Feasibility of using the RAMAS-Metapopulation Model to Assess the Risk of a Non-indigenous Copepod (*Pseudodiaptomus marinus*) Establishing in Vancouver Harbour from Ballast Water

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by

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ABSTRACT

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We assessed the feasibility of using a readily available model to predict the risk of establishment of a non-indigenous species (NIS) in Vancouver Harbour. Using life-history data from the literature and the RAMAS Metapop program, we conducted simulations using a single population and a metapopulation to assess the risk of population explosion of the copepod *Pseudodiaptomus marinus* released into the harbour from ballast water. Parameters which affected the explosion included initial density, population structure, and transport or dispersal rate. In general, this model provided a useful tool for assessing the risk of invasion and establishment by NIS. However, this approach is not comprehensive since it only considers survival after release from a ballast tank and it assumes a niche is available in the recipient habitat. The model may be useful to compare risk of establishment between NIS with varying life history parameters, and to identify which parameters most affect NIS establishment.

RESUMÉ

Barry, K.L., and C.D. Levings. 2002. Feasibility of using the RAMAS-Metapopulation model to assess the risk of a non-indigenous copepod (Pseudodiaptomus marinus) establishing in Vancouver Harbour from ballast water. Can. Tech. Rep. Fish. Aquat. Sci. 2401: 25 p.

Nous avons évalué la faisabilité d'appliquer un modèle facilement disponible pour estimer le risque qu'une espèce non indigène (ENI) s'établisse dans le port de Vancouver. Nous nous sommes servis du programme RAMAS Metapop et de données publiées sur le cycle vital du copépode *Pseudodiaptomus marinus* pour simuler la dynamique d'une seule population et celle d'une métapopulation afin d'évaluer le risque d'une flambée de population de cet organisme introduit dans le port par la vidange d'eau de ballast. La densité initiale, la structure de la population et le taux de transport ou de dispersion étaient des paramètres qui influaient sur la flambée de population. En général, ce modèle constitue un outil utile qui permet d'évaluer le risque d'invasion et d'établissement d'une ENI. Toutefois, cette démarche n'est pas exhaustive puisqu'elle n'aborde que la survie d'un organisme après son introduction à partir d'une citerne de ballast et qu'elle suppose qu'une niche libre convenable est présente dans le milieu récepteur. Le modèle pourrait s'avérer utile pour comparer les risques d'établissement d'ENI dont les paramètres du cycle vital diffèrent et pour déterminer les paramètres qui influent le plus sur l'établissement d'une ENI.

A. INTRODUCTION

Risk assessment is generally defined as the process of estimating the likelihood and consequences of undesired events (Hayes, 1997). Traditionally, risk assessment has been used to evaluate the effects of chemical pollution on living organisms, but this approach has the potential for a much broader range of applications, such as the evolving field of ecological risk assessment (ERA). ERA is based on the same framework as standard risk assessment methods, but the key feature of ecological risk assessment is that it considers effects beyond the individual, and includes effects at the population, community or ecosystem level.

One of the more recent applications of ecological risk assessment is in the study of non-indigenous species (NIS). The introduction NIS presents a unique application for ERA since the abundance and dispersal of biological invaders are obviously not subject to the same relationships as chemical pollutants. The ultimate effects of NIS can be difficult to quantify because biological invaders can (1) reproduce and multiply, (2) disperse in the environment using a variety of means at varying rates, (3) interact with biotic and abiotic components of the ecosystem, and (4) evolve over time, potentially altering their original characteristics. The introduction and subsequent establishment of NIS involves an array of physical and biological factors. Due to these complex mechanisms, there have been relatively few quantitative ecological risk assessments of NIS introductions, with the possible exception of genetically modified organisms (Ginzburg, 1991).

To be a useful tool for estimating the effects of NIS introductions, it is necessary to identify specific risk assessment endpoints (Hayes, 1997). These refer to the situation or state which is to be protected. Different risk assessments use different endpoints depending upon the purpose of the ERA. For example, the endpoints used in pollution risk assessments are often related to human injury or mortality. In the case of NIS, assessment endpoints may include the establishment of a NIS or the environmental damage caused by the invading organism. The latter effect is often a much more complex issue. In many cases, the establishment of a NIS is an undesired event in and of itself. In other words, there is a desire to preserve the existing species assemblage and prevent the introduction of NIS, because they may outcompete endemic species and reduce biodiversity (e.g. Ruiz et al., 1997).

Our goal was to evaluate an existing model (RAMAS (Risk Analysis Management Alternative System) Metapop) (Akçakaya, 1998), as a tool to assess the risk of NIS introductions via ballast water released into Vancouver Harbour, British Columbia (BC). Presently, there are no standardized quantitative risk assessment models for ballast water introductions. However, in 1993, the Australian Quarantine and Inspection Service (AQIS) commissioned the development of a risk assessment model specific to ballast water introductions in order to address the issue of NIS dinoflagellates in Australian waters (Hayes and Hewitt, 1998). This model will provide a much-needed tool, however it has not been completed.

Vancouver Harbour, located in Burrard Inlet, is an international port with a large proportion of vessels arriving from Asia. Recent monitoring conducted on vessels in Vancouver Harbour indicated that *Pseudodiaptomus marinus*, a calanoid copepod endemic to Japan (Fleminger and Kramer, 1988), was present in the ballast tanks of 25.4% of ships sampled, occurring in densities from 2 to 54 per m^3 (Piercey et al., 2000). The endpoint used in this study was the establishment of a reproductively viable population of *P. marinus*, assuming the organism was discharged via ballast waters into Vancouver Harbour. This species is thus a potential colonizer of Vancouver Harbour.

Calanoid copepods of the genus *Pseudodiaptomus* occur exclusively in shallow estuarine and protected coastal waters. This family consists of approximately 70 species (Fleminger and Kramer, 1988). Three species are indigenous to east Pacific coastal waters bordering North, Central and South America (*P. wrighti, P. culebrensis, P. euryhalinus*). *P. marinus* is native to Japan and was first described in 1913 (Fleminger and Kramer, 1988). Since then, it has been reported from China, Russia, Hawaii, India, California, and Australia. According to previous work, the only *Pseudodiaptomus* species occurring in coastal waters between Baja California and Oregon was *P. euryhalinus*. In 1988, however, breeding populations of *P. marinus* were discovered in Southern California (Fleminger and Kramer, 1988). More recently, another Asian pseudodiaptomid (*Pseudodiaptomus inopinus*) was discovered in the Pacific Northwest region in the Columbia River Estuary (Cordell et al., 1992). There are few published records of the life history characteristics for *P. inopinus,* whereas *P. marinus* is relatively well studied. Hence the latter species was the focus of the present study.

B. METHODS

I. GENERAL LIFE HISTORY CHARACTERISTICS OF *P. MARINUS*

Pseudodiaptomus marinus is an egg-carrying calanoid copepod with 6 naupliar stages (NI – NVI) and 5 copepodid stages (CI – CV) (Uye and Onbe, 1975). At 20°C, nauplius I stage lasts only 2-4 minutes, while the other naupliar stages are 1-3 days in duration. The duration of each copepodid stage is 3 days. Unlike free-spawning copepods, survival of *P. marinus* is high during the early stages and lower for later stages (Liang and Uye, 1997a). This species can reproduce throughout the year but seasonal abundance peaks occur in summer (June – July). On average, 61.4% of the population are females. Reproductive rate is affected by water temperature, increasing linearly with higher temperature, and is optimal at 20°C. Some areas of Vancouver Harbour are known to reach this level at the surface during summer months (Levings and Samis, 2001). Although salinity can also influence population growth, the effect is minor in comparison to the temperature effect, and thus salinity effects were not included.

II. RAMAS METAPOP MODEL

A set of populations of the same species that may exchange individuals through dispersal (migration) or transport is known as a metapopulation. The RAMAS Metapop model software simulates the metapopulation's future in terms of growth or decline. The model computes the probability of growth to a specific population size or "explosion" and the risk of decline toward possible extinction. For the purposes of the model, an explosion is defined as total explosion where there is a population increase to a certain level at least once during the specified time. A "quasi-explosion" is a partial increase where the population exceeds a range of threshold values at lease once (Akçakaya, 1998).

