To the Graduate Council

I am submitting herewith a dissertation written by Lee Hooi Ling entitled "Use of a Spatially Explicit Model to study the distributional dynamics of Unionid mussels." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for degree of Doctor of Philosophy, with a major in Ecology.

Donald L. DeAngelis, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

USE OF A SPATIALLY EXPLICIT MODEL TO STUDY THE DISTRIBUTIONAL DYNAMICS OF UNIONID MUSSELS

A Dissertation
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Degree
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Abstract

The United States has one of the richest and most diverse communities of freshwater mussels in the world. However, since early in this century, anthropogenic activities have had negative impacts on mussel communities. Destruction of natural habitats and reduction in number of fish hosts are some of the more severe effects of man's actions. This has resulted in many species of mussels presently being on the brink of extinction.

For my research purposes, I developed a computer model to test hypotheses concerning the diversity and spatial distribution of the Unionid mussels. The model is a generalized Leslie matrix model formulated for 35 different species with 15 age classes per species. In the model, each species of mussel is parameterized individually with regard to its characteristics and environmental sensitivities. The computer model uses a parallel computing approach and is designed to run on the MasPar MP-2.

Results from simulation runs of the computer model suggest that mussels propagate into new habitats in the form of a traveling wave front. Furthermore, a correlation was discovered linking the speed of the traveling wave front to mussels' characteristics and habitat.

I examined also the role of fish hosts in the spatial distribution of mussels in light of the core-satellite

hypothesis. In addition, the characteristics of different mussel communities were investigated to uncover the mechanisms involved in producing a bimodal core-satellite species distribution of mussels.

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PART I

INTRODUCTION TO THE UNIONIDS

General introduction to Molluscs

The Mollusc phylum is one of the oldest and largest in the animal kingdom. The earliest molluscs first evolved more then 550 million years ago during the Cambrian period (Vermeij, 1993). The first molluscs were marine animals, as all Cambrian life was marine in nature. Since that time, evolutionary changes have occurred to produce marine, non-marine and terrestrial molluscs. The phylum mollusca is divided into 8 distinct classes:

1. Polyplacophora (chitons)
2. Apalacophora (wormlike animals)
3. Monoplacophora (a mixed group of primitive univalve molluscs)
4. Gastropoda (snails - univalves)
5. Cephalopoda (squids, cuttlefishes and octopuses - no external shell)
6. Pelecypoda/Bivalvia (mussels, clams and oysters - bivalves)
7. Scarphopoda (animals with tubular shell)
8. Rostroconchia (lived between 250-500 million years ago during the Paleozoic period, presently extinct).

Gastropoda, Cephalopoda and Bivalvia are the three largest classes in the phylum mollusca. Gastropoda, with more

than 74,000 species, is the most diverse class (Russell-Hunter, 1983), and are found in all three types of environments. Gastropods are also the only successful land molluscs.

In comparison, the Cephalopoda are all marine animals. However they include the molluscs with the largest body size, ranging in length from 2 cm to more then 10 m for giant squids. There are presently 550 living species and 7000 known extinct species (Russell-Hunter, 1983).

In contrast, the Bivalvia has 31,000 species and are the most numerically abundant (Russell-Hunter, 1983). The majority of the Bivalvia are marine species, but three successful freshwater superfamilies have evolved: Unionacea, Corbiculacea and Dreissenacea. The Bivalvia are generally filter-feeders, except for a few highly specialized deep sea species which prey on small crustaceans (Vermeij, 1993). All of these animals have a soft body enclosed on each side by a hard calcareous shell/valve. The valves are joined in the center by an elastic ligament which controls the opening and closing of the valves. Figure 1.1 shows an external and internal view of a typical valve. Although the Bivalves are sedentary animals, their widespread spatial distribution and numerical abundance has led Goldberg (1975) to propose them as indicator organisms in a global environmental monitoring program known as the "Mussel Watch" program.

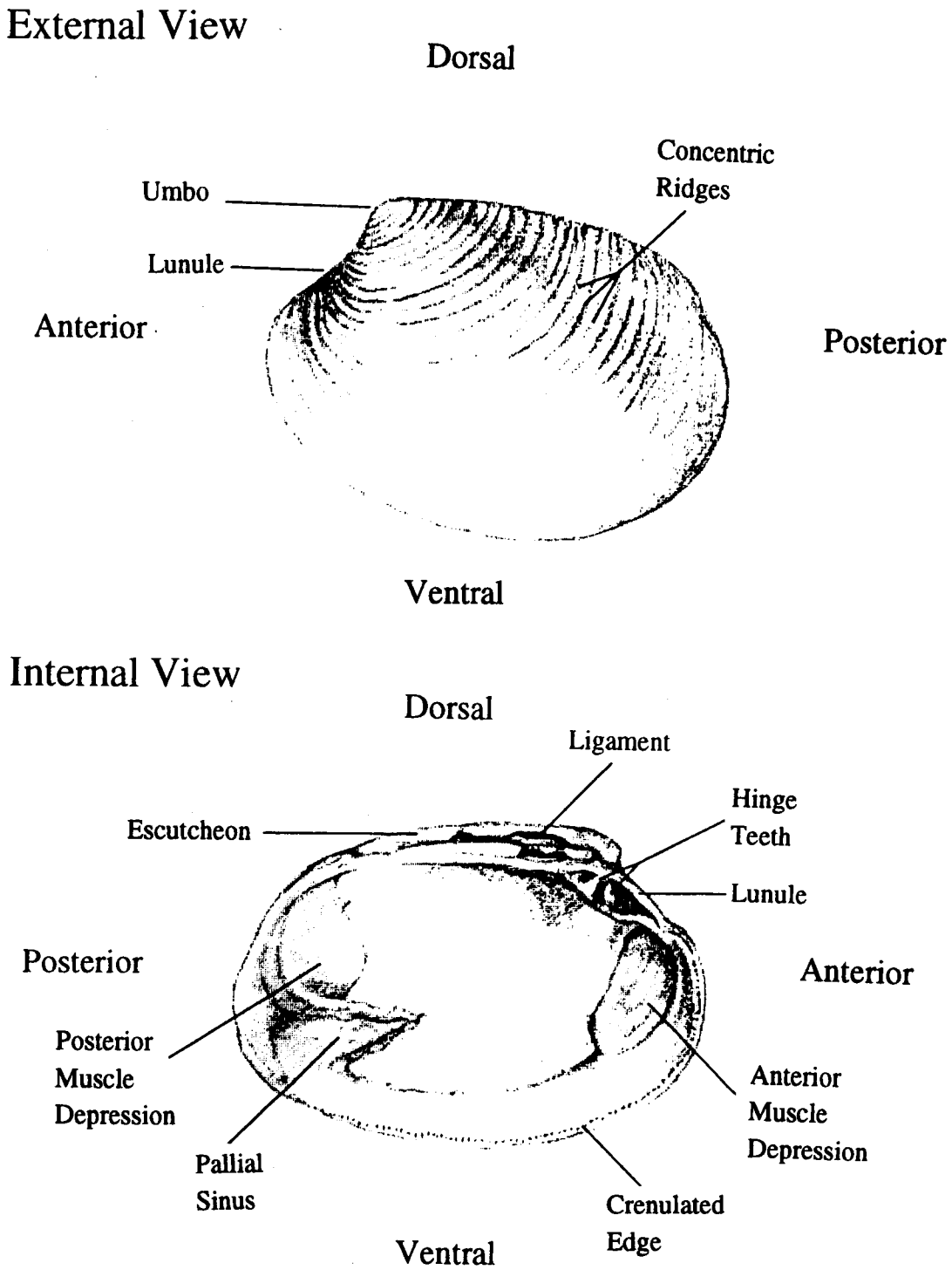

Figure 1.1. External and internal views of a typical valve.

Assumption of numerical abundance for freshwater mussels, however, is not accurate for all species. While the Asiatic Clam (Corbicula fluminea) and the Zebra Mussel (Dreissena polymorpha) have flourished so prolifically as to become pests in many of the major freshwater systems of the world today, the Unionid species on the other hand have steadily degenerated and are now heading slowly towards extinction.

The continent of North America is home to many species of Unionids, and its collection of mussels is unrivaled in terms of species diversity and richness. The malacologists van der Schalies (1950) divided North American mussel distribution into six major zoogeographical regions: the Pacific, Ozarkian, Mississippian, Cumberlandian, Apalachicolan and Atlantic.

This dissertation focuses on the distributional patterns of the Unionid mussels in the Cumberlandian region. The primary research topics are:

1. The temporal distribution patterns of the Unionids.
2. The spatial distribution patterns of the Unionids.
3. The development of a Unionid population computer model.

Description of the Unionids characteristics

The Unionids consist of both dioecious and hermaphroditic species. During the breeding season the male mussel sheds sperm, which are carried by water currents to the gill marsupia of the female for fertilization and incubation purposes. The breeding season varies from early spring to

fall depending on the species. Environmental parameters, especially temperature, prompt the mussels to start the breeding season. A drop of 5°C in temperature from 27°C To 22°C will stimulate the release of sperm in the male (Edgar, 1965). However, a sudden drop in temperature in "pregnant" females can cause abortion of the egg mass (Matterson, 1948).

The fertilized ova is often subjected to attacks by bacteria and protozoans while being incubated in the marsupium (Fuller, 1974). Ellis (1929) has observed that these attacks can cause a high degree of mortality among larvae. Despite that, the mussels still manage to release larvae in the millions after the incubation period (Merrick, 1930). The larvae are called glochidia and have a parasitic relationship with some species of fishes.

Upon release from the marsupium, glochidia are suspended in water by a lacework of mucous (Matterson, 1955; Yokley, 1972), awaiting contact with appropriate fish hosts. Glochidia of some species of mussels can remain alive as plankters up to 11 days (Murphy, 1942). Unfortunately, the majority will not succeed in finding a fish host and will instead fall prey to fish and other animals (Chamberlain, 1934). For those that do succeed in infecting an appropriate fish host, encystment will occur on the fish host for the duration of their development period. With completion of development, the glochidia will drop from the fish host to begin life as free living juvenile mussels. Conditions in the

habitat the juvenile mussels fall into will determine their survival rate. Juvenile mussels usually prefer yielding but firm and stable substrates (Negus, 1966) into which they can burrow. Different species of mussels have different preferences with regard to fish host species.

This parasitic link of mussels to fish hosts is unique to the Unionacea group of mussels and functions as an excellent dispersal mechanism. Unfortunately, this link is also tenuous at best and is easily disrupted by anthropogenic activities or natural changes in the environment. The fish host species of choice for many species of mussels are often those species distinguished as "trash fish" by fishermen. For example, the Gizzard Shard is the host fish of at least 4 species of mussels (Fuller, 1974). When attempts were made to eradicate the Gizzard Shards, the mussels were unwittingly endangered instead. Thus an improvement of the fish fauna from the fisherman's perspective is not necessarily an improvement of conditions for mussels. Furthermore, repeated glochidial infestation can induce immunity in the fish hosts to the glochidia itself (Arey, 1932). Some species of fish, after being infected by Copepods, become immune to glochidia infestation and vice versa (Cope, 1959; Wilson, 1916).

Similar to predation pressures faced by glochidia, adult mussels are also subjected to predation by a variety of fish species, such as Catfish (Kendall, 1910) and Freshwater Drum. Nonetheless, fishes that prey on adult mussels are often the

fish hosts of glochidia. To illustrate this point, consider the Freshwater Drum, which feeds almost exclusively on mussels (Forbes and Richardson, 1908) and is itself host to 11 species of glochidia (Fuller, 1974). In addition to fishes, other aquatic animals such as leeches and aquatic earthworms also prey on adult mussels. Water mites, depending on species and stage of life, can have either a parasitic or a commensalistic relationship with the mussels. Other mussel predators include small mammals such as otters, muskrats, raccoons, minks and waterfowls.

However, the greatest threat to mussels in the Tennessee river system is from anthropogenic activities along the river. The building of dams in the Tennessee river system has deprived mussels of many of their fish hosts. The reservoirs formed by dams have also destroyed many mussel beds by drowning/suffocating them. Isom (1971) estimated the loss of 60 species of mussels due to periodic oxygen sag from the creation of Fort Loudon Reservoir. Siltation and extreme changes in temperature from the release of hypolimnion waters are some of the other dangers the dams pose to the mussel communities.

The other major impact is the increased level of pollution in mussel habitats from the industrialization of the Tennessee Valley. Heard (1970) noted that pollution from a paper mill on the Fenholloway River in Florida had decimated all flora and fauna up to 15 miles downstream to the Gulf.

Similar effects, but on a smaller scale, have been observed in the Tennessee mussel communities (Orthman, 1918). Last, but not least, is the threat from the shell harvesting industry. This multi-million dollar industry, has in the past, destroyed many mussel communities in the Tennessee river system due to indiscriminate and over harvesting. In addition to the outright removal of animals, this activity also carries profound secondary effects, such as the depreciation of breeding stock, abortion in gravid females due to disturbances in their environment (J. F. Boepple in Simpson, 1899) and death of many adult mussels which cannot rebury themselves after being needlessly uprooted (Imlay, 1972).

Overview of the dissertation

The following four parts in the dissertation are designed as four complete individual papers which can stand by themselves. In parts 2 and 3, I examine the influence of various mussel characteristics, such as fecundity rate and maximum life span, on the spread of mussel populations through time. I also incorporate into those two papers the effects of habitat varieties and their relative sizes on the mussel communities. From my research, I discovered that mussels tend to propagate into new habitats in the form of a traveling wave front and the speed of the traveling wave front has a direct correlation with habitat sizes and environmental conditions.

Part 4 focuses on the effects of fish host movement range sizes on the mussel populations. Here, I investigate the characteristics and species that make up a metapopulation and relate them to the Core-Satellite species hypothesis proposed by Ilkka Hanski.

For all my studies, I developed a mussel population computer model to assess the impact of the various effects on the mussels. The computer model is written in FORTRAN 90, using a parallel algorithm approach. In part 5, I review the parallel algorithm and compare its performance to a similar sequential algorithm. My computer model uses an age-structured approach based on the generalized Leslie matrix to model mussel populations. I chose the age-structured approach to ensure that the methodology used in the computer model to assess mussel populations is conceptually similar to the method most often used in field surveys of mussel populations.

Growth of mussels in the field is usually assessed by one of the following methods:

1. Using a mean or modal size-frequency distribution.
2. Measuring marked mussels periodically.
3. Counting annual disturbance rings on the mussel's shell.

Method 1 is most widely used, as the size-frequency distribution of most bivalves is usually polymodal (Seed, 1976), with each size representing an individual year. By approximating the age of a mussel by its size as in method 1, it is assumed that the individual growth rates within each

year are fairly uniform for the mussels concerned. Likewise in the age-structured computer model, it is assumed there is uniform growth for the mussels within an age-class.

