global climate change, heat caused by industrial effluents) aspects in the future.

Simulation was also conducted with simple conditions of hydrological factors in this study: water current was slow without shear force and turbulence. In general the slope of urban streams is low compared with the streams in the mountainous areas since the cities are mostly located in flat areas. In addition pollution effects could be more readily observed at the area with slow current (i.e., less than $0.2 \, \text{m s}^{-1}$). The macroinvertebrates usually inhabit under the substrates (i.e., interstitial space), and would not be directly affected the flow current if the velocity is sufficiently low. Overall, stress due to pollution (e.g., oxygen depletion)

would be the main controlling factor in community establishment in polluted streams, although there would be effects caused by hydrological factors in some degree.

Spatial heterogeneity is a major factor in streams in defining spatial and temporal dynamics of organisms in streams (Hauer and Lamberti, 2006; Allan and Castillo, 2007), including patchy distribution (Dole-Olivier *et al.*, 1997; Mattaei *et al.*, 1999). Pools and riffles may be a main geomorphological character and would determine spatial heterogeneity by controlling important hydrological factors such as water velocity, substrate compositions, etc. In addition higher toxicity may be observed at pool areas due to sedimentation (Connolly *et al.*, 2004). Considering that the length of the stream (5 km) used in this model is substantially long, the river continuum concept (Vannote *et al.*, 1980) could be also an important factor in revealing the location-oriented, continuous effects of stream flows on biological organisms and environmental factors. These factors related with spatial heterogeneity need to be considered in IBMs in the future in elucidating ecological processes in stream ecosystems more effectively.

In addition to simplification of environmental and biological factors, there was also a limit in the size of cross section in the model. In this study we defined the neighbor sizes as 7×7 to allow movement of individuals (intermediate and old larvae) in natural conditions (see "(1) Movement" in "5) Design concepts and submodels"). This size of neighbors, however, was larger than the system size (5) of cross section in the model (Table 2). When we used the same size of 5×5 in the model, however, there was a higher chance of the individual staying at the boundary at the cross sections. Suppose the neighbor size is 5 in cross section and the individual was assumed to stay at the center. The individual may have the chance of remaining (say 0), or moving 1 site (say 1), or 2 sites (say 2) in either direction. Thus chance of remaining at the boundary would be 1/2 in this case in case the individual moves, since "2" will put the individual at the boundary. The similar results were also obtained when individuals were located at other places beside the center site on the cross section. If neighbor size is larger than 5, however, individuals may have less chance of staying at the boundary. Suppose the system size is 7 and the individual is located at the center of cross section. The individuals will have their choices to

movement of 0, 1, 2, and 3 sites from the center site in one direction, similar to the case of system size equal to 5. In case the individual moves, the movements 1 and 3 (i.e., due to reflection) would put the individual off the boundary while 2 will only put the individuals at the boundary. Consequently the chance of staying at the boundary would be lower with 1/3, compared with the case of neighbor size equal to 5.

Considering physical (i.e., pool and riffles), and biological (i.e., drifting, patch distribution) simplifications, and the limit in system size in cross section in 2 dimensions, an extended 2 dimensional model would be required to accommodate spatial heterogeneity, and physiological (e.g., development) and behavioral (e.g., drifting) events as well to elucidate complex ecotoxicological processes more realistically.

McGill *et al.* (2007) explained that five properties could be dealt with IBMs, including statistical theories, branching processes for life organisms, population dynamics, niche partitioning, and spatial distribution. The IBMs in this study seemed to contribute to elucidation of population dynamics, and partly to revealing niche partition. The simulation study additionally broadened the scope of IBM to the community level by exploring the complex individual-population-community relationships in an integrative manner.

CONCLUSIONS

The complexity of community responses to disturbance was clarified with the use of IBMs. The power law and negative exponential function governing natural and toxic survival rates at individual level were used in the IBM to illustrate different SADs of benthic macroinvertebrate communities that were observed across different levels of pollution in field conditions. IBMs could be used to elucidate the complex individual-population-community relationships in one system and thus could be useful for monitoring and characterizing community structures in stressful conditions.

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