A key feature of RAMAS Metapop is that it is designed to incorporate as many factors as possible and available on the ecology of the species in question, including stage structure, environmental variability (stochasticity), density dependence, and spatial structure (e.g. dispersal and correlation among populations). The program is flexible and allows the model to be based on a single population, or a metapopulation consisting of any number of subpopulations. In this study, analyses were based on a single population as well as a metapopulation.

Since risk assessment is based on probabilities, natural variability is an important component of any risk assessment. One of the reasons why RAMAS Metapop is well suited for risk assessments is that environmental stochasticity can be incorporated into the model. The risk of NIS establishment can be determined using the risk of explosion feature in RAMAS Metapop, in which the probability of the population abundance exceeding a certain level during a specified time period is determined. These calculations are based on vital rates, including survival and fecundity.

III. INPUT INFORMATION FOR RAMAS METAPOP MODEL

Some input information can be arbitrarily used in the model, tailored by the user to the particular application. Important factors to consider are processing speed, and desired degree of precision. Other types of input are based on the ecology of the species of interest, and require real data on the life history characteristics. In the case of *P. marinus*, the demographic characteristics are not a function of age, but rather the life history stage; therefore, a stage-based model was used. Age and life history stages are, however, correlated.

a. Single Population Analysis

To construct the *Stage Matrix* (Table 1), stage-specific survival data was obtained from Iwasaki and Kamiya (1977), who conducted a population growth experiment with *P. marinus* at 4 temperatures (10°, 15°, 20°, 25°C). Survival rates of each stage were calculated as the mean survival at each temperature. The *Standard Deviation Matrix* (Table 2) was constructed using the standard deviations of mean survival at each temperature. Only one standard deviation matrix was used in each simulation.

Using an example of a single population, the input parameters were as follows (Tables 1 and 2):

- *Replications*: 100 (at least 4 simulation replications are required for risk analysis)
- *Duration*: 30 days
- *Density dependence*: assumed to affect all vital rates, but modified later on in the procedure (see p. 26 in Akçakaya (1998) and below)
- *Constraints*: are in effect to check if the matrix elements in a given column when summed are >1.0, and if so, adjusts them (see p. 26 in Akçakaya, 1998)
- *Stages*: 3 (Nauplius, Copepodid, Adult)
- *Stage Matrix*: only one stage matrix was used in each simulation

- *Populations*:
  1. General: Initial density = 300 m^{-3}
  2. Density Dependence: Density dependence type: exponential
  3. Catastrophes: none; however, the model enables consideration of rare or extreme events which affect population abundance, vital rates, or carrying capacity due to local or regional catastrophes (see p. 54-59 in Akçakaya, 1998)
- *Initial abundance*: Based on a stable stage structure, the software computed the density of each life stage as follows: nauplius- 135 m^{-3}; copepodid- 110 m^{-3}; adult- 56 m^{-3}.
- *Demographic Stochasticity*:
  - Environmental stochasticity distribution: lognormal
- Explosion threshold: 1000 organisms
- *Catastrophe 1*: none
- *Catastrophe 2*: none
- *Dispersal*: not applicable; single population
- *Correlation*: none. The model allows options for situations where two populations experience the same environmental variables (e.g. weather for terrestrial animals), and therefore may have correlated changes in vital rates (see p. 65-67 in Akçakaya, 1998)
- *Population Management Actions*: none. The model allows options for assessing management options such as harvest management (see p. 100 in Akçakaya, 1998)

These settings were the default settings and remained constant in all simulations. To assess how specific variables affected the risk of explosion, simulations were run while altering one variable at a time, as described below. Detailed explanations of all variables and menu choices can be found in the RAMAS Metapop User Manual (Akçakaya, 1998). Important variables included initial population size, population structure, and density dependence. The effect of each of these variables was studied in turn.

b. Metapopulation Analysis

This analysis allows for the description of the dynamics of a number of interacting populations of the same species. In this case, these are populations released from the ballast tanks of ships. To approximate the situation in Vancouver Harbour, known anchorage locations were studied as potential release sites of five copepod populations (Figure 1).

The advantage of metapopulation analysis is that allows the inclusion of spatial factors such as dispersal. Colonization of new areas is a function of the organism's mobility, and the distance to the new patch where other individuals are located. In the case of ballast water discharge, the transport of *P. marinus* is influenced directly by currents, which we assumed to reflect dispersal. Estimates of surface currents were obtained from a modelling study conducted by Triton Consultants (2000) in which trajectories of ballast water released from anchorage sites were determined from current velocity and direction. Initial density data (Table 3) were chosen to cover a broad range of concentrations of plankton organisms similar to those found in ballast water tanks by Piercey et al. (2000).

Relative rates of transport between each population were ranked according to the modelled trajectories and distances between anchorages. Longer trajectories were the result of the stronger surface currents predicted in the Triton (2000) modelling work. Values were adjusted based on the assumption that the transport rate equals 10% of one population moving to another per time step (Table 4). In constructing this matrix, the sum of any column must be equal to or less than one.

Stage abundances of *P. marinus* after the metapopulation simulation are in Table 5. Input parameters were the same as those for Single Population Analysis, except that the explosion threshold for demographic stochasticity was set at 7500 organisms m^{-3}, and dispersal (transport) was as in Table 4.

C. RESULTS

I. COMMENTS ON DESCRIPTION OF KEY GRAPHICAL OUTPUTS

The results menu for RAMAS offers several types of graphical output, shown in Figure 2 to 8 and briefly described below. All risk graphs include 95% confidence intervals which are a function of the number of replications. The graphical results of primary interest are as follows: the *Trajectory Summary* (Fig. 2) shows a statistical summary of the abundance of the population as it changed through time. The mean abundance of the metapopulation is shown (with standard deviation) and maximum abundance. Since it often shows a skewed distribution, the average population size displayed on this graph should not be interpreted as the expected population size. The trajectory summary should only be used as a general summary of the population trend. (Akçakaya, 1998, p. 103).

*Final Stage Abundance (*Fig. 3) displays histograms of the distribution of the mean abundance, standard deviation, and maximum number of individuals in each life history stage in the population after 30 d, the final time step of the simulation (Akçakaya, 1998, p. 103).

Interval Explosion Risk (Fig. 4) shows the probability that abundance will exceed a range of abundance at least once during the simulation. In this example there is a 3% probability that the abundance of *P. marinus* will exceed 100 000 at least once during the next 30 days of the simulation (Akçakaya, 1998, p. 104).

Terminal Explosion Risk (Fig. 5) is similar to *Interval Explosion Risk*, but shows the probability that abundance will be above a given range at the end of certain time steps. For example, there is a 3% probability that after 30 days abundance of *P. marinus* will be greater than 20 000. (Akçakaya, 1998, p. 104).

Interval Percent Decline (Fig. 6) is similar to *Interval Explosion Risk,* except that it shows the probability that the total abundance will decline by a specific percentage from its initial value at least once during the simulation. For example, there is a 50% probability that the abundance of *P. marinus* will be 80% less than the initial abundance, at least once during the 30 days of simulation.

Terminal Percent Decline (Fig. 7) is similar to *Interval Percent Decline*, but shows the probability that abundance will decline by a specific percentage from its initial value at the end of the simulated time period. For example, there is a 42% probability that, after 30 days, the abundance of *P. marinus* will be 60% less than the initial abundance. The y-value of the line at 100% is the risk of total extinction.

Time to Quasi-Explosion (Fig. 8) shows the distribution of the times it takes the population size to exceed the specified explosion threshold. The histograms show the probability that the metapopulation size will exceed the specified threshold exactly at a specific time step, while the cumulative distribution (continuous line) shows the probability of exceeding the threshold at or before a specific time step. For example, there is a 5% probability that the population abundance will exceed 1000 on Day 2, and there is a 56% probability that the population abundance will exceed 1000 on or before Day 30. The median is indicated by the vertical dashed line.