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PART II

A SIMULATION STUDY OF THE SPATIO-TEMPORAL DYNAMICS OF THE UNIONID MUSSELS

Introduction

Freshwater mussel populations (Phylum: *Mollusca*), which spread and thrived throughout the freshwater systems of North America since the last ice-age, have steadily declined in size for the past hundred years. Anthropogenic activities and competition from non-native species of freshwater mussels are threatening the survival and existence of many species of the native freshwater mussels, especially those of the *Unionidae* family (Stansbery and Clench, 1974; Bates and Dennis, 1978; Ahlstedt, 1984).

While many studies regarding the Unionid mussels have been conducted, they have focused primarily on the physiology of the Unionids. In this paper, a study of the potential spatial-temporal dynamics of a Unionid population is performed through computer simulations. This includes a description of the spread and formation of new populations, as well as recolonization of habitats where local populations have gone to extinction. The computer model that is used incorporates many qualitative characteristics of the Unionids and their natural environment as well as parameterization by field data.

Studies on the movement of the Crown-of-thorns outbreaks on the Great Barrier Reef (Van Der Laan and Hogeway, 1992) and Asiatic Clam (*Corbicula fluminea*) invasion of North America (Pojeta, 1964; Eckblad, 1975; Clarke, 1981; Counts, 1981) have shown that these organisms and many others tend to move spatially and temporally as traveling wave fronts. Murray, (1989) describes a traveling wave to be "a wave which travels without any change of shape and the speed of the propagation of this shape is a constant". The mode of dispersal of Unionid mussels leads one to expect that the dispersal of Unionid mussels into currently unoccupied habitat might take the form of a traveling wave front. If this colonization or recolonization of habitat by mussels can be described by a traveling wave front, then from the theory of these wave fronts, the speed of movement can be related in a simple manner to the intrinsic growth rate of the population in the habitat and a coefficient of diffusion representing the spatial spread. This wave front speed would be a convenient index of the population's ability to maintain itself in rivers and streams despite a disturbance regime that caused frequent local population extinctions. Thus it would be a measure of the efficiency of the "rescue effect" (Brown and Kodric-Brown, 1977) that can be important in maintaining metapopulations.

The first objective of this study was to develop a realistic simulation model of a Unionid mussel population in a stream or river. Then the model's implications for the

spread of the population into unoccupied habitat were examined to see if wave front-like behavior resulted. Next, the relationships between wave front speed and parameters of the mussel life cycle and its interaction with its environment were studied. Finally, the wave front speed was examined in heterogeneous environments in which favorable and unfavorable mussel habitats alternated along a stream.

Life-cycle of the Unionids

There are approximately thirty-five extant species of Unionids in the United States, with most species located in the south-eastern region (Dennis, 1984). The Unionids prefer well-oxygenated shallow water habitats with stable coarse sand or sand-gravel mixture beds (Stone et al., 1982; Salmon and Green, 1983; Cooper, 1984; Machena and Kautsky, 1988; Way et al. 1990). The mussels have life-spans ranging from nine years up to ninety years (Stein, 1971; Lewandowski and Stanczykowska, 1975; Burky, 1983; Jirka, 1986). The onset of sexual maturity occurs anywhere from one year to as late as six years depending on the species (Pennak, 1953; Burky, 1983; McMahon, 1991). Environmental parameters and neurosecretory controls trigger the start of the breeding season, normally in spring or early summer.

Fertilization and incubation of the fertilized eggs take place in the gill marsupia of the female mussels. The fecundity and incubation period of the mussels are species-

dependent. Fecundity rate ranges from 200,000-17,000,000 glochidia/female mussel/breeding season (Young and Williams, 1984; Paterson and Cameron, 1985; Parker et al., 1984). The glochidia are the obligate parasitic larval stage of the mussels. The glochidia, upon release by the female mussels, attach themselves to suitable fish hosts before dropping off to settle on the substrate after completion of their development into juveniles.

Despite the large number of glochidia released, few find suitable fish hosts and even fewer survive to the juvenile stage. The juvenile and adult mussels are generally sessile. Figure 2.1 shows the life-cycle of the Unionids. When this simplified outline of the Unionid mussel life cycle is filled out with quantitative values for parameters, plus quantitative information on habitat favorability and the movements of fish hosts, a spatially explicit, age-structure population model can be formulated.

A description of the computer model

The computer model used in this study is based upon the Roughgarden et al.(1985) concept of a single-species, open marine population with space-limited recruitment. Due to the unique life-cycle of the Unionids and their riverine environment, it was necessary to generalize or alter Roughgarden et al.'s original concept in several ways to mimic reality as closely as possible. The present model allows the

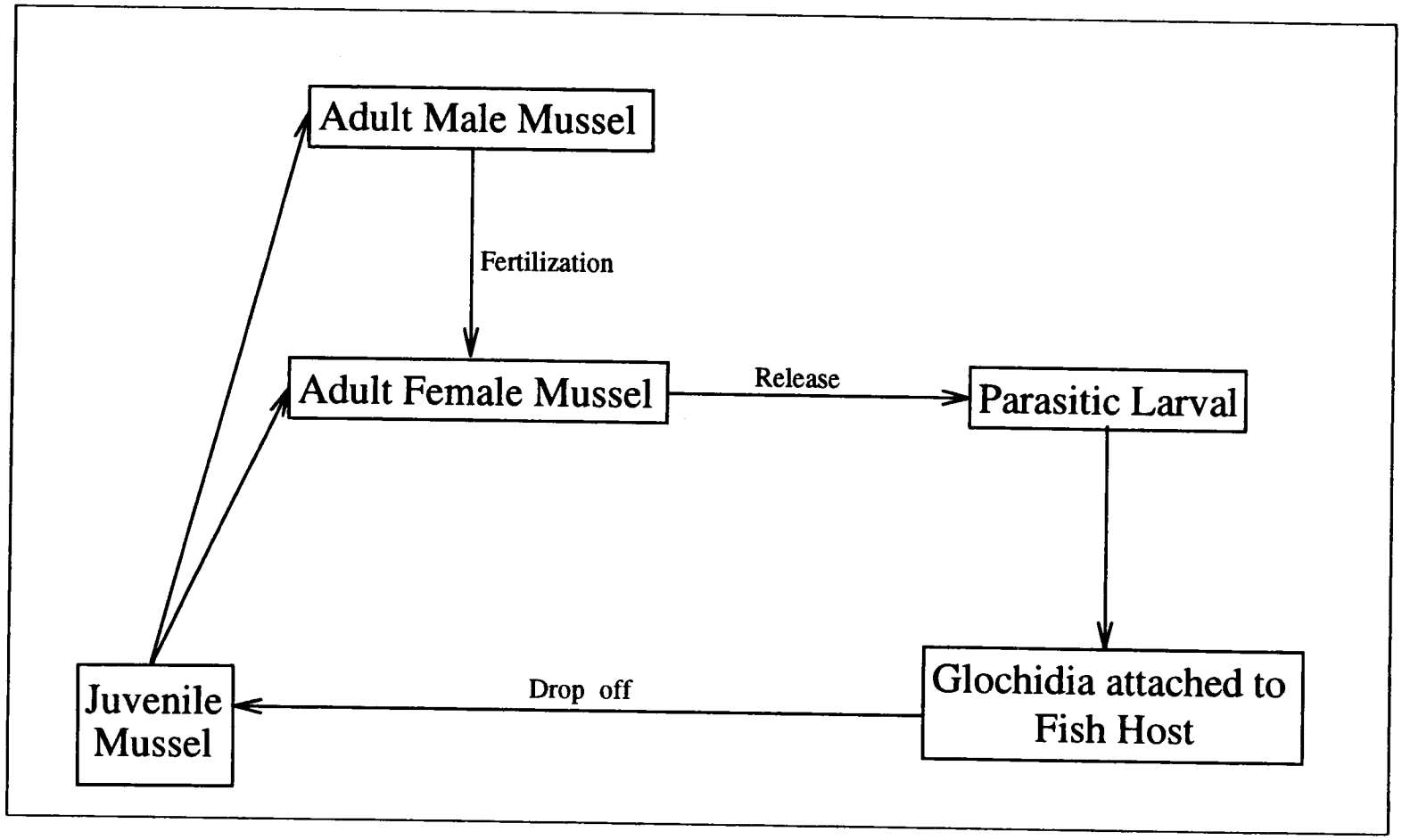

Figure 2.1. Life-cycle of the Unionids.

inclusion of many different species up to a maximum of thirty-five compared to only one in Roughgarden et al.'s model. Another feature is the use of multiple spatial cells, which interact during the dispersal period of the glochidia, as opposed to only a single spatial cell in the original model. A cell in the model is conceptually an area in the river that is internally uniform in properties affecting the mussels. Hence, a given stretch of river can be divided into as many different sized cells as needed, as shown in Figure 2.2. Each cell has its own suitability rating as a habitat for the Unionids. While Roughgarden et al.'s (1985) model assumed that at any particular time there exist a very large number of larvae in the water, the present model assumes that glochidia are only in the water for a fixed time period and the number of glochidia is directly dependent on the existing adult mussel and fish host populations.

Because the rate of spread of an organism that is mobile only in its early life history is clearly going to depend on features of its life history such as age of maturity, an age class model was used to describe the mussel population. The model has up to a maximum of fifteen different age classes for each species of mussel in each cell. It is assumed there is an abundance of food resource for the mussel community. Hence, the physiological growth of the mussels is described by a deterministic function form that can be parameterized for each species. The model describes the growth of a mussel by

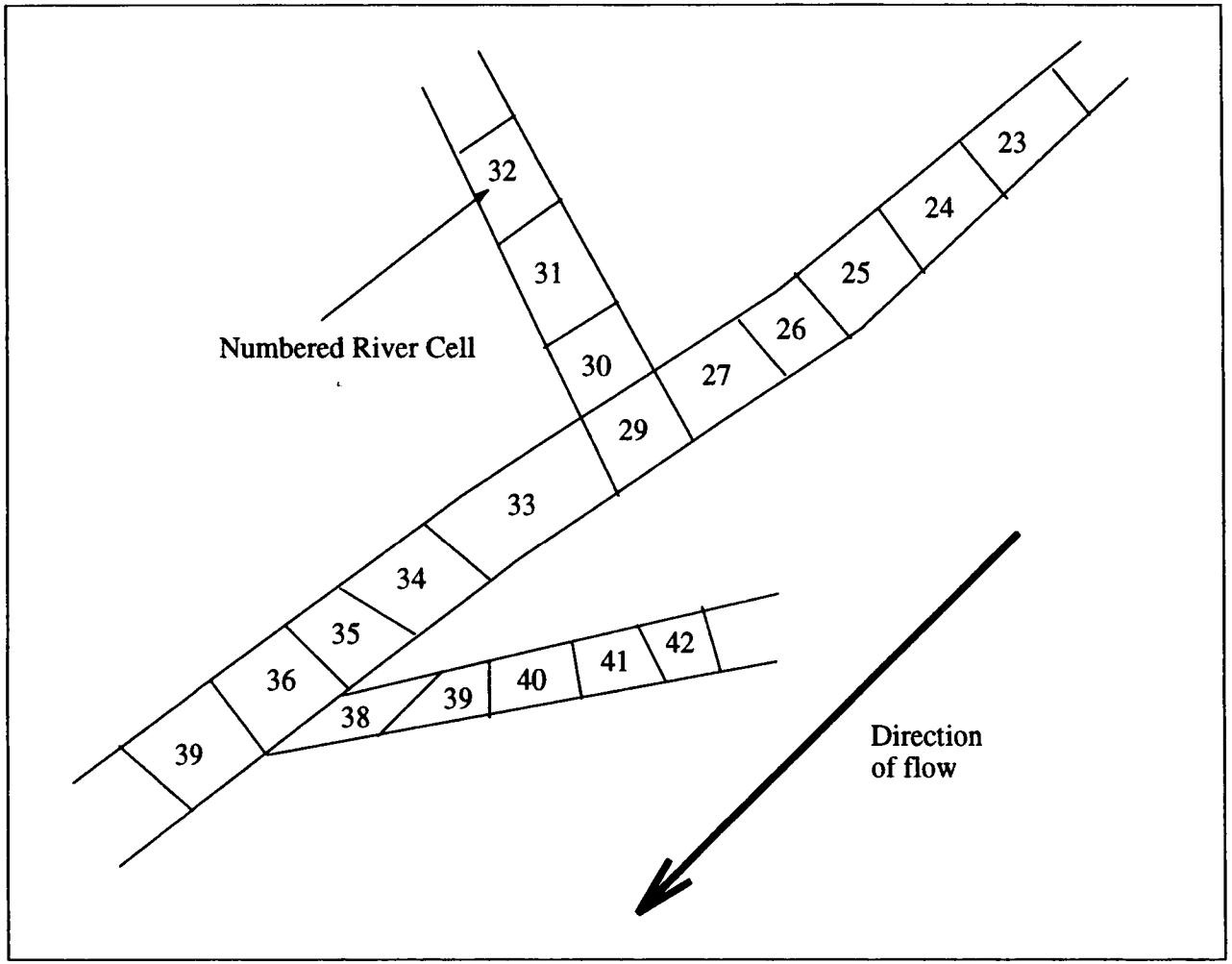

Figure 2.2. Segmentation of a hypothetical river.

relating the size of the whole organism deterministically to its age.

