How risky is risk assessment: The role that life history strategies play in susceptibility of species to stress

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Measurements of toxicity based on individuals, such as the LC_{50} (concentration that kills 50% of a population), and effects on reproduction are used extensively in determining ecological risk, in particular, for endangered or threatened species. An underlying assumption is that individual-based toxicity metrics for one species can be directly compared with that for another species. However, this assumption overlooks the fact that different species have different life-history strategies and variables, such as lifespan, time to first reproduction, and number of offspring produced over a lifetime. Using a simple model and laboratory-derived parameter values, we tested the impact of differences in life-history traits on predicted responses to stress. The model predicts the delay in population growth. We compared seven invertebrate species by imposing 50% chronic mortality, 50% reduction of offspring, and both of these effects. The model predicted substantial differences in population delay among all of the species. Furthermore, the intrinsic rate of increase of each population was negatively correlated with the delay in population growth; species with high intrinsic rates of increase were less susceptible to equal levels of stress than species with lower intrinsic rates of increase. These results suggest that the susceptibility of species to pollutants is more complicated than previously thought and that differences in life-history variables must be considered in analyses of population persistence for threatened and endangered species.

toxicity | conservation biology | delay-in-population-growth model | demography

For more than half a century both the scientific community and the general public have been acutely aware of the hazards of the extensive use of pesticides to both the environment and human health. Rachel Carson's *Silent Spring* (1) was the harbinger of a growing environmental movement that has developed at the grass-roots level and has also found a voice in the political/legislative realm. The United States Congress manifested this sentiment with the passage of the Food Quality Protection Act (2), which severely restricts the use of many pesticides in a wide range of uses. This piece of legislation, inspired by the desire to protect producers and consumers (especially children), illustrates the rising tide of public concern about the dangers of environmental contaminants to human health and natural ecosystems (3, 4). Although much effort has been put into assessing the risk of pesticides on human health (3, 4), and a great deal of work has been conducted on ecological risk assessment (5), more work on the effects of pollutants on other ecologically and economically important species still needs to be done. Conservation biologists, documenting global declines in amphibians, birds, and reptiles, have highlighted the need to better understand the interaction between population declines and environmental contaminants (6, 7). This lack of knowledge has been exacerbated, in part, by the continued use of simplistic models to evaluate toxicities in laboratory tests, and the failure of toxicologists to better incorporate meaningful ecological indicators into risk assessment. Although toxicologists continue to use individual measures of effects, such as acute lethal concentration/dose estimates (LC_{50}) and the no observable effect concentration for reproduction, as measures of toxicity, applied ecologists and conservation biologists routinely use more sophisticated measures of population responses to contaminants (e.g., refs. 8 and 9). This discrepancy between established theory and actual practice, which likely stems from the fact that short-term toxicity estimates are simple and inexpensive to derive, is becoming increasingly important as management issues become more complex and focus shifts away from individual to population-level effects and single-species conservation in favor of community- or ecosystem-based approaches.

Efficient and accurate risk assessment is critical in determining the extent to which chemicals pose a risk to the environment and to ecological communities. One of the major approaches involves plotting estimates of the chemical concentration that kills 50% of a population (LC_{50}) and/or chronic no observable effect concentration for reproduction for a range of organisms along with a distribution of expected environmental concentrations of the chemical. Any overlap between the 10th percentile of toxicity values and the 90th percentile of the environmental concentration then serves as an indication that the chemical poses a risk to aquatic ecosystems (10–12). In this application, the acute LC_{50} arguably plays an invaluable role as a quantitative measure in ecological risk assessment. However, as with any environmental indicator, certain underlying assumptions and simplifications are associated with the acute LC_{50} methodology and other methods of measuring toxicity in individuals. One important assumption inherent in the commonly used toxicity endpoints is that values generated for one species are directly comparable with values for other species. However, life-history traits such as lifespan, time to first reproduction, and number of offspring produced over a lifetime may vary substantially among species (13). As such, we would expect that species with different life-history strategies would react differently to stressors, such as exposure to toxicants, over the long term. In this study, the impact of differences in life-history traits on predicted responses to stress was tested. In particular, we tested whether 50% population mortality or a 50% reduction in per capita reproductive output, or a combination of both, results in the same population effect for seven species with widely ranging life-history traits. Using a modification of the delay-in-population-growth index model developed by Wennergren and Stark (14), we evaluated the responses of several economically and environmentally important invertebrate species ranging across trophic levels, habitats, and feeding guilds.