II. SINGLE POPULATION ANALYSIS

a. Risk of Population Explosion

The RAMAS model offers several ways to assess the risk of population explosion, including interval and terminal explosion risk (Fig. 4, 5). Extinction risk (Fig. 7) can provide information about whether the population is likely to persist over time. Another type of useful prediction provided is the time to quasi-explosion (Fig. 8), which estimates the median time for the population to exceed a pre-defined explosion threshold. In an example using the single population analysis for *P. marinus*, the time to quasi-explosion was 28 d, with a moderately low risk of extinction (19%). This indicates there was a 19% chance that the population will decline to zero, but if not, it would take approximately 28 d to explode.

b. Parameters Affecting Risk of Population Explosion

1. Initial Population Density

The density of organisms in ballast tanks can vary significantly, both between vessels, and among tanks on a particular vessel (Piercey et al., 2000). To address this variability, simulations were run with different initial population densities while all other parameters were kept constant (Table 6).

The model predicted that higher initial densities of copepods would result in increased risk of population explosion, as expected (Table 6). Over the 30 d simulation period, the risk of population extinction was relatively high if initial density is <100 m^{-3}. If initial abundance exceeded 500 m^{-3}, population explosion would occur in less than 1 week.

2. Population Structure

Within given ballast tank, the population structure of the organisms may vary. That is, the proportion of each life history stage may be different in each tank or between tanks on various vessels.

Population structure affected the likelihood that *P. marinus* would become established (Table 7). When only adult *P. marinus* were present, the time to explosion was very short and the extinction risk was low. Time to explosion was longest when no adult *P. marinus* were present. When the density of each life stage was approximately equal, the time to explosion was moderate while extinction risk was relatively low.

3. Density Dependence

There are three categories of density dependence provided in the RAMAS model. The first category (including logistic and Ricker equations) is based on worsening survival when resources are shared more-or-less equally among individuals. It is analogous to scramble competition. The second category (Beverton-Holt function) is based on diminishing returns when available resources are shared unequally. It is analogous to the effects of contest competition. The third category (ceiling model) is also similar to contest competition, but affects the population dynamics only when it reaches the population ceiling rather than continuously. All three types of density dependence are based on declining recruitment or growth rate as density increases. Another type of density dependence involves Allee effects, in which the recruitment or growth rate declines as density decreases. In other words, if a population declines to a critical level, if only by chance, then Allee effects can decrease it even further. Allee effects can be combined with any other type of density dependence.

Density dependence is often very difficult to identify in natural populations. Previous work indicated that some copepods are affected by density dependent functions only when densities are unnaturally high (i.e. 1 female • ml^{-1}) (Miralto et al., 1996). It is likely that most natural populations are affected by climate and resource variability more often than, or just as often as density dependent factors.

Due to the lack of data about density dependent effects on *P. marinus* and the difficulty in estimating these parameters, the density dependence function was set to exponential (i.e. no density dependence) in most of the simulations. A few simulations were also run to examine how density dependent effects would influence model results.

To assess how different types of density dependent mechanisms could affect the explosion risk of *P. marinus,* specific simulations were run using each type of density dependence, while keeping all other variables set to their default values as described above (Section BIII).

Density dependence mechanisms affected the model results quite strongly (Table 8). Under each type of density dependence, the time to explosion was usually greater than 30 days and the risk of extinction was high. In general, density dependence decreased the population growth of *P. marinus* so that the probability of explosion was substantially lowered. The only case in which there may be a population explosion within 30 days was when Allee effects were invoked under an exponential situation. Using an exponential setting (i.e. no density dependence), either alone or in combination with Allee effects may provide a conservative estimate of whether or not a NIS is likely to show a population explosion.

III. METAPOPULATION ANALYSIS

a. Risk of Population Explosion

In a simulation for a metapopulation consisting of 5 subpopulations, the chances of explosion were much higher than in the single population scenario (Table 9). The time to explosion was quite fast at 4.2 days, and the extinction risk was zero, which indicates that this metapopulation will increase in abundance and it is likely to expand rapidly.

b. Parameters Affecting Risk of Metapopulation Explosion

1. Number of populations

The simulation results indicated that there are many interacting factors which contribute to a high risk of explosion (Table 9). The time to explosion was shortest (11.3 days) for the metapopulation consisting of 3 populations and high transport rates (see Table 4). The time to explosion seemed to depend more on transport rate than initial density. That is, metapopulations with high initial density but low or moderate transport rates had explosion times which exceeded 30 days. In general, the times for explosion were quite long. This may be due to the fact that the explosion threshold was set quite high (7500 organisms m^{-3}) for all simulations, even those which had low initial density.

2. Transport Rate

Generally, as transport rates decreased, the time to quasi-explosion increased (Table 10). This indicates that when organisms are unable to colonize new areas, the probability of population explosion will be reduced. Overall, however, the pattern was not exceptionally strong. Perhaps when the probability of explosion is very high, the effect of transport is not as evident. In this case, the time to quasi-explosion was probably controlled by a combination of initial density and transport rate.

D. DISCUSSION

The RAMAS Metapop program could be a useful tool to evaluate the probability of NIS introductions, particularly those with varying life history characteristics, from the ballast water of ships. The preliminary results from this simulation study indicate that it is possible for *P. marinus* to expand its population quickly if habitat and niche conditions allowed. The parameters which significantly affected the risk of population explosion included population abundance, population structure, and transport rate. Therefore, as the number of ships using the harbour and the density of adult *P. marinus* in ballast tanks increases, the likelihood of a successful invasion could rise. However, invasion success is a function of species-specific and site-specific characteristics and a population explosion may not be a valid indicator of NIS colonization. The strength of this model is its ability to incorporate species-specific parameters, since it is based on real life history characteristics. As an egg-carrying copepod, *P. marinus* exhibits a lower fecundity than free-spawning calanoid copepods (Kiørboe and Sabatini, 1994; Liang and Uye, 1997b). Having fewer eggs than free-spawners to be fertilized, *P. marinus* may have a relatively low reproductive rate. At the same time, however, during times of low copepod population density, egg-carrying may favour survival because the nauplii, after hatching, are positioned more closely together than scattered nauplii that have hatched from pelagic eggs. This aggregation of *P. marinus* nauplii gives each individual a greater chance for survival because its likelihood of being captured by a predator is reduced (Alcock, 1998). Nonetheless, during times of high copepod density, free-spawners, because of their higher fecundity, have a higher reproductive rate and may therefore give different model results and hence may be more likely to become established in Vancouver Harbour. To test this, the reproductive rate in the stage matrix was increased to 5.0 from 2.4. With the higher reproductive rate, simulation results indicated that the probability of population explosion (to 500 000) was 55%, whereas with the lower rate it was less than 10%. Similarly the time to quasi-explosion decreased from 18 days to only 3.6 days. Clearly, species-specific life history characteristics, such as reproductive rate, have a significant effect on whether the population will explode and to what degree.

The model also allowed a certain degree of site-specificity in that the effect of Vancouver Harbour currents on transport of copepods was used to simulate dispersal rates. However, without empirical data, it is difficult to estimate the number of individuals that could move from one population to another. In this regard, without data on the density of organisms as the population is being dispersed after being pumped out of a ballast tank, it is difficult to estimate population density and hence estimate if density dependent effects could be operating. This is potentially one of the major sources of error in this study.

There is furthermore a temporal aspect to modelling population explosions, since the conditions in the receiving environment are not static. This aspect was incorporated in the model as environmental stochasticity. There may, however, be other types of temporal variation which are underestimated in the model, such as the effects of changing wind and tides on organism transport. Another key aspect of modelling is that the results will only be as good as the amount and quality of available data for the given species. Thus, this model would not be appropriate to evaluate the risk of introduction of a species for which little population biology is known.