Studies by Coe and Fox (1942), Stubbings (1954), Savage (1956), Seed (1969) and Meaney (1970) on the *Mytilus* mussels have shown that increasing age is accompanied by a decline in growth rate. For convenience and flexibility, in the model there exist three different stages of growth, each with its own growth rate for each species of mussel as shown in Figure 2.3. The growth functions are:-

Stage 1: $$S_j^i = 0.990 MS^i \frac{A_j^i}{MA^i} + 0.001 MS^i$$

Stage 2: $$S_j^i = 4.000 MS^i \frac{A_j^i}{MA^i} - 0.300 MS^i$$

Stage 3: $$S_j^i = 0.143 MS^i \frac{A_j^i}{MA^i} + 0.857 MS^i$$

where

S_j^i = Size of species i mussel in cell j (m^2)

MS^i = Maximum size of the species i mussel (m^2)

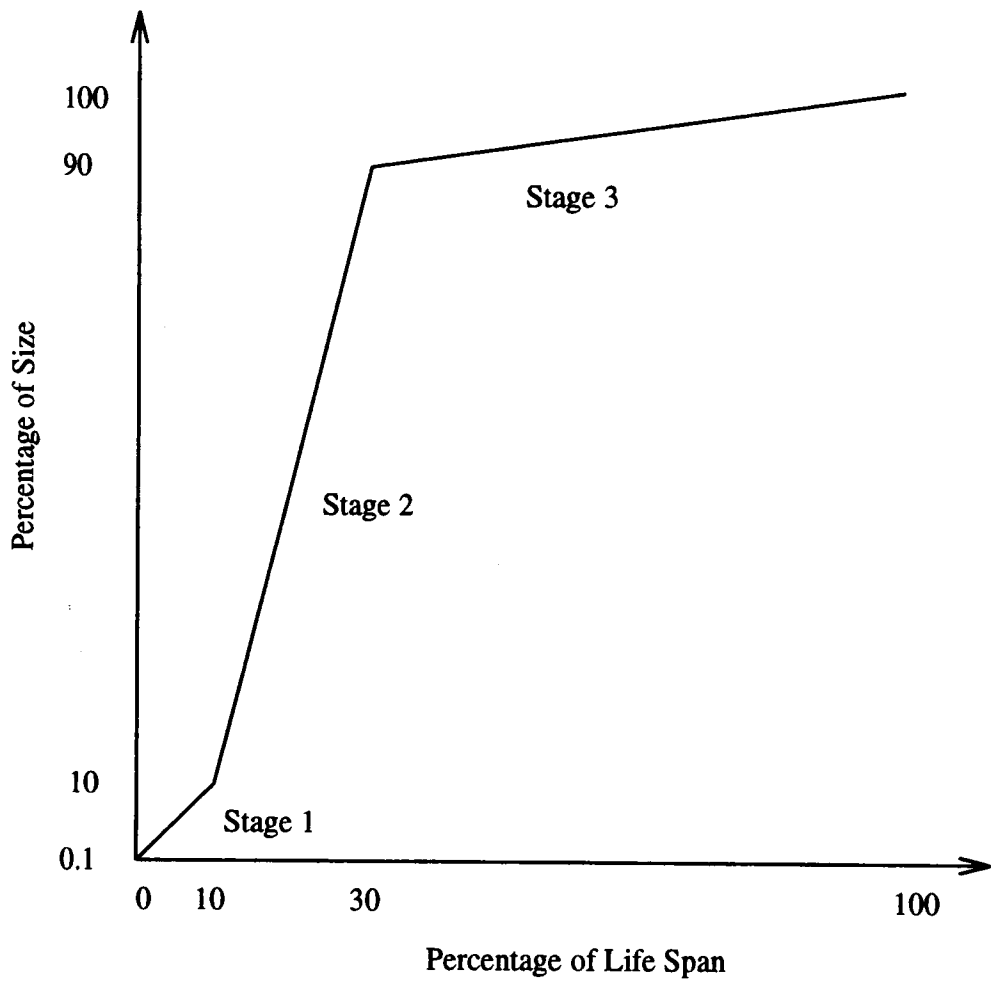

Figure 2.3. Graph of growth functions.

A_j^i = Age of species i mussel in cell j(days) and

MA^i = Maximum life span of species i mussel (days).

The first growth function represents the initially slow rate of growth of the juvenile mussels. The second equation shows the extremely fast rate of growth of the juveniles until maturity that follows the initial stage. The third and final equation represents the steady rate of growth of the mussels after maturity.

The probability of survival from one age class to another is a function of the mussel's species, age and its immediate environment. The probability of survival function is:-

$$PSURV_j^i(A_j^i) = \left[\frac{A_j^i - 0.1MA^i}{0.6MA^i}(PMAX^i - PMIN^i) + PMIN^i\right]\left[1.0 - \exp^{-M^i\left(\frac{F_j}{TA_j}\right)}\right]$$

where

$PSURV_j^i$ = Probability of survival of species i mussel of age A_j^i in cell j

$PMAX^i$ = Maximum probability of survival of species i mussel

$PMIN^i$ = Minimum probability of survival of species i mussel

M^i = Space-dependent survival coefficient of species i mussel

F_j = Free space available in cell j (m^2)

TA_j = Total bed area in cell j (m^2) and

A_j^i and MA^i are as defined before.

The function describing probability of survival is a revised version of the equation used in Roughgarden et al.'s model for sessile marine organisms. The survival function assumed that the probability of survival increases with age for all species of mussels. But each species of mussel has its own individual maximum and minimum probability of survival, which incorporates mortality risk from the surrounding environment due to predation, inter- and intra-specific competition and other factors. In addition, it is assumed that mortality increases when the amount of free space decreases, a situation that can arise with the invasion of a fast growing invading non-native species of mussel, such as the Asiatic Clam (*Corbicula fluminea*). But because the present Unionid mussel populations modeled here tend to be far less dense than the marine populations modeled by Roughgarden et al. (1985), the effect of density dependence as a limiting constraint on the population size is less pronounced in the freshwater mussel community than in the case of the marine population.

Reproduction begins when sexual maturity is reached and occurs at the same time each year. The recruitment/settlement of juveniles on a given cell is a function of the availability

of free space in the cell and the suitability of the habitat. Studies by Cherry et al. (1980) and McMahon and Williams (1986a, 1986b) have shown that adult population of *Corbicula fluminea* has an inhibitory effect on successful juvenile settlement and this might be also true for the Unionids. Hence, the fecundity function is:-

$$JM^{i}_{kj} = 0.1 AM^{i}_{k} B^{i} \frac{F_j}{TA_j}$$

where

JM^{i}_{kj} = Total number of species i juveniles produced by species i mussels from cell k settling in cell j

AM^{i}_{k} = Total number of species i sexually mature mussels in cell k

B^{i} = Fecundity coefficient of species i mussel and

F_j and TA_j are as defined before.

Dispersal of glochidia occurs through the movements of the fish hosts. The fish hosts are not modeled explicitly. Instead it is assumed based on literature data (Fuller, 1974; Kat and Davis, 1984; Bauer et al., 1991; McMahon, 1991; Weaver et al., 1991; Jirka and Neves, 1992) that a certain fraction of glochidia successfully find fish hosts and are carried, with equal probability in the upstream or downstream

direction. The distance of transport for a given individual is chosen randomly from a normal distribution. After the glochidia are released they are assumed to be juvenile mussels.

Computer simulations

Computer simulations of the model were performed by starting with small, spatially localized mussel populations in a river system of similar cells to determine if the population spread resembled a traveling wave front. The example displayed in Figure 2.4 shows that as the mussels colonizes new downstream habitats, the spread of the mussel populations has the general appearance of a traveling wave front.

Further computer simulations were performed to determine the correlations between velocity of the traveling wave and (A)rate of attachment of glochidia to host fish and their survivorship, (B)age of maturity, and (C)size of the segments of unsuitable habitat between segments of suitable habitat. The computer simulations were grouped into sets designated by A, B, and C, where each set of computer simulations tested only one of the above mentioned parameters. To determine patterns despite the stochasticity occurring in each simulation, each parameter being tested was repeated in at least 5 replicate computer runs, where all parameters were identical except for the initial random number seed. Hence each set of computer simulations was made up of at least 20

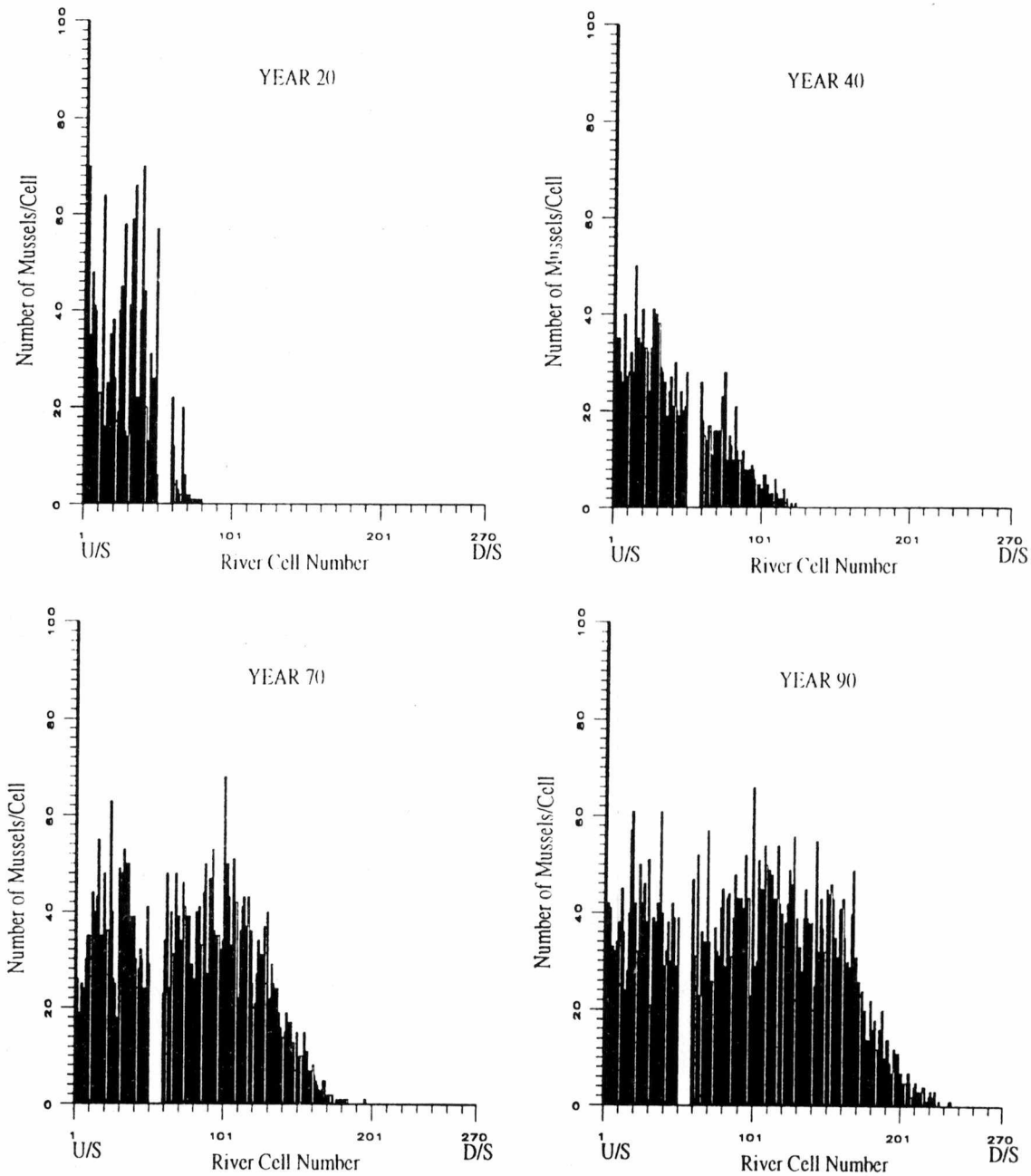

Figure 2.4. Propagation of a wave front. Each cell is 500 m by 500 m and U/S is upstream and D/S is downstream.

individual runs, each with its own initial random number seed to test four different values of a parameter. To simplify the modeling exercise, a hypothetical stretch of river of length 135km with no tributaries was divided into 270 consecutive 500m X 500m cells. Cells 1 and 270 are the extreme upstream and downstream cells respectively. Five cells from cell 1 to cell 50 were chosen randomly and seeded with a small initial population of mussels of mixed age class. All the cells were rated as suitable habitat except for the interval segment from cell 51 to cell 60.

The effect of different rates of attachment of released glochidia to fish host was tested in simulation set A by varying it from 300 glochidia/female mussel to 1200 glochidia/female mussel for the runs. The varying rate of attachment of glochidia to fish hosts in the simulations mimicked the natural conditions of the mussels' environment, where varying numbers of fish hosts can be found. Simulations in set B were performed by varying the life span of the mussels between 10 to 30 years. Because age of maturity is linked allometrically to life span (mussels reach the age of maturity when they attain 1/3 of their maximum life span), this causes the age of maturity to be varied also. In the final set, C, the size of the unsuitable environment was varied from 5km to 20km.

Results from each run are plotted individually as shown in Figure 2.5. To lessen the effects of stochasticity, the

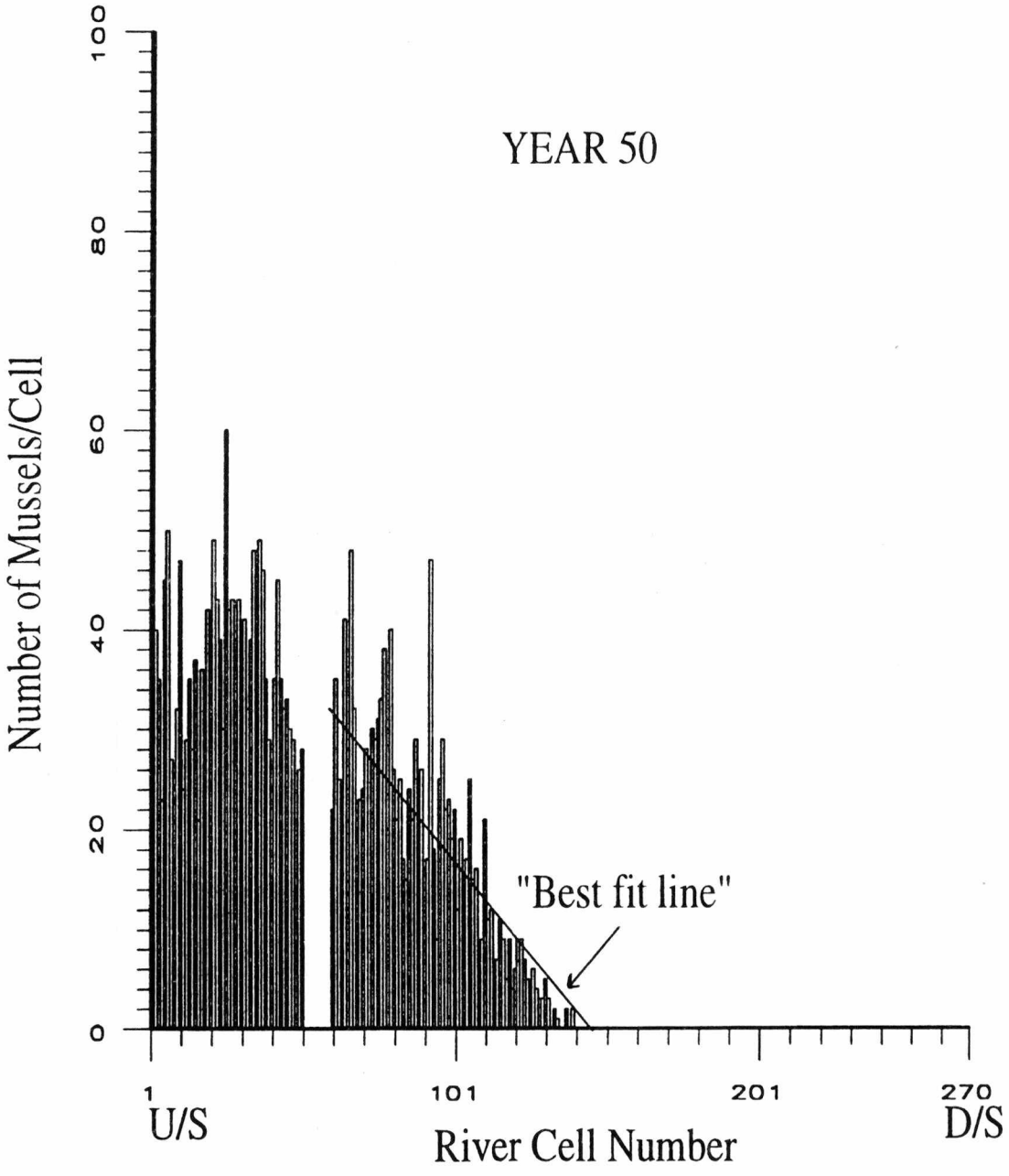

Figure 2.5. Spatial distribution of mussels from simulation set A. U/S is upstream and D/S is downstream.

total number of mussels counted in each cell excluded mussels of age class-1 where variability in number is much greater than in other age classes. The velocity of the wave front was calculated in three different ways using the plots as shown below:-

Method 1 :-

$$V = \frac{Cell\ J_z - Cell\ I_{z-s}}{s} \left(500m\ X\ \frac{1km}{1000m}\right)$$

where

V = Velocity of the traveling wave [km/year]

Cell J_z = The cell numbered J furthest in the direction of movement that has mussels at time z

Cell I_{z-s}= The cell numbered I furthest in the direction of movement that has mussels at time z-s

z,s,z-s = Time [years]

Method 2 :-

$$V = \frac{Cell\ JN_z - Cell\ IN_{z-s}}{2s}$$

where

V = Velocity of the traveling wave [km/year]

Cell JN_z = The cell numbered J furthest in the direction of movement that has N number of mussels at time z

Cell IN_{z-s}= The cell numbered I furthest in the direction of movement that has N number of mussels at time z-s

z,s,z-s = Time [years]

Method 3:-

A "best fit line" is drawn as shown in Figure 2.5 and calculation is similar to method 2 except that the cell chosen is based on the line. The "best fit line" is a straight line representing the general position of all data points, a "best fit" to the data.