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Table 1. Life table parameters for each species evaluated

	*A. pisum**	*C. septempunctata*†	*D. rapae*†	*D. pulex*‡	*B. dorsalis*§	*F. arisanus*¶	*F. vandenboschi*¶
Intrinsic rate of increase, *r*	0.295	0.085	0.218	0.236	0.160	0.12	0.08
Net reproductive rate, Ro	62	73	25	271	418	27	10.1
Birth rate	0.31	0.09	0.22	0.24	0.21	0.15	0.1
Death rate	0.02	0.005	0.003	0.0015	0.05	0.03	0.002
Generation time	14	50	15	24	37	27	30
Doubling time	2.3	8.1	3.2	3.0	4.3	5.8	8.7

*Data from ref. 19.
†Data from ref. 23.
‡Data from ref. 22.
§Data from ref. 20.
¶Data from ref. 21.

Materials and Methods

When a toxicant does not kill all individuals, populations will eventually recover from the stress; therefore, an alternative to simple calculations of mortality is necessary in the evaluation of pesticide effects (14). Simply put, we might ask the following question as a means of comparison: how long does population recovery take? Wennergren and Stark (14) developed a method called the delay-in-population-growth index to predict population growth delays after a stressful event such as exposure to a pesticide. This method, which involves life table parameters and a matrix-projection model, is mathematically simple yet ecologically much more sophisticated than traditional ''spray-and-count'' methods such as the LC_{50}.

For this study, we developed a modification of the delay-in-population-growth index developed by Wennergren and Stark (14). Whereas Wennergren and Stark (14) examined the delay as the time for a population exposed to contaminants to recover to the same number of individuals as a control population, we modified the model to predict the time it takes for a population to grow from 10 to 100,000 individuals. However, the justification for the use of a 10,000-fold increase is that the population growth rates for two of the species tested, the ladybeetle, *Coccinella septempunctata*, and the parasitoid, *Fopius vandenboschi*, are so much lower than the other species that they don't level off until they reach ≈50,000 individuals (see Fig. 1). Running the model until 100,000 individuals had been reached ensured that all species had reached stable growth rates (stable age distribution). The delay model can be run with lower numbers, for example, until only 1,000 or 10,000 individuals are reached. However, this might result in somewhat different outcomes. This modification to the delay model of Wennergren and Stark (14) allows comparisons among species and allows for the incorporation of varying amounts of stress into the model. Thus, for example, any level of mortality, reduction of offspring, or combinations of lethal and reproductive effects may be imposed on a population.

The delay model is based on an age-structured Leslie matrix model (15–18) and consists of a matrix with the life-history elements, survivorship and fecundity. The matrix is multiplied by an initial condition vector, $n(t)$, containing information on the age distribution of the population. Repeated multiplication yields a projection for population growth across time, which in this case corresponds to a 1-day projection of the population across t days of population change. Survival and fecundity parameter values were obtained from life tables (see below) that were generated from daily measurements taken throughout the life of the sample population. Mortality and fecundity were manipulated in the matrix, not in the initial vector, and as such represent chronic mortality and chronic effects on reproduction. Furthermore, the model assumes a closed system with no immigration or emigration and it is not density-dependent. For the mathematical details of the delay model, refer to Wennergren and Stark (14).

The following species/systems were evaluated.

1. A community common in agroecosytems: the pea aphid, *Acyrthosiphon pisum* Harris; an aphid predator, the Seven-Spot ladybeetle (C-7), *C. septempunctata* L.; and an aphid parasitoid, *Diaeretiella rapae* (M'Intosh).
2. A community consisting of the tephritid fruit fly, the oriental fruit fly, *Bactrocera dorsalis* (Hendel), and two parasitoids that attack this fly, *Fopius arisanus* (Sonan) and *F. vandenboschi* (Fullaway).
3. An aquatic organism, the water flea, *Daphnia pulex* Leydig, a commonly used indicator species for pollutants.