Although this study focused on the probability of survival and establishment post-release, in reality there are many steps in ballast water risk assessment, including (Hayes and Hewitt, 1998):

1. The probability of organisms living in water from which ballast is drawn,
2. the probability of uptake into tanks,
3. the probability of survival during ballasting,
4. the probability of surviving in tanks during transit,

5. the probability of surviving deballasting, and
6. the probability that the receiving environment is a suitable habitat and that an ecological niche is available

In this study, we assumed that steps 1 through 6 had probabilities of 100%. Perhaps the most significant assumption in this study is that which refers to habitat suitability. Although RAMAS Metapop is able to take environmental variability into account through the standard deviation matrix, it is not able to incorporate habitat suitability, which is critically important to the survival and establishment of a new species. It is generally very difficult to infer anything about the above steps from historical data. Consequently, there is a great need for empirical data in order to successfully address the question of the risk of ballast introductions. Information needed includes biology of ballast tank assemblages, physiological tolerances, and viability experiments, to name a few. Since ballast tanks can be considered as self-contained mesocosms with varying physical conditions and species assemblages, research on the survival, reproduction and growth of species in ballast tanks can provide much useful information (e.g. Gollasch et al., 2000).

E. CONCLUSIONS

Although relatively simplistic, this modelling exercise provided valuable information about the probability of NIS establishment in Vancouver Harbour. The results indicate that the probability of *P. marinus* invading Vancouver Harbour might be significant if large numbers of adult copepods were released from ballast tanks at closely spaced anchorages. Key characteristics which should serve as indicators of a species likely to invade include high adult density in tanks, high reproductive rates, fast dispersal or transport rates, and physiological and ecological tolerance of conditions in the recipient environment.

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TABLES

Table 1. Stage-specific matrix survival rates for *P. marinus* averaged over all incubation temperatures (from Iwasaki and Kamiya, 1977).

	Nauplius	**Copepodid**	**Adult**
Nauplius	0.175	0.075	2.383
Copepodid	0.725	0.263	0.111
Adult	0.000	0.500	0.138

Table 2. Standard deviation of stage-specific survival rates, computed over four incubation temperatures (from Iwasaki and Kamiya, 1977).

	Nauplius	**Copepodid**	**Adult**
Nauplius	0.236	0.150	1.371
Copepodid	0.150	0.431	0.194
Adult	0.000	0.367	0.094

Table 3. Numerical code used for anchorages (see Fig. 1) where ballast water was released into Vancouver Harbour, initial density of *P. marinus* populations, and current transport factors used in the metapopulation analysis.

Numerical code for anchorage where population released from ballast tanks	**Initial Density (m^{-3})**	**Currents**	**Distance to Nearest adjacent anchorage (arranged closest to farthest)**
1 Outer Burrard Inlet	1000	Weak	3, 2, 4, 5
2 West Vancouver	1000	Strong	3, 5, 4, 1
3 English Bay North	2500	Moderate	4, 2, 1, 5
4 English Bay South	100	Weak – moderate	3, 2, 1, 5
5 Inner Burrard Inlet	500	Moderate	2, 3, 4, 1

Table 4. Matrix showing relative rate of transport of *P. marinus* populations between five anchorages in Vancouver Harbour (Fig. 1), based on current predictions from Triton (2000).

Population	Anchorage 1	Anchorage 2	Anchorage 3	Anchorage 4	Anchorage 5
Anchorage 1	-	0.100	0.100	0.100	0.001
Anchorage 2	0.025	-	0.200	0.150	0.200
Anchorage 3	0.025	0.300	-	0.300	0.100
Anchorage 4	0.025	0.200	0.300	-	0.050
Anchorage 5	0.001	0.200	0.010	0.010	-

Table 5. Density (m^{-3}) of each life stage of *P. marinus* after the metapopulation simulation.

Population	Nauplius	Copepodid	Adult
Anchorage 1	450	364	186
Anchorage 2	225	182	93
Anchorage 3	902	727	371
Anchorage 4	45	36	19
Anchorage 5	225	182	93

Table 6. Time to explosion and extinction risk for populations of *P. marinus* with different initial densities.

Initial Population Density (m^{-3})	Median Time to Quasi-Explosion (days)	Extinction Risk (%)
100	< 30	16
300	16	12
500	6.5	7
750	3.3	3
1000	0.8	2
1500	0.6	0

Table 7. Simulation results with varying proportions of three life history stages of *P. marinus*. Total initial density in each simulation was 300 m^{-3}.

Nauplii (m^{-3})	**Copepodid (m^{-3})**	**Adult (m^{-3})**	**Median Time to Quasi-Explosion (days)**	**Terminal Extinction Risk (%)**
100	100	100	11.5	5
125	125	50	15.0	8
50	125	125	9.3	8
125	50	125	13.0	6
0	150	150	11.0	5
150	0	150	15.0	4
150	150	0	>30	12
300	0	0	19.8	11
0	300	0	24.8	9
0	0	300	6.0	4

Table 8. Explosion time and extinction risk for a single population of *P. marinus* with different density dependent functions. NA indicates not applicable.

Density Dependence Type	**Median Time to Quasi-Explosion (days)**	**Extinction Risk (%)**
Scramble	> 30	81
Contest	> 30	85
Ceiling	NA	100
Allee - exponential	26.5	24
Allee - scramble	> 30	88
Allee - contest	> 30	89
Allee - ceiling	NA	100

Table 9. Explosion times resulting from different combinations of metapopulations at five anchorages in Vancouver Harbour.

Metapopulation at various anchorages	**Final Total Abundance (m^{-3})**	**Median Time to Quasi-Explosion (days)**
1, 5	1500	28
2, 5	1000	26
2, 4	600	>30
1, 2	1500	>30
2, 3, 4	2600	11.3
1, 4, 5	1600	>30
1, 3, 5	3500	>30
1, 2, 4, 5	2100	23
2, 3, 4, 5	3100	20
1, 2, 3, 4	3600	>30

Table 10. Effects of transport rate on time to quasi-explosion and extinction risk.

Transport rate	**Median Time to Quasi-Explosion (days)**	**Extinction Risk (%)**
No transport	4.2	0
Low	1.9	0
Medium	1.8	0
High	1.7	0

LIST OF FIGURES

Figure 1. Map of Vancouver Harbour showing the location of the five anchorages used as simulated ballast water release sites in the metapopulation simulation analyses. 1- Outer Burrard Inlet; 2- West Vancouver; 3- English Bay North; 4- English Bay South; 5- Inner Burrard Inlet.

Figure 2. Example of output "Trajectory Summary" showing general trend of abundance for *P. marinus* during the 30 d simulation period. Mean abundance and standard deviation are data close to the x-axis. Maximum values shown by the symbol " ◊ ".

Figure 3. Example of output "Final Stage Abundance" showing distribution of mean abundance and standard deviation of each life history stage of *P. marinus* after 30 d simulation. Maximum values shown by the symbol " ◊ ".

Figure 4. Example of output "Interval Explosion Risk" showing probability that abundance will exceed threshold levels at least once during a 30 d simulation period. Dashed line is 95% confidence interval.

Figure 5. Example of output "Terminal Explosion Risk" showing risk that abundance will exceed various threshold levels at the end of the 30 d simulation period. Dashed line is 95% confidence interval.

Figure 6. Example of output "Interval Percent Decline" showing risk that abundance will decline by specific percentage at least once during the 30 d simulation period. Dashed line is 95% confidence interval.

Figure 7. Example of output "Terminal Percent Decline" showing risk that abundance will decline by specific percentage from initial value at end of the 30 d simulation period. Dashed line is 95% confidence interval

Figure 8. Example of output "Time to Quasi-explosion". Histograms show the risk that abundance will exceed 1000 at an exact day in the 30 d simulation (x-axis). Solid line indicates the risk that the population size will exceed 1000 at or before a specific day. Dashed line is 95% confidence interval.