Results

Table 2.1 shows the result of set A simulations which examined the effects of rate of glochidia attachment on wave front speed. The velocity of the wave front for species 1 and species 2, ranges from 0.87-1.06 km/yr and 2.21-2.47 km/yr respectively. Doubling or tripling the rate of attachment of the glochidia to fish does not appear to affect the velocity of the traveling wave front significantly. This indicates that the velocity of the wave front is not sensitive to the rate of attachment of the glochidia to fish host. Besides that, the values from the three different methods of computing the velocity of the wave also do not differ much.

The results of set B simulations, which examined the effects of age of maturity on wave front velocity, are shown in Table 2.2. The relationship of the velocity of the traveling wave front and the maximum life span of the mussel can be expressed by a significant linear regression of the form

$$y = 2.7279 - 0.8179x$$

Table 2.1. Velocity of the wave front.

	[a]Max. Size [cm^2]	[a]Max. Life span [yr]	[b]Rate of Attach.	[d]Aver. Vel. Meth.1 [km/yr]	[d]Aver. Vel. Meth.2 [km.yr]	[d]Aver. Vel. Meth.3 [km/yr]
[c]S.1	30	30	300	1.00	0.95	0.97
			600	0.99	0.95	0.93
			900	1.06	0.87	0.91
[c]S.2	3	10	300	2.47	2.26	2.28
			900	2.41	2.21	2.23
			1200	2.40	2.41	2.47

[a]Max. = Maximum
[b]Rate = Rate of attachment of glochidia to fish host
[c]S. = Species
[d]Aver.= Average Velocity Method 1, 2 or 3

where y = ln (velocity of the traveling wave; km/yr)

x = ln (maximum life span of the mussel; yr)

and $r^2 = 0.9998$.

Hence, it can be concluded that as the age of maturity of the mussels increases, the velocity of the traveling wave decreases.

In simulation set C, which examined the effects of different sizes of unsuitable habitats on the traveling wave front, cell 1 to cell 50 were randomly seeded initially with a mussel with a maximum life span of 10 years and maximum size of 3 cm^2. The rate of attachment of glochidia to fish host was assumed to be 300 glochidia/female mussel. From cell 51 onwards the river environment included unsuitable habitats as well as suitable habitats. These suitable and unsuitable habitats were alternately arranged to the end of the river, as

Table 2.2. Effects of life-span on velocity of the wave.

Computer Run Number	Max. Life-span of 10 years [km/yr]	Max. Life-span of 20 years [km/yr]	Max. Life-span of 30 years [km/yr]
1	2.4125	1.0166	0.8500
2	2.0875	0.7656	0.8071
3	2.2225	0.8222	0.6875
4	2.6167	1.0389	0.6889
5	2.4250	1.0071	0.5643
6	2.4375	0.8667	0.5444
7	2.5667	1.2125	0.6222
8	2.3900	0.9111	0.5125
9	2.3625	0.9889	0.5813
10	2.3167	1.0389	0.6500
11	2.0875	0.9063	0.5857
12	2.1375	1.0063	0.5813
13	2.4335	0.9889	0.6444
14	2.3250	0.7722	0.5500
15	2.2375	0.8750	0.6250

shown in Figure 2.6. The length of each kind of habitat (l_1 for suitable and l_2 for unsuitable) was fixed for each simulation. A suitable habitat was capable of supporting mussels while an unsuitable habitat was not. Five different combinations of lengths l_1 and l_2 were chosen. For each pair of l_1 and l_2 eight individual simulations were performed.

Figure 2.7 shows graphically the result of one of the simulations for a given year. The results of all the simulations are tabulated in Table 2.3. When the length of both l_1 and l_2 are 5km the velocity of the wave front is 1.72km/yr. Doubling the unsuitable length of l_2 to 10km (l_1=5km) causes the velocity to drop to 1.40km/yr, while increasing the length of l_1 from 5km to 10km and 15km (l_2=5km) causes an almost proportional increase in the velocity, i.e.; 1.94km/yr and 2.11km/yr respectively. However, increasing the length of both l_1 and l_2 from 5km to 10km causes the wave front to slow down from 1.72km/yr to 1.49km/yr. When l_1 is 15km and l_2 is 10km, the velocity of the wave front is 1.50km/yr. Computer runs where l_1 is 5km, 10km, and 15km and where l_2 was equal to 15km were also performed. The preliminary results suggests that the velocity of the wave front is slowed down significantly.

Shigesada et al. (1986) suggested in their paper "Traveling Periodic Waves in Heterogeneous Environments", that the velocity of the traveling wave can be computed by another method that is different from the three methods used in this

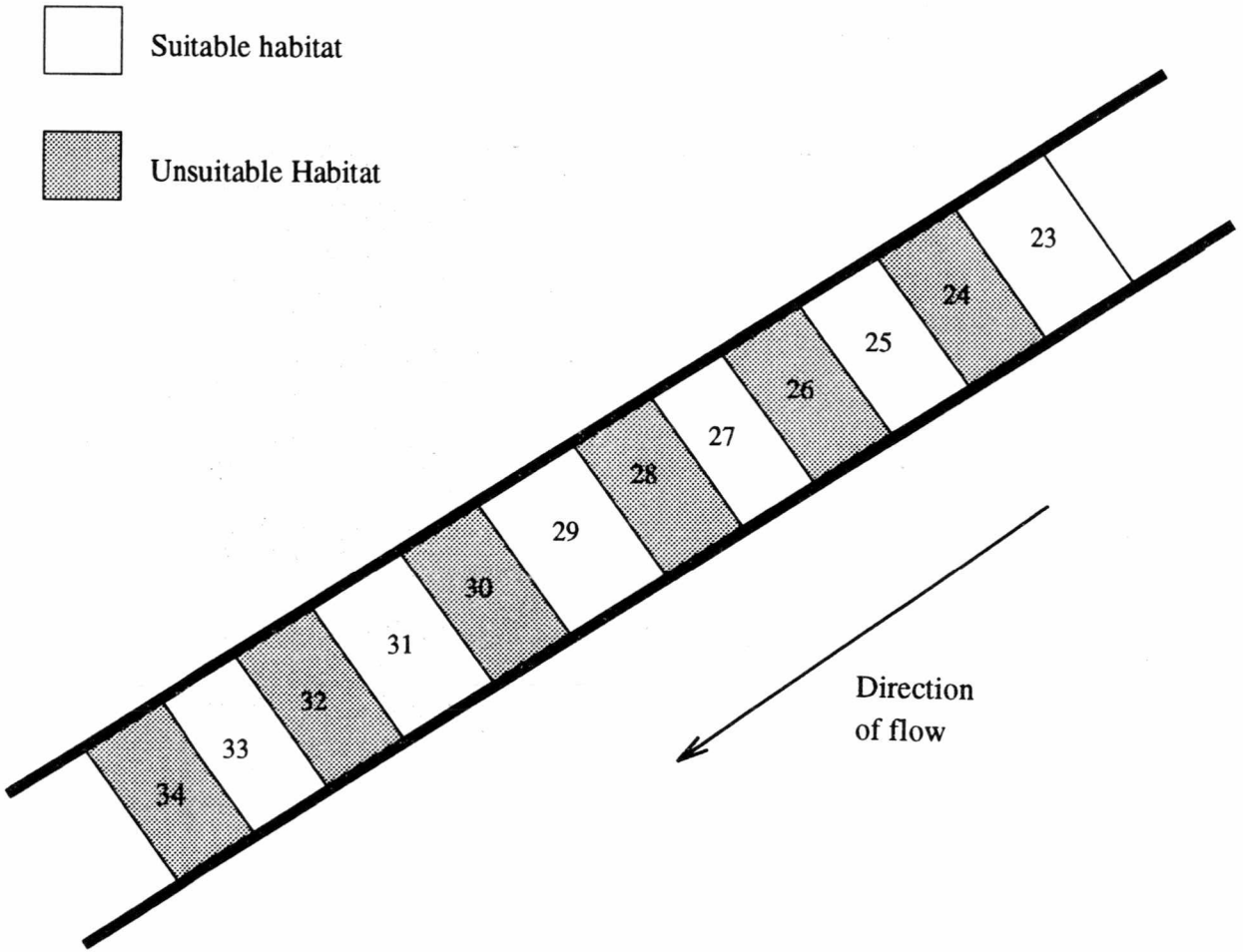

Figure 2.6. Schematic map of the distribution of suitable and unsuitable habitats in a river.

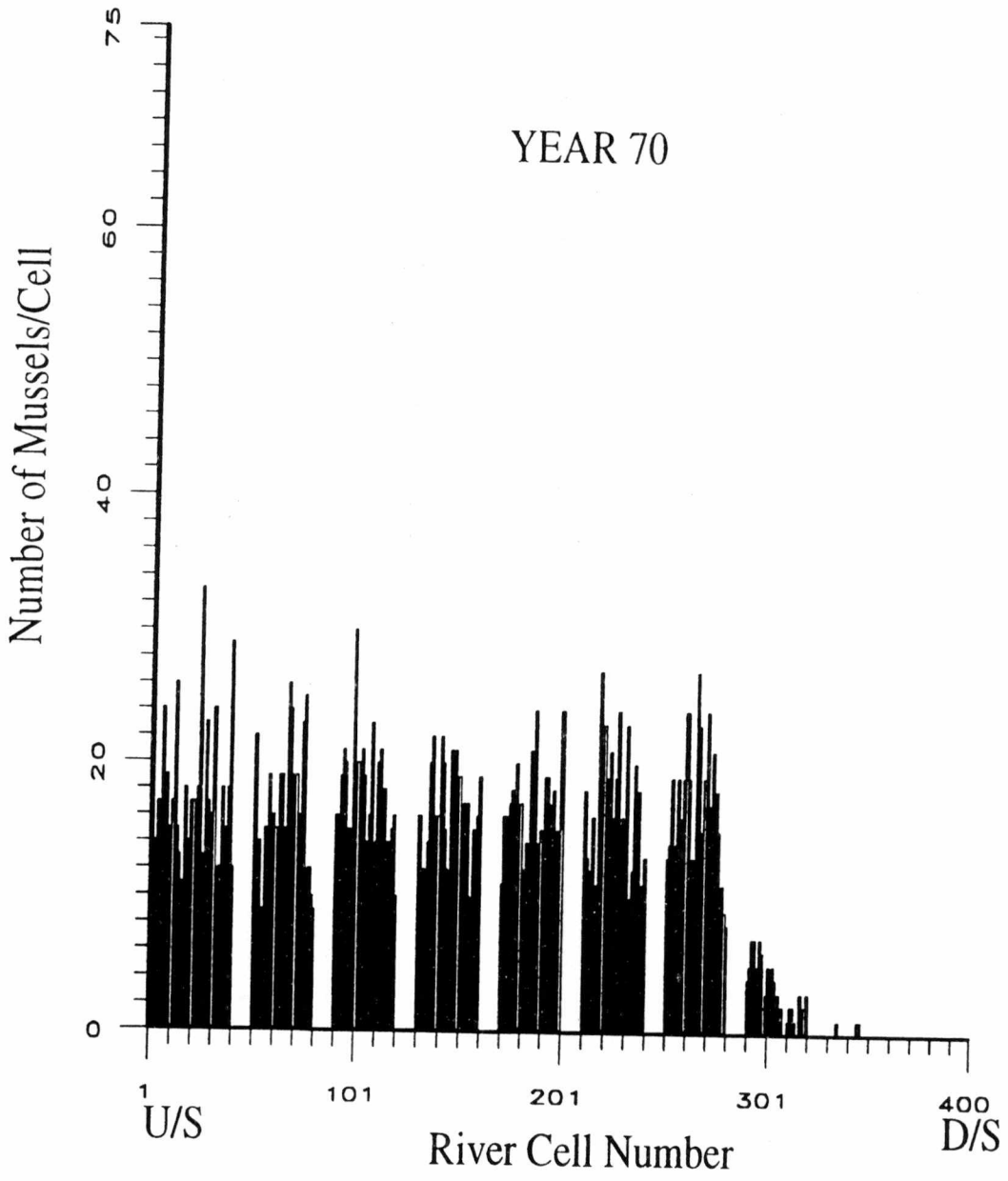

Figure 2.7. Spatial distribution of mussels from simulation set C. U/S is upstream and D/S is downstream.

Table 2.3. Comparison of velocities values.

Width of habitats	[a]Aver. Vel. [km/yr]	[b]Aver. Vel. [km/yr]	Time Period t^* [yr]	[c]Disper. d_1 [km^2/yr]
l_1= 5km l_2= 5km	1.72	1.67	6.0	0.0050
l_1= 5km l_2=10km	1.40	1.47	10.2	0.0048
l_1=10km l_2= 5km	1.94	2.03	7.4	0.0052
l_1=10km l_2=10km	1.49	1.42	14.0	0.0049
l_1=15km l_2= 5km	2.11	2.04	9.8	0.0053
l_1=15km l_2=10km	1.50	1.57	15.9	0.0051

[a]Average velocity value determine from Simulations.
[b]Average velocity value determine by equation (1).
[c]Dispersion values.

paper. Shigesada et al. (1986) used :

$$C_r = \frac{l_1 + l_2}{t^*} \qquad (1)$$

where

C_r = velocity of the wave [km/yr]

l_1, l_2 = length of habitat 1 and 2 respectively [km]

t^* = periodicity of the wave [yr].