All these species exhibited differences in key life-history variables (Table 1).

Life Table Data

Life table data were taken from previously published studies [*A. pisum* from Walthall and Stark (19), *B. dorsalis* from Vargas *et al.* (20), *F. arisanus* and *F. vandenboschi* from Vargas *et al.* (21)], *D. pulex* from Stark and Vargas (22), *D. rapae* and *C. septempunctata* from Stark *et al.* (23). All life table data were developed under similar environmental conditions (25°C, 50% relative humidity, 16 h light:8 h dark/light regimen).

The delay-in-population-growth model for all species was started with a vector consisting of 10 individuals (neonates or eggs) and ended when population size reached 100,000 individuals. Survival and fecundity of each species was manipulated in the model such that a population was reduced 50% (mortality), the number of offspring produced was reduced by 50% (sublethal effect) and the population was reduced 50% and a 50% reduction of offspring occurred (lethal and sublethal effect). In all cases, population responses to treatment effects were compared with control populations. That is, the delay in population growth was calculated as the difference between the number of days it took the control population to reach 100,000 individuals and the number of days that it took a population exposed to stress to reach 100,000 individuals. Note that factors, such as density dependence, and other natural stressors, such as changes in weather, predation, etc., will all influence these recovery times in the real world and, as such, the recovery times we generated serve only as a comparison among species under contrived conditions. The life-history variables listed in Table 1 were compared with the delay in population growth (in days) with Pearson product moment correlation for mortality, reduction of offspring, and the combination of both these impacts, to determine whether a relationship existed between life-history variables and the delay (24).

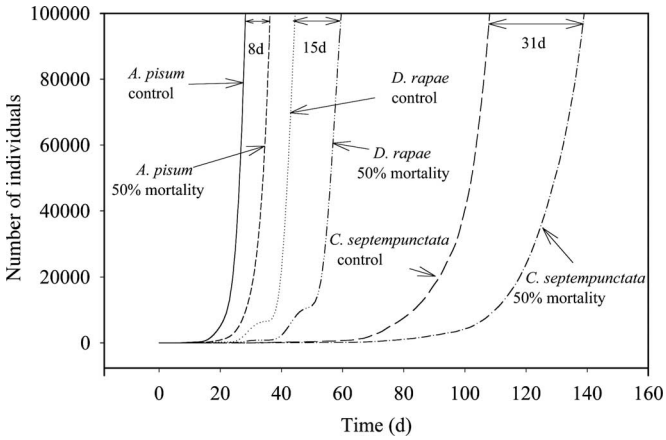

Fig. 1. A comparison of the delay in population growth for untreated populations of the pea aphid, *A. pisum*, the aphid parasitoid, *D. rapae*, and the seven-spot ladybeetle, *C. septempunctata*, and populations that have been subjected to 50% chronic mortality.

Results

The delay in population growth was different for the pea aphid, the aphid parasitoid, *D. rapae*, and the ladybeetle after 50% mortality (Fig. 1). The pea aphid population exhibited the shortest delay, followed by *D. rapae*. Ladybeetle population growth was delayed much longer than the other two species after 50% mortality.

A similar scenario occurred after a 50% reduction of offspring. Again C-7 was the most susceptible species based on a delay of population growth (Table 2). The reduction in offspring resulted in a similar delay in the pea aphid but less of a delay for *D. rapae* and C-7. A combination of 50% mortality and a 50% reduction of offspring resulted in a much longer delay than either factor alone (Table 2), indicating a synergistic rather than additive interaction. That is, addition of the delay in days for 50% mortality and a 50% reduction of offspring was always lower than the combination of the two effects run in the model. This synergistic effect was observed in all the species evaluated except the oriental fruit fly, *B. dorsalis*.