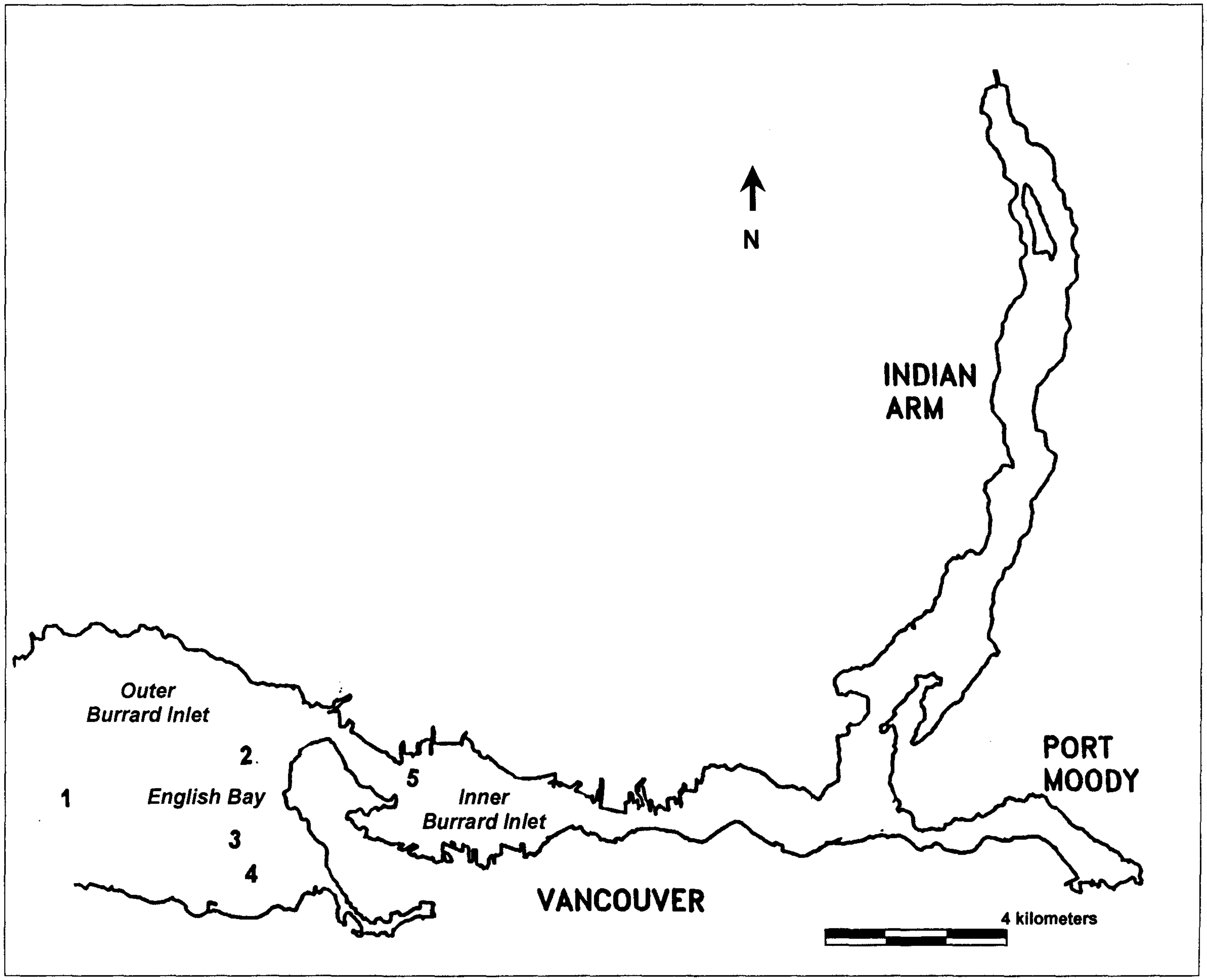

N
INDIAN ARM
Outer Burrard Inlet
2
1
English Bay
3
4
5
Inner Burrard Inlet
PORT MOODY
VANCOUVER
4 kilometers

Figure 1.

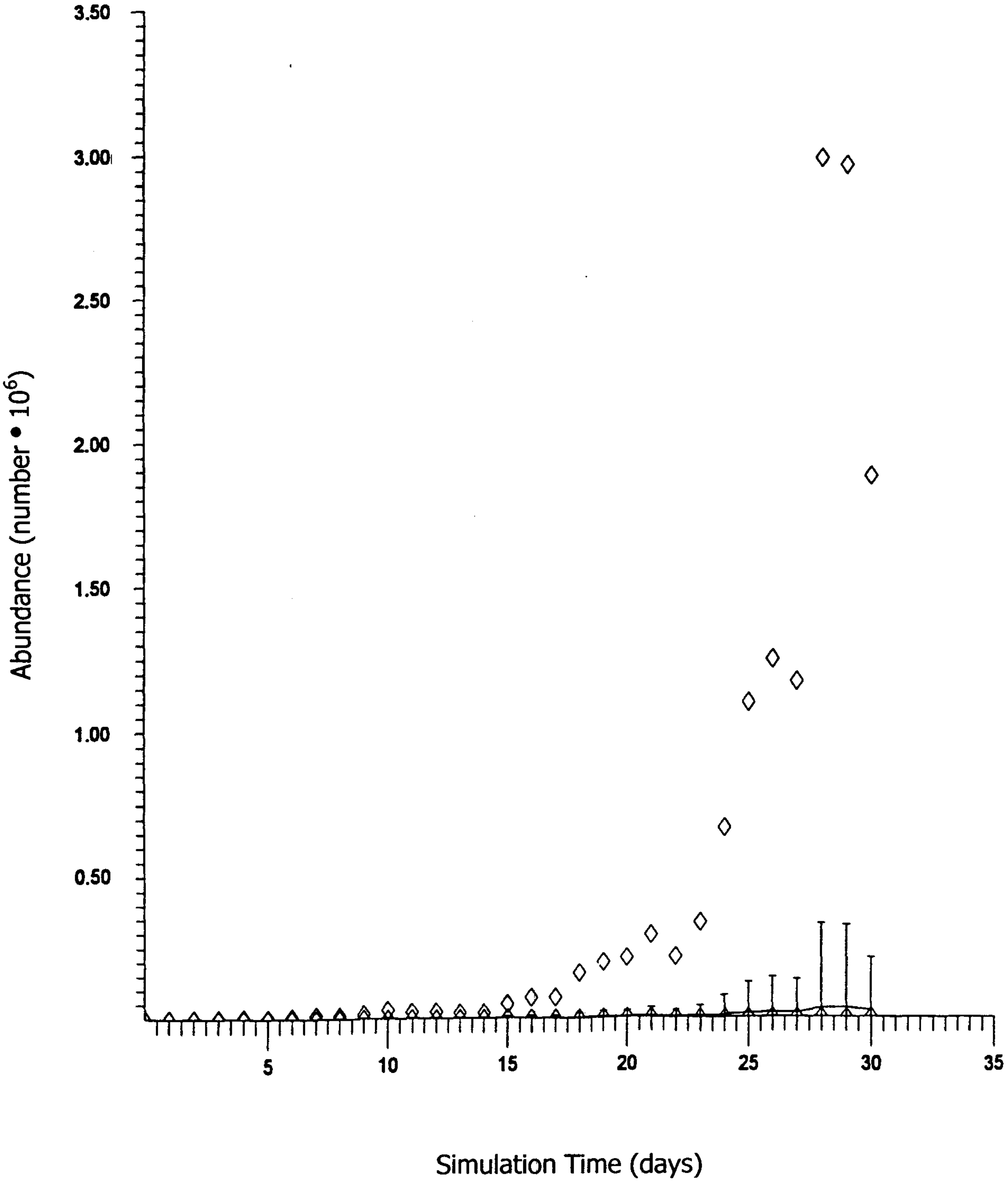

3.50
3.00
2.50
2.00
1.50
1.00
0.50
Abundance (number • 10^6)
5
10
15
20
25
30
35
Simulation Time (days)

Figure 2.