As can be seen in Table 2.3, the velocities determined by the computer simulations are within 10% of the value projected by Shigesada et al. (1986) equation. More detailed comparison of the computer simulations of the current model and Shigesada et al. (1986) analytic model will be pursued in a later paper.

Discussion and conclusion

Overall, the results presented here suggest that the spread of the mussels into a new environment may resemble a traveling wave front. The overriding factor determining the velocity of the wave front in a homogeneous environment is the life-span of the mussels. But in a heterogeneous environment, the habitats themselves also play a key role in determining the velocity of the wave. However at present, there is not much field data to verify the above observations. Simple field tests might be carried out by selectively removing the mussels from a selected tributary and observing how long does it take before recolonization occur. It is also useful to determine how long it will take the mussels to recolonize former habitats after being wiped out by natural disturbances, such as spates or droughts, or anthropogenic disturbances such as chemical releases or sedimentation from erosion.

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PART III

USING TRAVELING WAVE FRONT TO ESTIMATE PROPAGATION RATE OF THE UNIONID MUSSELS

Introduction

Freshwater bivalve mollusks are made up primarily of three superfamilies; the *Unionacea*, *Corbiculacea* and *Dresseniacea*. Representatives of the *Unionacea* and *Corbiculacea* can be found all over the world (Fuller, 1974). The habitats of these bivalves are generally more transient and spatially discrete in nature compared to those of the terrestrial and marine organisms. Although certain freshwater mussels such as the pisidiid clams (*Corbiculacea*) can be found in relatively small temporary bodies of water, the Unionids need habitats that are temporally more permanent. Thus, the Unionids are largely confined to the major freshwater drainage systems of the world (Burky, 1983). The continent of North America is considered to be the "mussel central" of the world (Williams and Neves, 1992). It is very rich in the biodiversity of freshwater mussels, especially those from the *Unionacea* family.

However, since the early 1900's, human activities and the accidental introduction of foreign species of mussels have had a negative impact on the population size and species richness of the native mussels. As a consequence, today many species of native freshwater mussels are threatened with extinction

(Stansberry and Clench, 1974; Bates and Dennis, 1978; Ahlstedt, 1984).

While an increasing amount of literature on the physiology of the Unionids is becoming available daily, there have been few attempts to model the spatial and temporal dynamics of the Unionid populations. Lee and DeAngelis (1996) have developed a computer model for the Unionid population dynamics, and this paper is a follow-up on the earlier work. The present paper focuses primarily on the dispersal rate of the Unionids in heterogenous environment through the use of computer simulations.

In Lee and DeAngelis (1996), it was established that a modeled Unionid population disperses into unoccupied habitats in a pattern that resembles a travelling wave front. A travelling wave is described by Murray (1989) to be "a wave which travels without any change of shape and the speed of the propagation of this shape is constant". In addition to noting that modeled population spread resembles a travelling wave, Lee and DeAngelis also found correlations between the travelling wave front speed and certain parameters of the mussels' life-cycle, such as fecundity rate and the condition and size of the mussels' habitat. A continuation of the study of the relationship between the travelling wave front speed and the mussels' heterogeneous environment is pursued here using the computer model developed by Lee and DeAngelis. Lastly, a detailed comparison of the computer model with

Shigesada et al (1986) analytic model will be performed.

Characteristics of the Unionids

The upper Clinch River in Virginia and Tennessee, in the eastern United States, is especially rich in Unionid mussels. The maximum life-span of the Unionids ranges from 9 to 90 years depending on species (Stein, 1971; Lewandowski and Stanczykowska, 1975; Burky, 1983; Jirka, 1986). The preferred habitats of these mussels are stable coarse sand beds with shallow running water (Stone et al., 1982; Salmon and Green, 1983; Cooper, 1984; Machena and Kautsky, 1988; Way et al., 1990). The onset of sexual maturity is species dependent and can occur as early as one year to six years (Pennak, 1953; Burky, 1983; McMahon, 1991). The breeding season of the mussels is in early summer. Being sessile, the mussels depend on water currents to carry the sperm to receptive females. The fertilized eggs are incubated in the gill marsupia of the females before being released as the obligate parasitic glochidia. There are three kinds of glochidia:-

i. "hooked glochidia", which attach and encyst on external surfaces of the fish hosts (McMahon, 1991)

ii. "hookless glochidia", where attachment and encystment occurs among the gill filament of the fish hosts (McMahon, 1991)

iii. "axehead glochidia", whose sites of attachment on the fish host are unknown (Kat, 1984).

Upon completion of development, the glochidia drop off from their fish hosts onto the substrate. There, they begin life as independent juvenile mussels. Figure 3.1 briefly outlines the life-cycle of the mussels.

Problems threatening the survival of the Unionids

The decline in biodiversity and the abundance of the freshwater mussel communities in the Tennessee River system in recent years is caused in part by the presence of dams. The reservoirs formed by dams have "drowned" some of the upstream mussel beds in deep cold water and covered others with smothering silt. Downstream mussels are often chilled into a reproductive torpor when cold water is released or spilled from the dams. The dams have also disrupted the migratory routes of many species of fish, leading to a shortage or disappearance of appropriate fish hosts upstream. This, in turn, caused the death of many glochidia (Fuller, 1974; Kat and Davies, 1984). Furthermore, the dams have curtailed the foraging range of many existing fish hosts and indirectly interfered with the dispersal of the juvenile mussels.

Increase of suspended silt in the water can interfere with the filtering, consumption and gas exchange mechanisms in the mussels, and, in extreme cases, kill them. The mussels are also sensitive to the overall water quality of their habitats. Low pH in the water can affect growth and fecundity rates of some species (Hornbach and Cox, 1987). Pollutants

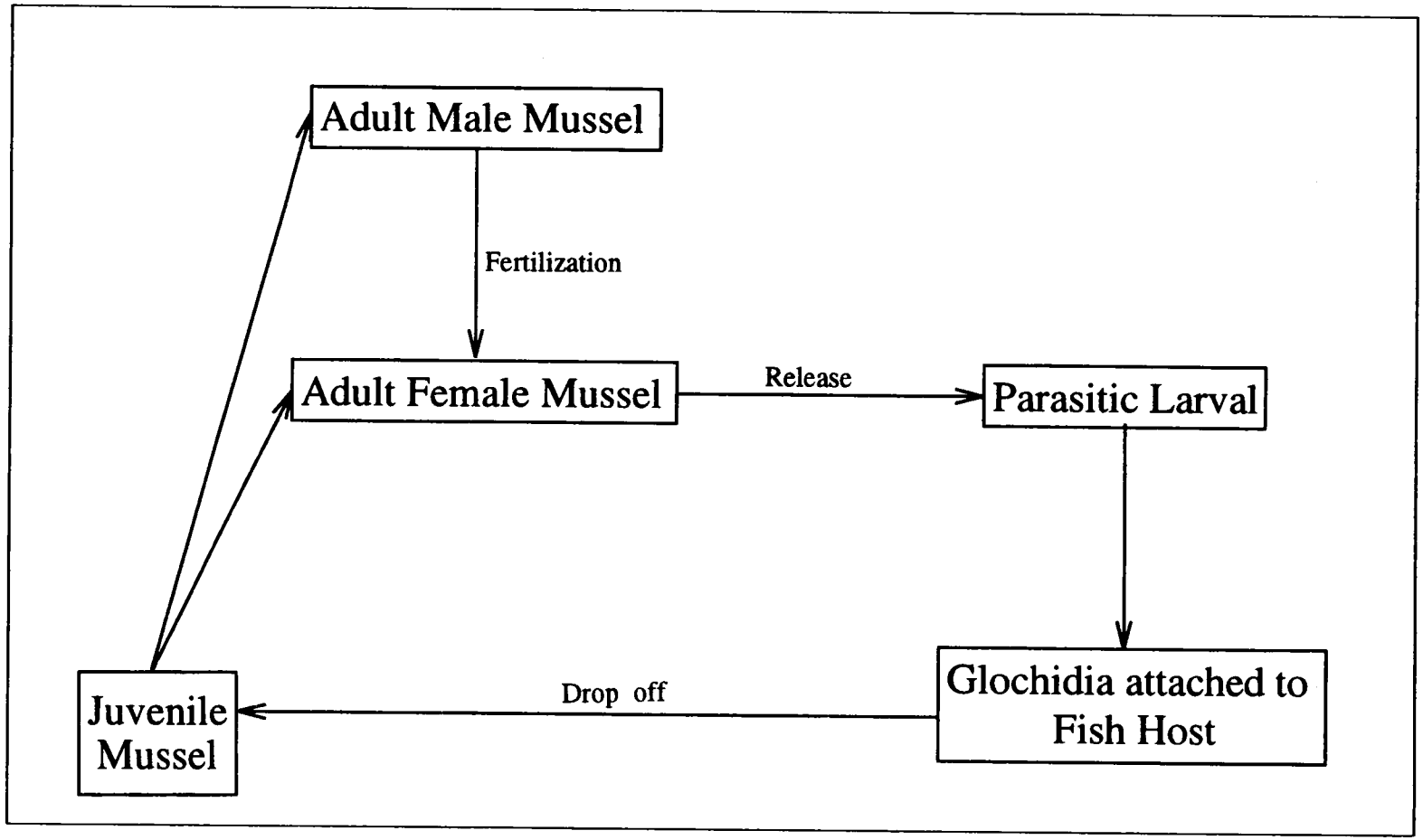

Figure 3.1. Life-cycle of the Unionids.

such as chlorine, paper mill effluents and acid mine drainage are lethal to the freshwater bivalves and their fish hosts (Fuller, 1974; Warren et al., 1984; Taylor, 1985). Finally, intense harvesting of mussels for their shells has also extracted a heavy toll on the Unionids community (Stolzenburg, 1992).

The computer model

The computer model is a generalized Leslie matrix model formulated for up to thirty-five different species of mussels interacting on local sites of arbitrary size. For each of the individual species, the model has some similarities with the Roughgarden et al. (1985) concept of a single-species model of recruitment. However, unlike the marine system modeled by Roughgarden et al., the freshwater populations here are modeled as a spatially extended, closed populations. In addition, unlike the barnacles modeled by Roughgarden et al., the freshwater mussels modeled here seldom seem to be limited by substrate space. The availability of fish hosts may be limiting, however.

For the modeling exercise, the river is divided into different size cells as shown in Figure 3.2. A cell is assumed to be an area in the river with homogeneous physical and chemical properties affecting the mussels. Some of the physical properties being considered here are substrate condition, water depth and level of suspended silt. The

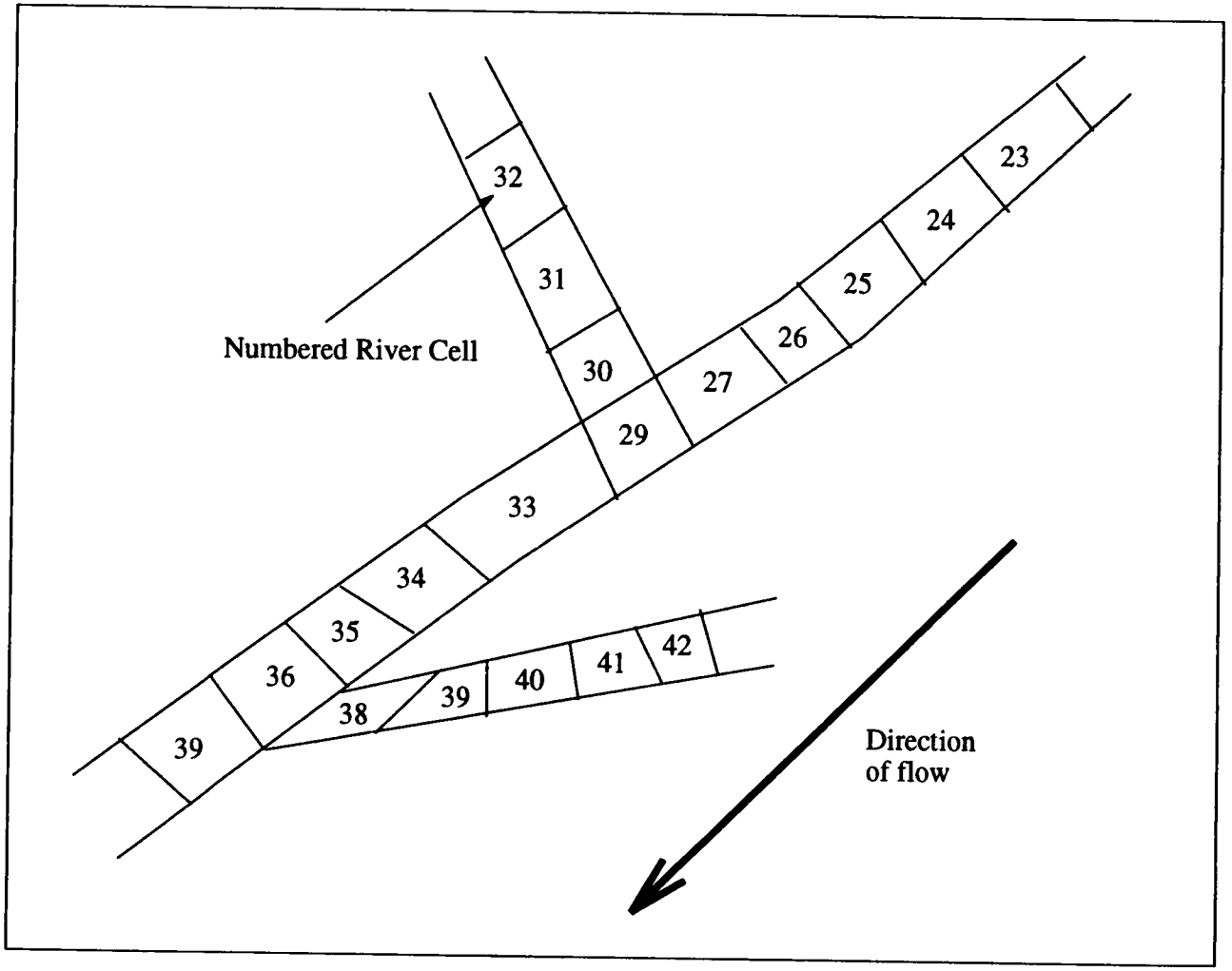

Figure 3.2. Division of a river into cells.

chemical properties refer to the overall water quality, such as pH and dissolved oxygen level. These properties and other factors, such as predation, allowed each cell to be rated with regard to its suitability as a mussel habitat. This suitability rating ranges from 0.0, unable to support mussel life, to 1.0, optimal conditions for mussel life. The suitability rating can affect all or some aspects of mussel life depending on species and the environment.