D. pulex was the least susceptible species tested based on the delay in population growth (Table 2). *D. pulex* was ≈6 times less susceptible than the C-7 ladybeetle.

The oriental fruit fly and the parasitoid species, *F. arisanus*, exhibited a similar delay after being subjected to 50% mortality or 50% reduction of offspring (Table 2). However, the combination of effects was much more detrimental to *F. arisanus* than to *B. dorsalis*. Furthermore, the parasitoid *F. vandenboschi* was the most susceptible of these three species (Table 2).

Statistical analysis revealed that a high negative correlation existed between the intrinsic rate of increase and the delay in population growth for mortality ($r = -0.81$, $P = 0.014$), reduction of offspring ($r = -0.93$, $P = 0.001$), and the combination of both impacts ($r = -0.87$, $P = 0.006$). In other words, a higher intrinsic rate of increase was associated with a shorter delay in population growth (faster recovery). Statistically significant positive correlations (mortality, $r = 0.81$, $P = 0.01$; offspring, $r = 0.93$, $P = 0.001$; combination, $r = 0.87$, $P = 0.006$) also existed between population doubling time and the delay in population growth. Statistically significant negative correlations (mortality, $r = -0.90$, $P = 0.01$; offspring, $r = -0.89$, $P = 0.001$; combination $r = -0.87$, $P = 0.006$) existed between birthrate and the delay. Generation time and the delay were positively correlated for mortality ($r = 0.77$, $P = 0.03$) and a reduction of offspring ($r = 0.79$, $P = 0.03$) but not statistically correlated for the combination of mortality and reduction of offspring ($r = 0.53$, $P = 0.18$). Death rate and net reproductive rate (Ro) were not correlated with the delay in population growth.

Table 2. Delay in population growth

Species	Delay in population growth, d		
	50% mortality	50% reduction offspring	50% mortality and 50% reduction offspring
A. pisum	8	8	20
D. rapae	15	12	38
C. septempunctata	31	23	67
D. pulex	5	4	12
B. dorsalis	20	17	30
F. arisanus	23	17	48
F. vandenboschi	20	31	67

Table 3. Comparison of the delay in population growth as a percentage of generation time

Species	50% mortality	50% reduction offspring	50% mortality and 50% reduction offspring
A. pisum	57	57	143
D. rapae	100	80	253
C. septempunctata	62	46	134
D. pulex	21	17	50
B. dorsalis	54	46	81
F. arisanus	85	63	180
F. vandenboschi	67	100	223

Values listed are percentages.

The least susceptible species, based on the delay in population growth, were *D. pulex* and the pea aphid, whereas the ladybeetle and the parasitoid, *F. vandenboschi*, were the most susceptible. Notably, mortality had a greater effect on C-7 than on *F. vandenboschi*, whereas a reduction of offspring had a greater effect on *F. vandenboschi* than on C-7. However, a combination of effects resulted in the same delay (67 d) for both species.

To investigate whether the predicted delays in population growth found are substantial in terms of potential damage to a population, we characterized the delay as a percentage of generation time. We found that delays caused by 50% mortality, 50% reduction of offspring, or the combination of both effects account for a large proportion of generation time for some of these species, sometimes being 2-fold longer than generation time (Table 3). When we ranked susceptibility by the delay in population growth and compared it with the delay in population growth as a percentage of generation time, we find very different rankings of susceptibility (Table 4). However, *D. pulex* is always the least susceptible species no matter how the data are analyzed.

Discussion

The results of the simulations carried out in this study clearly contradict the assertion that all species react to the same stress equally regardless of differences in life-history variables. In fact, the species tested reacted quite differently to the same levels of stress; some species were six times more susceptible than other species. All the species we evaluated were arthropods; differences among species that are more phylogenetically disparate could be even more pronounced. Furthermore, the predicted delays we observed accounted for a large proportion of the generation time for most of the species we evaluated. Therefore, simplistic measures of effects, such as lethal concentration estimates, that are so widely used in risk assessment may not tell us enough to protect endangered species.