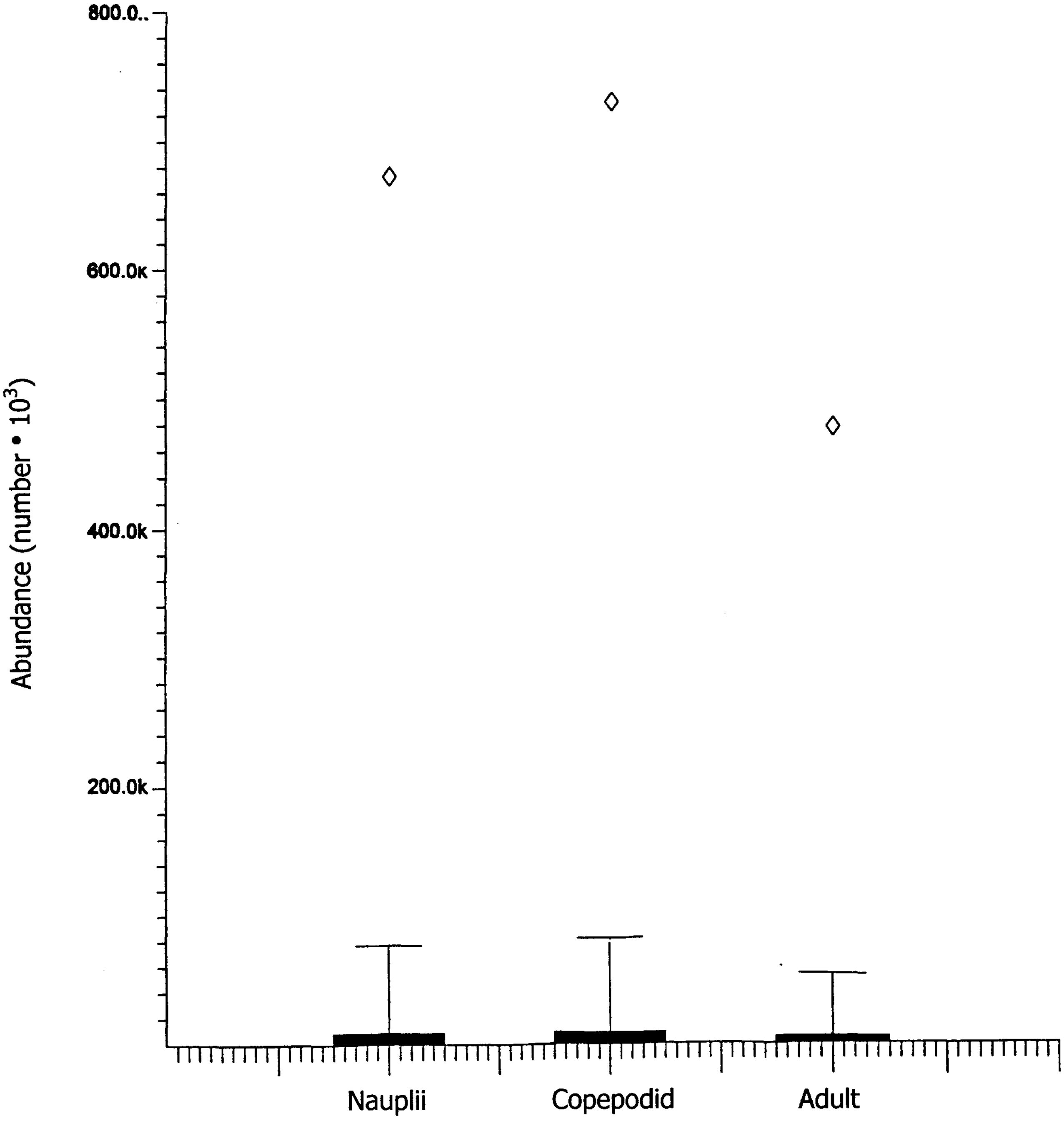

800.0..
600.0K
400.0k
200.0k
Abundance (number • 10^3)
Nauplii
Copepodid
Adult

Figure 3.

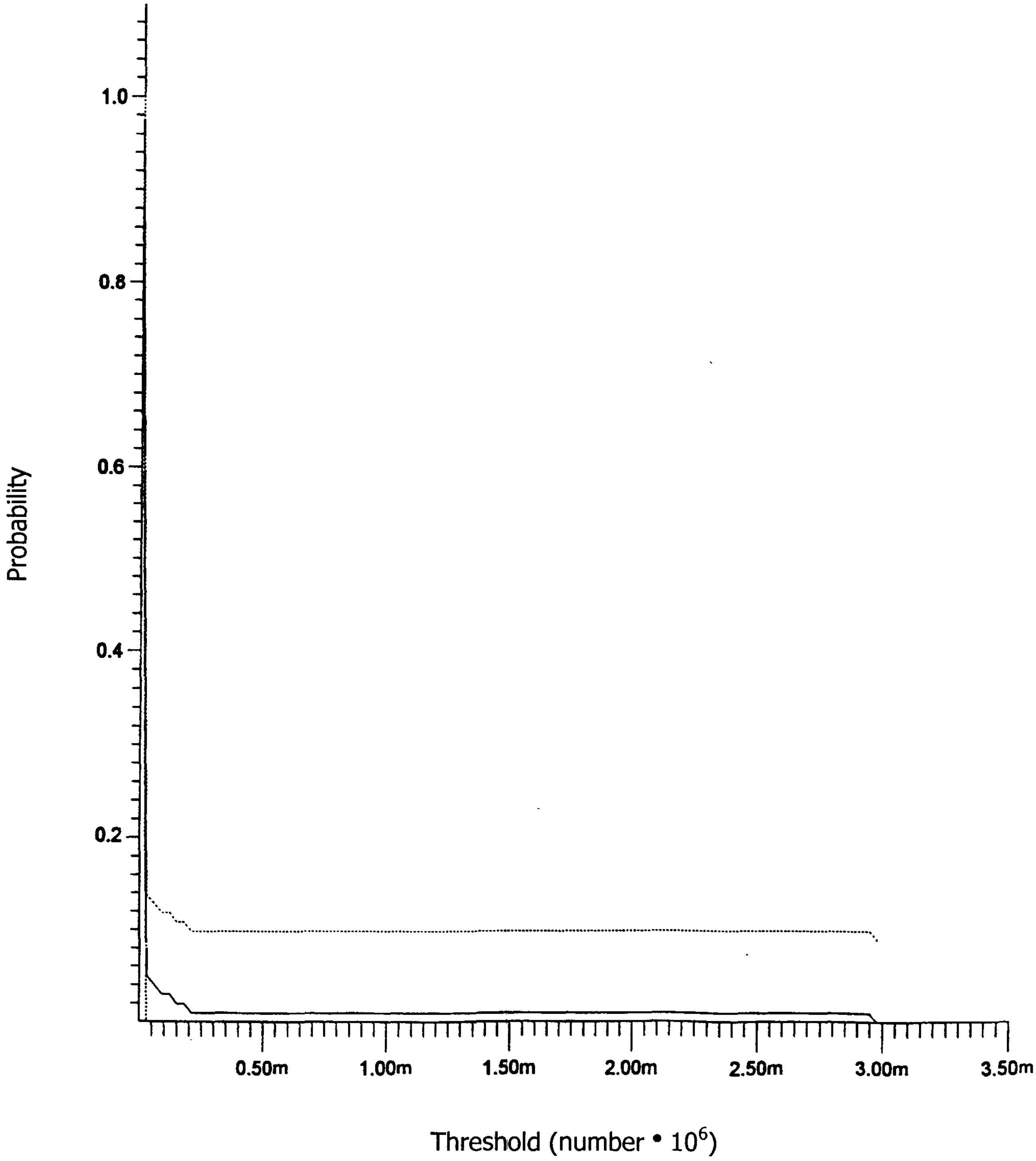
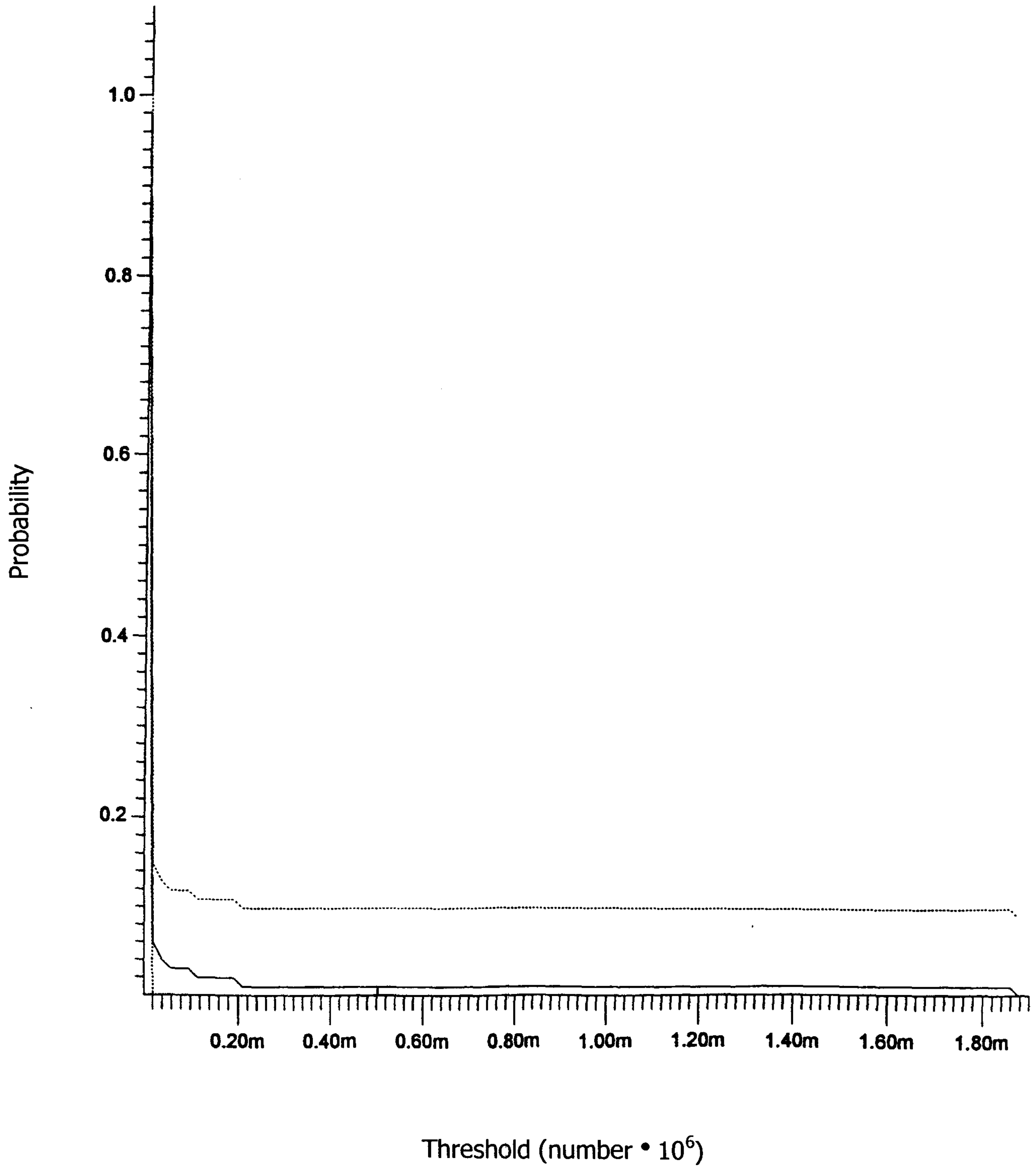