The computer model has 15 different age classes for each species of mussels in each cell. The probability of survival is lowest in the youngest age class and gets better as the mussel ages. However, upon reaching the maximum age, the mussel is killed instantaneously. Simple deterministic functions are parameterized individually for each species to describe the overall physiological growth of the mussels.

As an example, growth in the mussels is determined by relating the size of the mussel to its chronological age and habitat conditions. Though a mussel continues to grow in size throughout its life, its rate of growth (percentage gain in weight per unit time) decreases with age. Hence the mussel has different growth rate for different stages of its life. A detailed descriptions of the growth function is given in Lee and DeAngelis (1996). Figure 3.3 shows the general relationship between mass increase and age. Habitat conditions can affect the growth pattern significantly.

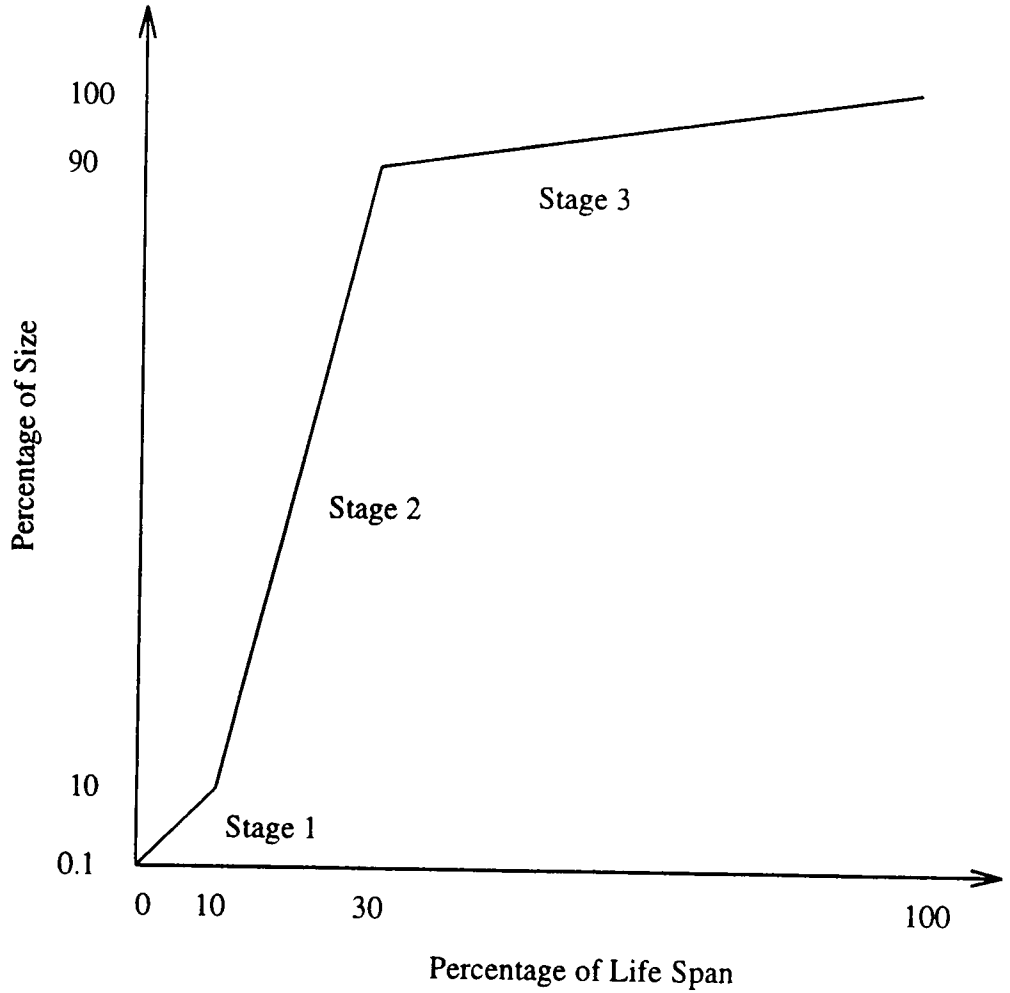

Figure 3.3. Graphical representation of increased in mass versus chronological age.

Reproduction occurs yearly once sexual maturity is achieved provided the mussels are large enough. The breeding season occurs at the same time each year for the same duration. Based on published data (Fuller, 1974; Cherry et al., 1980; Kat and Davis, 1984; McMahon and Williams, 1986a; 1986b; Bauer et al., 1991; McMahon, 1991; Weaver et al., 1991; Jirka and Neves, 1992), it is known that only a very small percentage of glochidia succeed in finding fish hosts and an even smaller percentage will manage to complete their development. The fecundity function is:-

$$JM_{kj}^{i} = \mu^{i} AM_{k}^{i} B^{i} \frac{F_j}{TA_j} \delta_j$$

where

JM_{kj}^{i} = total number of species i juveniles produced by species i mussels from cell k settling in cell j

AM_{k}^{i} = total number of species i sexually mature mussels in cell k

F_j = free space available in cell j (m^2)

TA_j = total area in cell j (m^2) and

B^{i} = fecundity coefficient of species i mussel and

μ^{i} = coefficient of availability of species i mussel's fish host

δ_j = scaling coefficient incorporating habitat conditions in cell j

The mussels have only one mobile stage in their life

cycle, the parasitic glochidia stage. Hence, the fish hosts are also vehicles for dispersal of the juvenile mussels. It is assumed that there exists equal probability for upstream and downstream dispersal of the mussels. The distance of dispersal is chosen randomly from a normal distribution, centered around the adult, for each juvenile mussel.

Overall, the probability of yearly survival increases with age for the mussels. However, this function is individualized for the different mussel species due to their varied biological characteristics and habitats. The probability function is:-

$$PSURV_j^i(A_j^i) = \left[\frac{A_j^i - \eta MA^i}{\lambda MA^i}(PMAX^i - PMIN^i) + PMIN^i\right]\left[1.0 - \exp^{-M^i \frac{F_j}{TA_j}}\right] v_j$$

where

A_j^i = age of species i mussel in cell j(days)

MA^i = maximum life span of species i mussel (days).

$PSURV_j^i$ = probability of survival of species i mussel of age A_j^i in cell j

$PMAX^i$ = maximum probability of survival of species i mussel

$PMIN^i$ = minimum probability of survival of species i mussel

M^i = space-dependent survival coefficient of species i mussel

λ, η = proportionality constant

v_j = scaling coefficient incorporating habitat conditions

in cell j and

F_j, and TA_j are as defined before.

A detailed explanation of the computer model and all the functions has been given in Lee and DeAngelis (1996) and will not be repeated here.

Computer simulations

The modeling exercise uses a hypothetical, idealized river of length 200km with no tributaries. The river is then divided into 2000 consecutive cells of 100m X 100m. Cell 1 is the upstream cell and cell 2000 is the downstream cell. Cells 1 to 50 are each given a habitat suitability rating of 1.0, meaning that all of these 50 cells are good habitat.

To begin a particular simulation, five of these 50 cells are randomly chosen and seeded with a mixed age class of mussels. Two generic species of mussels are employed here, species 1 and species 2.

Species 1 has a maximum size of 30 cm^2, maximum life span of 30 years, and the rate of attachment of glochidia to fish host is 300 glochidia/female mussel. Species 2 has a maximum size of 3 cm^2, maximum life span of 10 years and the rate of attachment of glochidia to fish host is 900 glochidia/female mussel.

From cell 50 onwards, the river environment consists of heterogeneous habitats. The lengths of reaches of suitable habitat are designated by l_1 and they are composed of some

integer multiple of 100m-long cells. Similarly, the lengths of reaches of less suitable habitat are designated by l_2 and they are composed of some integer number of cells. A typical situation of suitable and less suitable sites, arranged alternately, is shown in Figure 3.4. The length and suitability rating of each kind of habitat is fixed for each simulation. Three different combinations of lengths l_1 and l_2 are used. Furthermore, for each length of l_2 there are three different suitability ratings, r_2. The suitability rating (r_1) for all l_1 lengths is fixed at 1.0. For each combination of l_1, l_2, r_1 and r_2, at least five replicate computer runs are performed to lessen the inherent stochasticity in each run. In the replicate runs, all parameters are identical except for the initial random number.

Results from each runs are plotted individually for each species as shown in Figure 3.5. However, age class 1 mussels are excluded from the total number of mussels counted. The is due to the high variability in numbers of age class 1 mussels compared to the other age classes. The velocity of the wave is calculated in three different ways using similar plots to those shown in Figure 3.5.

Although the computer model does not parameterize the dispersal rate explicitly, it is still possible to calculate the consequent dispersal rate of each species of mussels in its habitats. The distances of dispersal of individual glochidia are randomly chosen from a normal distribution,

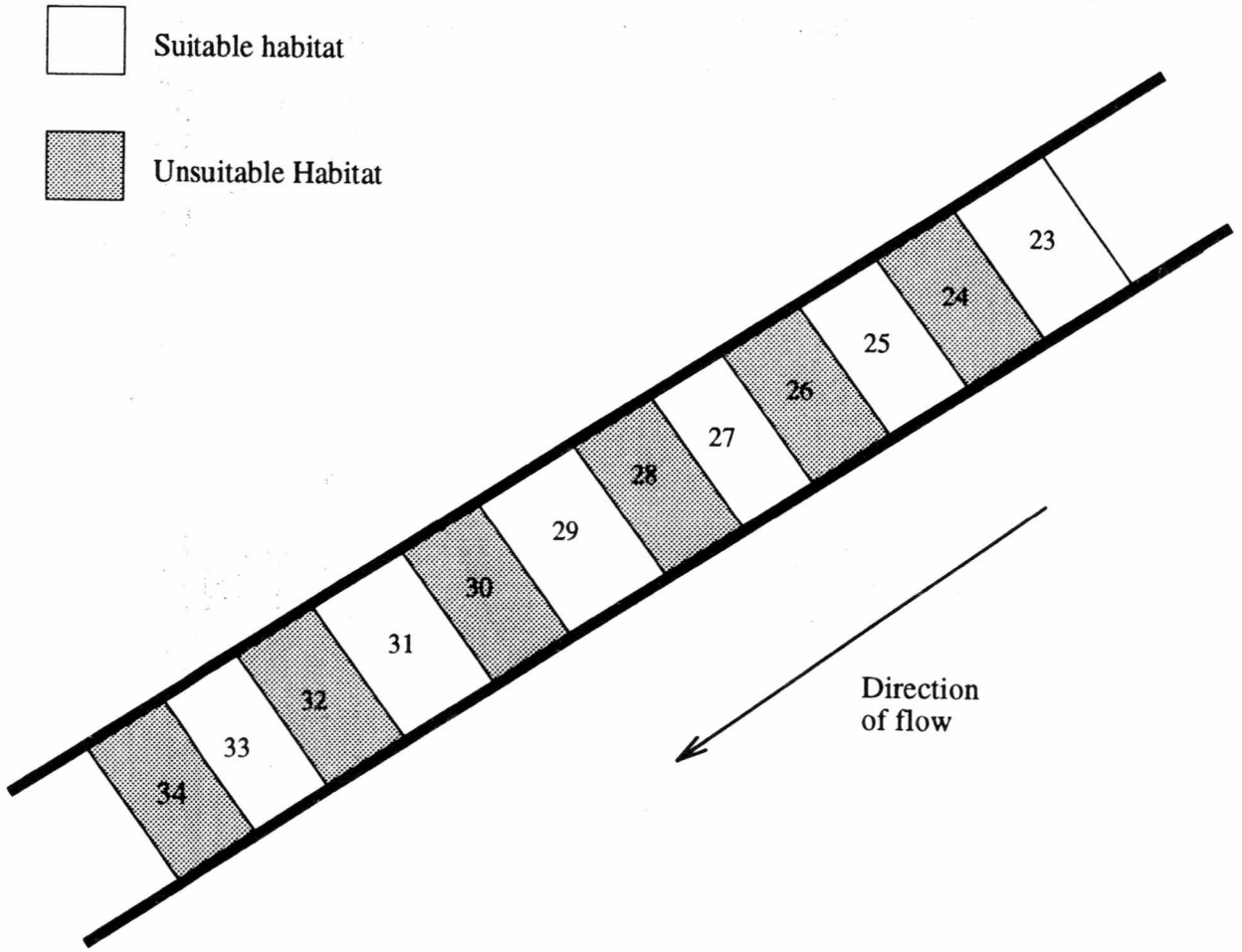

Figure 3.4. Distribution of suitable and unsuitable habitats in a river.

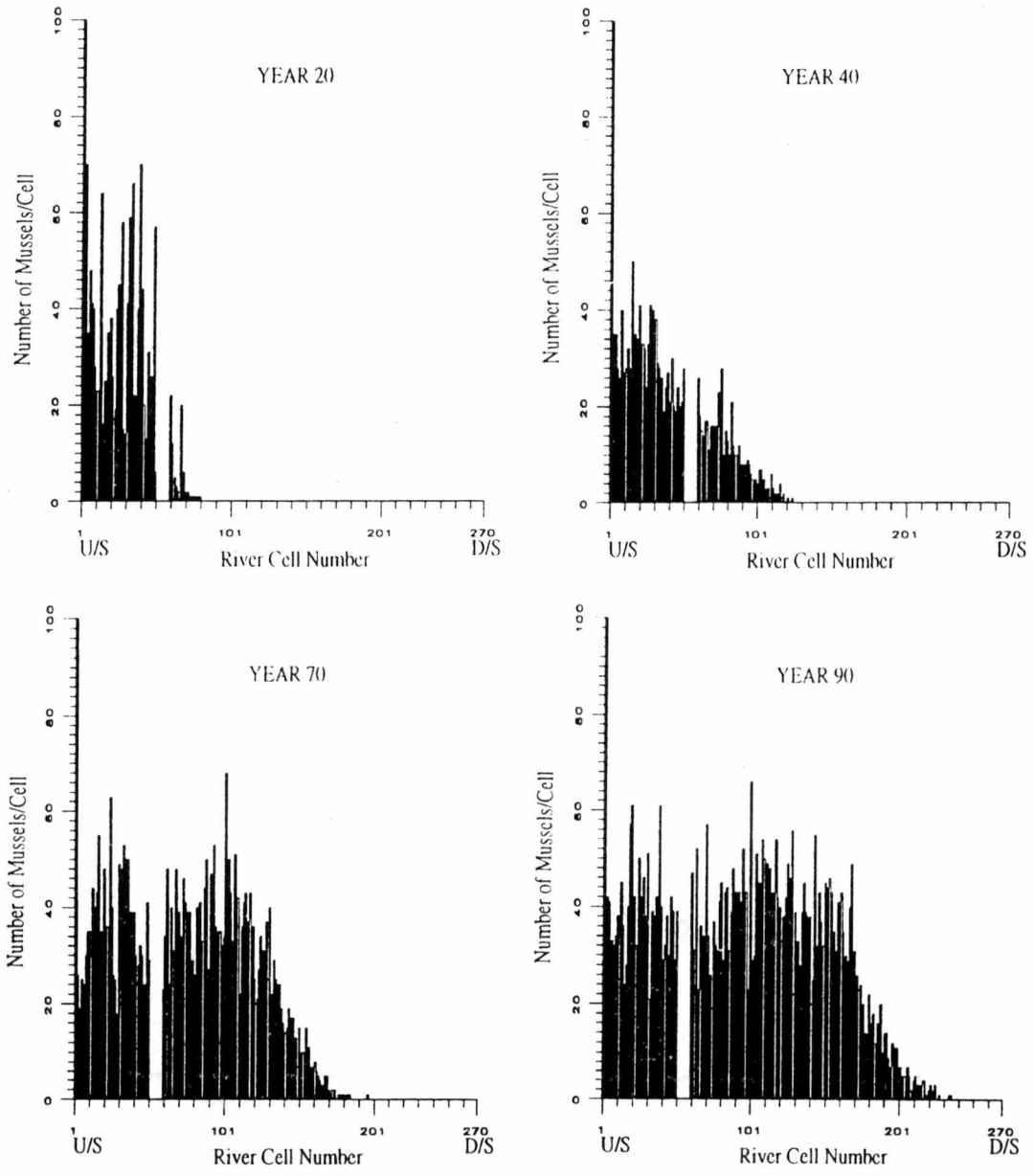

Figure 3.5. Propagation of a wave front for species 1. Each cell is 100 m by 100 m and U/S is upstream and D/S is downstream.

hence the equation is (Murray, 1984):

$$u(x,t) = \frac{Q}{2(\pi DT)^{0.5}} \exp^{-\frac{x^2}{4DT}}$$

where

$u(x,t)$ = number of mussels in cell x at time t

Q = number of mussels per unit area at x=0 and t=0

D = diffusivity of the species (km^2/yr)

x,t = variables in continuous time and space

Although it is not possible to solve for D directly in the above equation, it is still possible to estimate D easily using the Newton-Raphson method.