Table 4. Ranking of species susceptibility (from most susceptible to least) based on the delay in population growth or on the delay in population growth as a percentage of generation time

Mortality		Reduction offspring		Mortality and reduction offspring	
Delay	% generation time	Delay	% generation time	Delay	% generation time
C. septempunctata	*D. rapae*	*F. vandenboschi*	*F. vandenboschi*	*C. septempunctata*	*D. rapae*
F. arisanus	*F. arisanus*	*C. septempunctata*	*D. rapae*	*F. vandenboschi*	*F. vandenboschi*
B. dorsalis	*F. vandenboschi*	*B. dorsalis*	*F. arisanus*	*F. arisanus*	*F. arisanus*
F. vandenboschi	*C. septempunctata*	*F. arisanus*	*A. pisum*	*D. rapae*	*A. pisum*
D. rapae	*A. pisum*	*D. rapae*	*B. dorsalis*	*B. dorsalis*	*C. septempunctata*
A. pisum	*B. dorsalis*	*A. pisum*	*C. septempunctata*	*A. pisum*	*B. dorsalis*
D. pulex	*D. pulex*	*D. pulex*	*D. pulex*	*D. pulex*	*D. pulex*

Why were the C-7 ladybeetle and the parasitoid, *F. vandenboschi* the most susceptible of the species evaluated in terms of the delay in population growth? The most parsimonious reason is that they had the lowest intrinsic rate of increase compared with the other species. An examination of the life table parameters reveals that C-7 has a much longer generation time than *F. vandenboschi* but a higher net reproductive rate (Ro). These two species had similar doubling times, death rates, and birthrates. The least susceptible species, *D. pulex* and *A. pisum*, had the highest intrinsic rate of increase and shortest doubling times.

Species that have high intrinsic rates of increase, short generation times, and a short time interval for first offspring (e.g., *Daphnia*) are often used as indicator species of environmental pollutants, because they are usually easy to rear and their life-history traits enable large amounts of data to be gathered quickly. However, results of our study indicate that species that exhibit such traits (e.g., *Daphnia*) are also much less susceptible to stress at the population level than species with different life-history variables, such as C-7 and *F. vandenboschi*. Therefore, if a toxicant is being evaluated with a traditional toxicological approach, such as the LC_{50}, and an LC_{50} value of 25 μg/liter is estimated or the no observable effect concentration for reproduction is found to be 10 μg/liter for *Daphnia*, these concentrations may be devastating to populations of a species that have much lower intrinsic rates of increase, reproductive rates, and longer generation times. Thus, the use of environmental concentrations that are safe for *Daphnia* as aquatic life criteria for risk assessment (25) may have disastrous consequences for the conservation and preservation of other species with very different life-history traits.

Notably, risk assessment protocols in the United States and the European Union (26, 27) have incorporated a tiered structure to hedge against underestimates of toxicities on nontarget organisms. In particular, when data on acute toxicity of invertebrates are the only data available for risk assessment, uncertainty factors comprising a factor of 2–20 in the United States and a factor of 100 in the European Union are applied to the LC_{50} to account for the uncertainty in extrapolating from these values to the likely effects on nontarget aquatic organisms. The use of uncertainty factors certainly reduces the chance that simplistic toxicity measures will severely underestimate the true risks to populations subjected to pesticide exposure, but our results suggest that such margins might vary substantially among species with widely different life-history traits. Recently species sensitivity distributions have been discussed in the context of risk assessment, and this should certainly improve the risk assessment process (28).

One way to improve risk assessment is to compare life-history variables for organisms that are most likely to be exposed to a toxicant. Unfortunately, a dearth of life history data exists for many species, especially those that are threatened or endangered. Once more data are collected, we can move from individual or population responses to entire ecosystem responses to toxic disturbances (29, 30).

Our results indicate that differences in life-history variables among species greatly influence population susceptibility to stress. Equal levels of mortality and reductions in fecundity will have very different impacts on species with different life-history traits. Susceptibility to toxicants cannot be attributed solely to the toxic properties of a compound and/or the physiology of the exposed organism and will vary as a function of population growth rates. Therefore, life-history traits need to be incorporated into studies of species interactions under different disturbance regimes.

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