1.0
0.8
0.6
0.4
0.2
Probability
0.50m
1.00m
1.50m
2.00m
2.50m
3.00m
3.50m
Threshold (number • 10^6)

Figure 4.


Probability
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0.8
0.6
0.4
0.2
0.20m
0.40m
0.60m
0.80m
1.00m
1.20m
1.40m
1.60m
1.80m
Threshold (number • 10^6)

Figure 5.

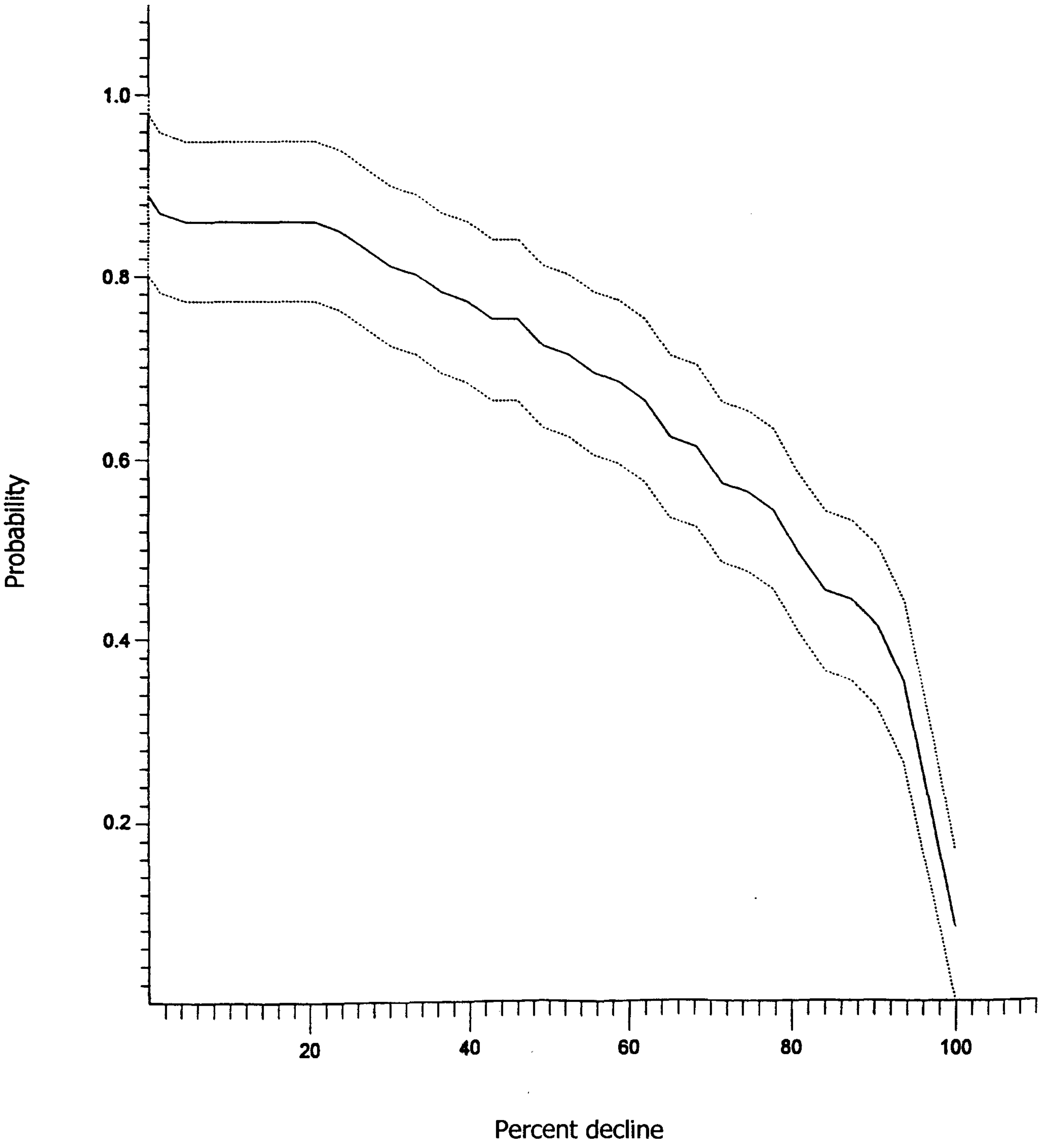

Figure 6.