Results

Tables 3.1 and 3.2 summarize the results of the computer runs for species 1 and 2 respectively. Overall, for both species of mussels, changing the suitability rating r_2 of habitat l_2, from 0.1 to 0.5 increases the velocity of the travelling wave front by less than 10%. For species 1 when l_1 is 1000m, l_2 is 500m, r_1 is 1.0 and r_2 takes on the sequence of values 0.1, 0.3 and 0.5, the velocity of the travelling wave is respectively, 0.94km/yr, 0.96km/yr and 0.99km/yr.

When the length of less suitable habitat, l_2 is doubled to 1000m (l_1=1000m, r_1=1.0), the velocity of the travelling wave front is slowed down proportionately to 0.86km/yr for r_2

Table 3.1. Computational results for species 1.

		r_2	ε_2	d_2	C_{model}	C_{min}	C_r	%
l_1=1000m l_2= 500m r_1= 1.0	ε_1=.445 d_1=1.21	.1	.096	.280	.944	1.185	.868	8.0
		.3	.246	.398	.957	1.425	1.044	9.1
		.5	.327	.450	.988	1.528	1.120	13.3
l_1=1000m l_2=1000m r_1=1.0	ε_1=.445 d_1=1.21	.1	.096	.280	.855	.957	.701	18.0
		.3	.246	.398	.870	1.241	.910	4.5
		.5	.327	.450	.911	1.373	1.006	10.4
l_1=1000m l_2=1500m r_1=1.0	ε_1=.445 d_1=1.21	.1	.096	.280	.793	.842	.617	22.2
		.3	.246	.398	.852	1.149	.842	1.3
		.5	.327	.450	.882	1.294	.948	7.4
l_1= 500m l_2=1500m r_1=1.0	ε_1=.445 d_1=1.21	.1	.096	.280	.680	.688	.504	25.9
		.3	.246	.398	.693	1.026	.752	8.5
		.5	.327	.450	.700	1.190	.872	24.6

ε_1, ε_2 = intrinsic growth rate in habitats 1 and 2 (1/yr)
d_1, d_2 = dispersion rate in habitats 1 and 2 (km^2/yr).
C_{model} = velocity calculated from the computer model (km/yr)
C_r = velocity calculated from SAM (km/yr)
% = percentage of difference between C_{model} and C_r

Table 3.2. Computational results for species 2.

		r_2	ε_2	d_2	C_{model}	C_{min}	C_r	%*
l_1=1000m l_2= 500m r_1= 1.0	ε_1=1.33 d_1=3.10	.1	.288	.450	2.159	.998	2.031	5.9
		.3	.737	.528	2.259	1.139	2.317	2.6
		.5	.980	.599	2.265	1.234	2.511	10.8
l_1=1000m l_2=1000m r_1=1.0	ε_1=1.33 d_1=3.10	.1	.288	.450	1.935	.785	1.597	17.4
		.3	.737	.528	1.948	.950	1.934	.7
		.5	.980	.599	1.955	1.059	2.155	10.3
l_1=1000m l_2=1500m r_1=1.0	ε_1=1.33 d_1=3.10	.1	.288	.450	1.723	.683	1.390	19.3
		.3	.737	.528	1.746	.863	1.757	.6
		.5	.980	.599	1.794	.979	1.992	11.0
l_1= 500m l_2=1500m r_1=1.0	ε_1=1.33 d_1=3.10	.1	.288	.450	1.435	.551	1.122	21.9
		.3	.737	.528	1.438	.755	1.537	6.9
		.5	.980	.599	1.465	.880	1.790	22.2

ε_1, ε_2 = intrinsic growth rate in habitats 1 and 2 (1/yr)
d_1, d_2 = dispersion rate in habitats 1 and 2 (km^2/yr).
C_{model} = velocity calculated from the computer model (km/yr)
C_r = velocity calculated from SAM (km/yr)
% = percentage of difference between C_{model} and C_r

= 0.1, 0.87km/yr for r_2 = 0.3 and 0.91km/yr for r_2 = 0.5. Tripling l_2 to 1500m while keeping all other parameters the same causes the velocity of the wave to slow down even more. The velocity in this case is, respectively, 0.79km/yr, 0.85km/yr and 0.88km/yr for r_2 of 0.1, 0.3 and 0.5.

In the final set of runs for species 1, l_1 is reduced to 500m (r_1=1.0) while l_2 remains at 1500m. The velocity of the travelling wave under this condition is the slowest of all cases. It is 0.68km/yr (r_2=0.1), 0.69km/yr (r_2=0.3) and 0.70km/yr (r_2=0.5).

Tables 3.3 and 3.4 show the results of the F-test performed on species 1. Two F-tests were performed. The first test was to determine the effect of the three different r_2 values on the velocity of the travelling wave. The second F-test dealt with the influence of the different l_2 lengths on the velocity of the travelling wave. The observed value of F_s is 3.18 and 21.43 for the first and second test, respectively. $F_{\alpha[2,40]}$ is 3.23 (α=0.05) and 5.18 (α=0.01). It appears that differences in lengths of l_2 affect the velocity of the

Table 3.3. F-test result from testing different r_2 values for species 1.

Source of Variation	Deg. of Freedom	Sums of Squares	Mean Squares	F value
Among groups (A. r_2 values)	2	0.0298	0.0149	3.1799
Error	42	0.1968	0.0047	

Table 3.4. F-test result from testing different l_2 lengths for species 1.

Source of Variation	Deg. of Freedom	Sums of Squares	Mean Squares	F value
Among groups (A.l_2 lengths)	2	0.1143	0.0572	21.4307
Error	42	0.1121	0.0027	

travelling wave significantly. Meanwhile, the effects of r_2 values on the velocity are negligible. However, the situation could easily change with different parameter values. Please note that data from the simulation when l_1 is 500m and l_2 is 1500m are not included in the sample size of the two F-tests.

The velocity of the travelling wave for species 2 is much higher than for species 1. This is due to the higher fecundity rate and the earlier age of maturation of species 2. Table 3.2 shows the results of the computer runs for species 2.

When l_1 is 1000m, r_1 is 1.0, l_2 is 500m, r_2 is 0.1, 0.3 and 0.5, the velocity is respectively 2.16km/yr, 2.26km/yr and 2.27km/yr. When l_2 is doubled to 1000m, the velocity is approximately 1.95km/yr for all three values of r_2. In the case when l_2 is set to 1500m, the velocity of the travelling wave drops to 1.72km/yr, 1.75km/yr and 1.79km/yr for r_2 of 0.1, 0.3 and 0.5, respectively. For the final set where l_1 is 500m (r_1=1.0) and l_2 is 1500m (r_2=0.1, 0.3 and 0.5) the velocity slowed down even further to 1.43km/yr, 1.44km/yr and 1.46km/yr.

Similar F-tests to those performed on species 1 were conducted on species 2. Tables 3.5 and 3.6 show the F-tests results. As expected, different r_2 values did not influence the velocity of the travelling wave significantly. The observed value of F_s is 0.34 while $F_{\alpha[2,40]}$ is 1.44 (α=0.25) and 2.44 (α=0.10). However, differences in lengths of l_2 do affect the velocity of the wave. The observed F_s value is 90.74.

Consider a generalized reaction-diffusion model of the following form:

$$\frac{\partial}{\partial t}u=\frac{\partial}{\partial x}(D(x)\frac{\partial}{\partial x}u) + f$$

where

$u(x,t)$ = population density at point x at time t

$D(x)$ = diffusivity of the population

f = a function of u, x and t

x, t = variables of space and time.

It is known that for such reaction-diffusion models the

Table 3.5. F-test result from testing different r_2 values for species 2.

Source of Variation	Deg. of Freedom	Sums of Squares	Mean Squares	F value
Among groups (A. r_2 values)	2	0.0339	0.0169	0.3450
Error	42	2.0636	0.0491	

Table 3.6. F-test result from testing different l_2 lengths for species 2.

Source of Variation	Deg. of Freedom	Sums of Squares	Mean Squares	F value
Among groups (A. l_2 lengths)	2	1.7034	0.8517	90.7443
Error	42	0.3942	0.0094	

asymptotic rate of spread in one-dimension (or propagating travelling wave) for a population living in a homogeneous environment with density-independent population growth (Andow et al., 1990) is

$$C = \sqrt{4\varepsilon D}$$

where

C = velocity of the wave [length/time]

ε = intrinsic growth rate [1/time] and

D = diffusivity of the population [length^2/time].

However in a heterogeneous environment the above equation is no longer valid.

For a heterogeneous environment, Shigesada et al. (1986) showed that the travelling wave speed can be estimated by the following equations:

$$C_{min} = 2\sqrt{\frac{L_1+E_bL_2}{L_1+\frac{L_2}{D_b}}} \qquad for\ \ L_1 \ll 1.0,\ \ L_2 \ll 1.0,\ \ L_1+E_b \geq 0 \tag{1}$$

where:

$$L_1=\sqrt{\frac{\varepsilon_1}{d_1}}l_1 \ , \qquad L_2=\sqrt{\frac{\varepsilon_1}{d_1}}l_2$$

$$E_b=\frac{\varepsilon_2}{\varepsilon_2} \ , \qquad D_b=\frac{d_1}{d_2}$$

and l_1, l_2=length of habitats 1 and 2 respectively (km)

ε_1, ε_2=intrinsic growth rate in habitats 1 and 2 (1/yr)

d_1, d_2=dispersion rate in habitats 1 and 2 (km^2/yr).

C_{min}, L_1, L_2, E_b and D_b are dimensionless.

Then the velocity of the travelling wave is:

$$C_r = \sqrt{\varepsilon_1 d_1}C_{min} \qquad L_1 \ll 1, \ L_2 \ll 1, \ L_1+E_bL_2 \geq 0$$
$$C_r = 0 \qquad \textit{otherwise}$$

where C_r = velocity of the travelling wave (km/yr) and C_{min}, ε_1, d_1 are as defined before. The heterogenous environment proposed by Shigesada et al. consists of good habitats (l_1) alternating with less favorable habitats (l_2) as shown in Figure 3.4. The lengths of l_1 and l_2 are fixed for each computation.

A comparison of results can be performed between Shigesada et al.'s analytical model (SAM) and the present model. Tables 3.1 and 3.2 show the results of the comparison. When l_2 ranges in length from 500m to 1500m, and l_1 is 1000m,

the velocities of the travelling wave of species 1 computed by the model are lower then the values predicted by SAM. Also, the differences are less then 20% except for one case of 22%. However when l_1 is reduced to 500m, the differences increase to approximately 25%.

For species 2, similar differences were observed. The difference in value between the two models is less than 20% for all cases. When l_1 is 500m and l_2 is 1500m, the difference is 22%.

Discussion and conclusion

Overall, there are significant differences in the velocities of the travelling wave computed by the model and SAM. This could be due in part to the inability to completely fulfill all the constraints imposed by equation (1), $L_1 << 1$ and $L_2 << 1$. In the model, although L_1 and L_2 are less than 1, they are not very much less, as required by equation (1).

Another major cause of difference between the computer simulation model and the mathematical model is the use of age-structure in the computer model. The SAM model does not represent age-structure in the population. This makes a fundamental difference with regard to diffusion across poor habitats. In the SAM model, the organisms diffuse continuously across both the good and bad habitats. But in the computer simulation model, this is not possible. The only mobile stage in the Unionid's life-cycle is the parasitic

glochidia stage. When a developed glochidia falls into a poor habitat, the probability of its dying before maturing is extremely high. Besides that, even if the glochidia survives and manages to grow into a mature mussel, it may never grow large enough to reproduce, despite being of mature age. Lastly, should it manage to reproduce, it still might not produce enough glochidia to ensure even one of its offspring finding a fish host and repeating the life-cycle. In most cases, a poor habitat for mussels is also a poor habitat for fish. Hence, the likelihood of a fish host foraging in a poor habitat is small. Most of the time, the Unionids can only diffuse across an extremely poor habitat by "jumping" across - when a fish carries a glochidia far enough to cross the poor habitat. This is the form of diffusion occurring in the simulations. Thus, the population sizes in the computer simulation are too small for the assumption of continuous-time diffusion to be valid.

Furthermore, the mussels in the model have two stages in their life cycle; a short unreproductive stage (mobile glochidia and sessile juveniles) and a long immobile but reproductive stage. This is the reverse of the life-cycle of the organisms being considered in SAM. SAM is more appropriate for organisms that are either mobile throughout their lives or that have a relatively long mobile and reproductive stage in their life-cycle.

Despite the major differences between the two model, it is still useful to compare the results. SAM can serve as a simple desk-top model to check the accuracy of the results of the computer model.

The present computer model can be a useful tool to determine the speed of the Unionids recolonizing the rivers of North America. It can be used to determine how far apart to locate detrimental chemical discharges/wastes along a river to ensure the survival of a viable population of mussels. Alternatively, the model can also give an idea on appropriate strategies to reseed the river with Unionids to enable recolonization to take place.