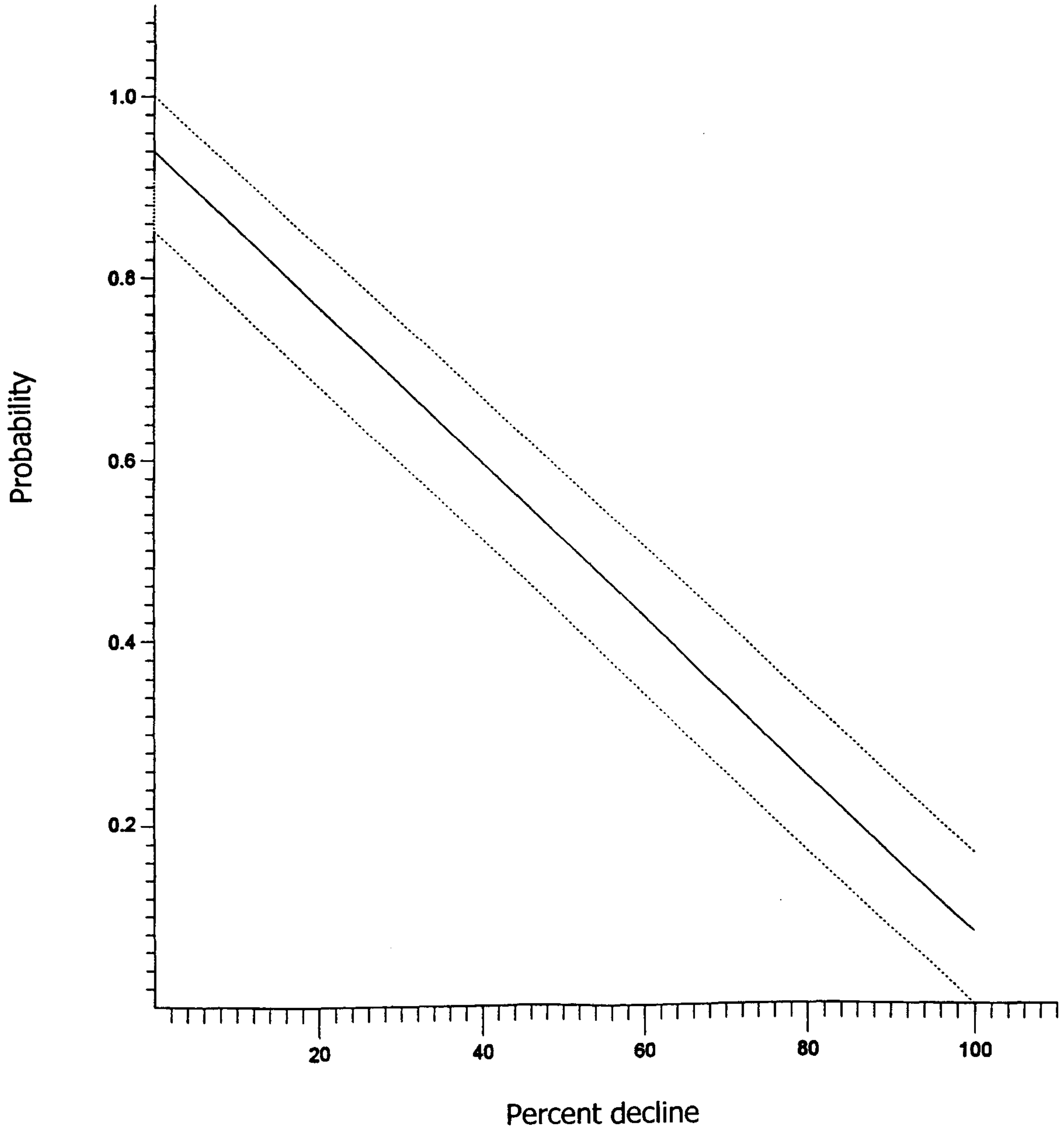

Figure 7.

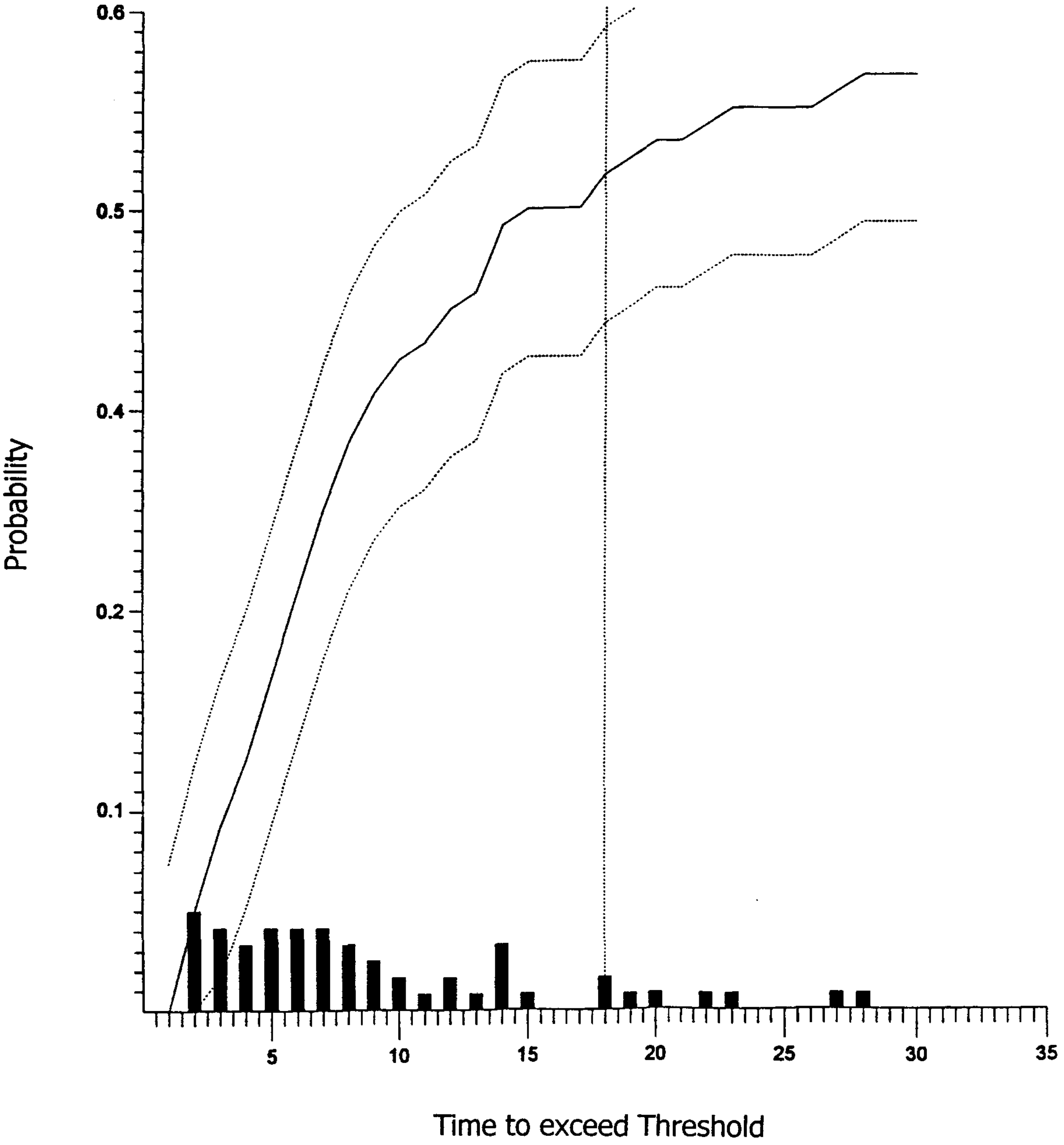
0.6
0.5
0.4
0.2
0.1
Probability
5
10
15
20
25
30
35
Time to exceed Threshold

Figure 8.