Lastly it must be stated that at present, the computer model has not been validated yet due to the insufficiency of field data. However this can be easily remedied by simple undestructive field tests, such as the selective removal of mussels from selected tributary and observation of the length of time before recolonization occurs.

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PART IV

SPATIAL DISTRIBUTION OF THE UNIONID MUSSELS AND THE CORE-SATELLITE HYPOTHESIS

Introduction

Russell-Hunter (1983) noted that the phylum Mollusca has approximately 110,000 living species and is one of the most successful forms of animal morphology. The biomass of mollusks dominates the lower trophic levels of many marine ecosystems. The Gastropoda, Bivalvia and Cephalopoda are three major classes in the phylum Mollusca. The organisms in these three classes all share the same basic anatomical structure, a soft body contained within a hard calcareous shell. The organisms in the class of Gastropoda are various species of marine and terrestrial snails. The Bivalvia are made up of marine and freshwater mussels, clams and oysters. The most diverse group of mollusks are the marine gastropods but the most abundant are the marine bivalves.

The Unionacea, one of the major superfamilies of bivalves (Fuller, 1974) are freshwater mussels and can be found worldwide. Until early this century, they were especially abundant in number and species on the continent of North America. Since then, various communities of freshwater mussels have steadily dwindled in size as well as species richness. Various studies have attributed this loss primarily to anthropogenic activities.

In this paper, we will study the spatial distributional pattern of the Unionacea within a geographically small area of habitat, a river or river segment, and relate it to the core-satellite hypothesis proposed by Hanski (1982). We use a computer model, which was developed earlier to study the temporal distributional patterns of the mussels. However some minor modifications in the computer model are necessary to facilitate the new study. Lee and DeAngelis (1996) showed that the mussels tend to spread spatially and temporally in the form of a travelling wave front. Furthermore, they also showed that it is possible to relate the velocity of the wave to certain characteristics of the various species of Unionids. As an example, the model predicts that mussels of different species with dissimilar life-spans and age of maturity will have different wave velocities in their spread. The wave front velocity can be used as a gross indicator to predict the time required for recolonization following the extinction of small local populations of mussels.

However, the study here will focus essentially on the spatial distributional patterns of the Unionids. The purpose is to judge which local populations of mussels are the core populations and which are the satellite populations. Besides that, it will also seek to identify the core and satellite species of mussels. It is hoped that by identifying possible core and satellite features, the model can help conservationists decide more accurately which populations or

species to protect and use to repopulate former habitats, or to rejuvenate local populations of mussels. This study, coupled with earlier travelling wave front studies, can serve as a tool in estimating the length of time, size of habitats, and size or species of mussel populations needed for recolonization purposes. Further explanation of the core and satellite hypothesis of Hanski (1982) will be given in a later section of this article.

Life-cycle of the Unionids

Freshwater mussels evolved before fish in the Mississippi basin. They spread and thrived throughout the freshwater systems of North America since the last ice-age. However in the last 100 years the populations of freshwater mussels in North America have steadily deteriorated in size as well as species richness, due to the effects of anthropogenic activities (Stansbery and Clench, 1974; Bates and Dennis, 1978; Ahlstedt, 1984).

In the past, as many as 70 different species of mussels existed in one section of the Tennessee river system known as Mussel Shoals (Conrad, 1834). However, currently there exist only 35 different species of Unionids in the entire river system (Dennis, 1984). The freshwater mussels are an integral part of the riverine ecology, as they are the prey items of numerous small terrestrial mammals (Stansbery, 1973). The extinction of the mussels would likely have a profound impact

on those creatures.

The Unionids prefer well-oxygenated shallow water habitats with stable substrate in depths between 4 m to 10 m (Stone et al., 1982; Salmon and Green, 1983; Stern, 1983; Cooper, 1984; Machena and Kautsky, 1988; Way et al., 1990). The densities of the mussel populations vary considerably with depth, the deeper the water the lower the density of mussels (Negus, 1966; Cvancara, 1972; Burky, 1983).

The Unionids are in general long-lived, with life spans ranging from 9 years to 90 years (Stein, 1971; Lewandoski and Stanczykowska, 1975; Burky, 1983; Jirka, 1986). Some of the species are dioecious while others are hermaphroditic (Burky, 1983). Sexual maturity can occur as early as 1 year to as late as 6 years or more depending on species (Pennak, 1953; Burky, 1983; McMahon, 1991). Reproduction occurs once a year, in the early summer in general. Environmental parameters, such as temperature and photoperiod as well as neurosecretory controls, cue the start of the breeding season. The male mussels will then shed sperm as packets or volvocoid bodies (Edgar, 1965) to be carried by water currents to the gill marsupia of the females for fertilization and incubation. The larvae (called glochidia) are released at the end of the incubation period through exhalant apertures on the females (Burky, 1983). The glochidia are parasitic and require fish hosts to complete their development. Figure 4.1 shows a brief summary of the life-cycle of the mussels.

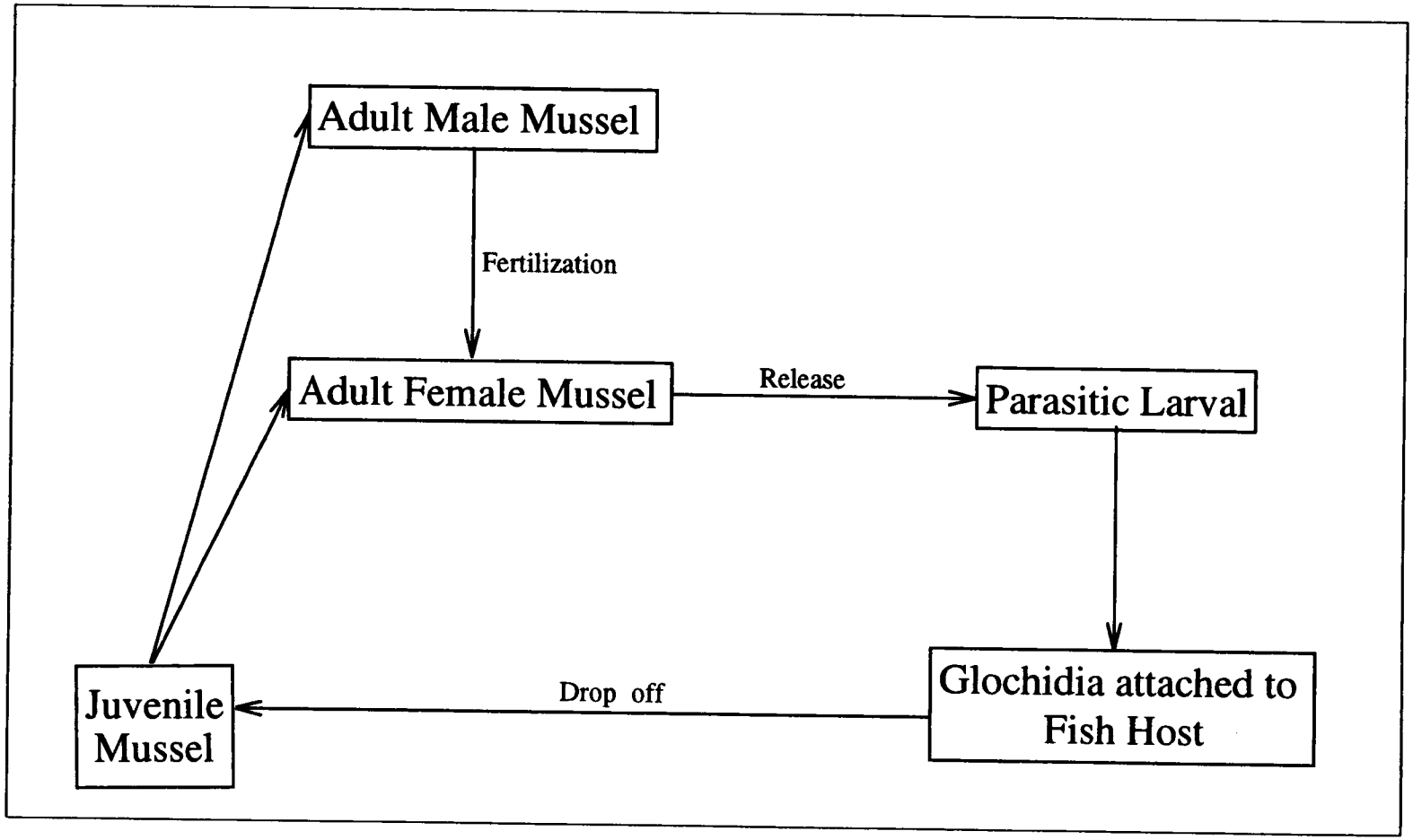

Figure 4.1. Life-cycle of the Unionids.

It is this required period of parasitism in their life-cycle which sets the Unionids apart from other species of mussels. This parasitic association of mussels and fish hosts is of great benefit to the mussels. It helps in the dispersal of the juveniles mussels as well as providing food and shelter to the developing glochidia. However this link is also most vulnerable to disruption by human activities. This is especially true for mussel species capable of infecting only a very limited number of fish host species. Lack of fish hosts possibly is one of the direct causes of the decline of the mussel communities in the Tennessee river systems.

Core-satellite species hypothesis

The Tennessee River system, home to the Unionid mussels, is a fairly large river system. Thus it is not unusual to find environmental conditions differing extensively from one place to another along the river system. This creates a rich diversity of niches, and encourages the co-occurence of a multiplicity of species of freshwater mussels.

Each of the different species of mussel has its own distributional pattern and density. Some species are numerous in nature while others are few in numbers and can only be found in very selected niches. This variability in distribution and density patterns suggests that the core-satellite hypothesis may be relevant to the mussel community. But what is the core-satellite hypothesis?

Hanski proposed the core and satellite species hypothesis in a 1982 article entitled "Dynamics of regional distribution: the core and satellite species hypothesis", and developed it together with Gyllenberg further in a 1993 article entitled "Two general metapopulation models and the core-satellite species hypothesis". In the studies, "abundance" is defined as the "number of individuals in a local population site" and "distribution" is "the number of population sites occupied by a given species". With these definitions in mind, the studies showed that many species of plants and animals, including freshwater mollusks, exhibit a bimodal distribution of site occupancy frequencies as shown in Figure 4.2; that is some species occupy many sites (and are locally abundant) and some species only a few sites. Relatively fewer species occupy an intermediate number of sites. This produces a bimodal distribution, which is termed the core and satellite (species) distribution.

Hanski (1982) suggested using the core-satellite species hypothesis as a null test to explain regional rarity with an important restriction in its application. The hypothesis terms locally abundant and widely distributed species "core species", and terms rare species "satellite species". The restriction in the hypotheses requires the many species being tested to be capable of colonizing the same habitats. It is not applicable when morphological distinction in species results in different habitat selection. The hypothesis

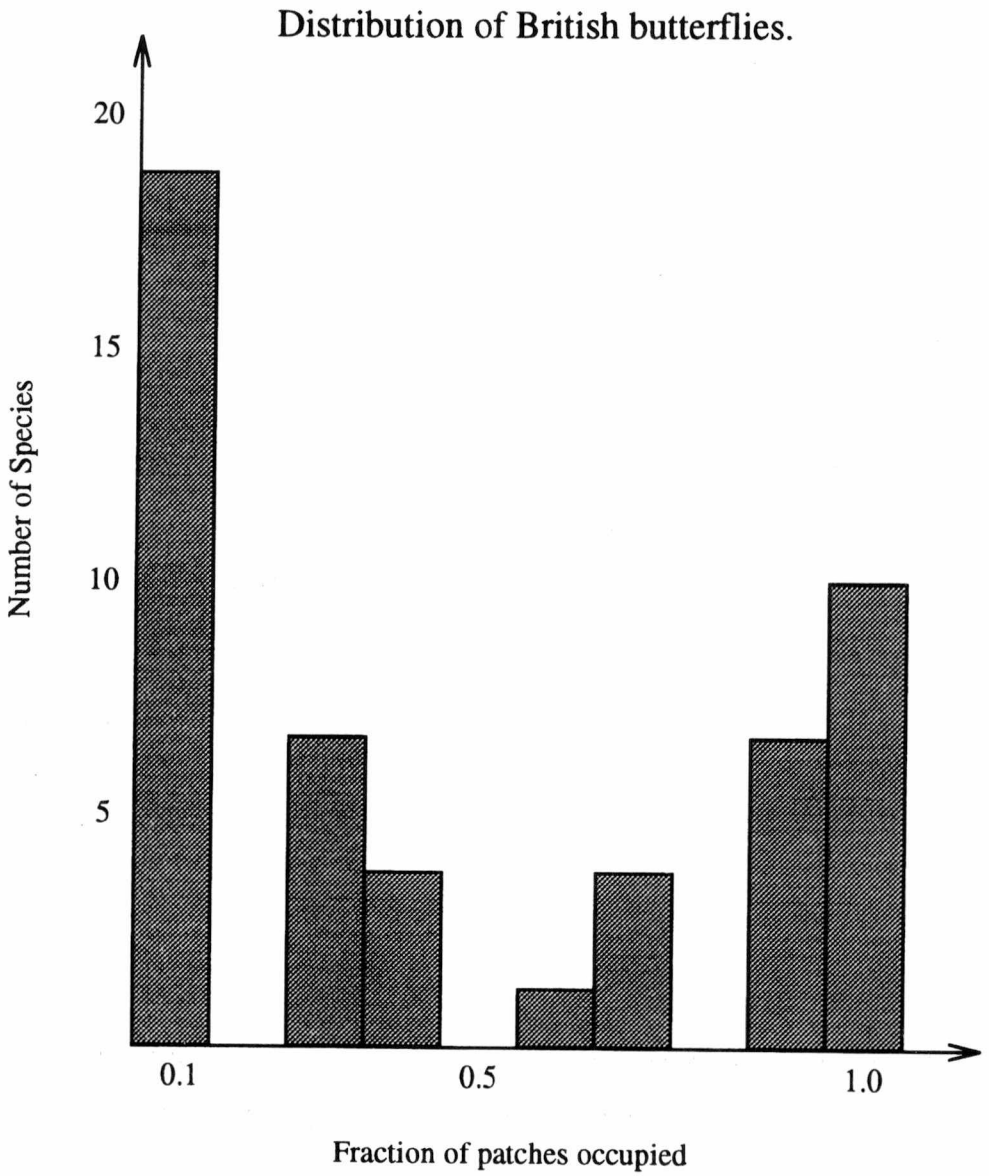

Figure 4.2. The distribution of British butterflies from data collected by Pollard et al. (1986).

further claims that the size of the region correlates positively to the number of satellite species in the region. It supposes also in intense inter-specific competitions, core species will normally outperform satellite species.

In Hanski's (1993) study, it was added that the bimodality of distribution can be attributed to:-

1. A strong rescue effect.

There is a strong and viable core population of organisms which have access to former habitats and are capable of repopulating those habitats.

2. Spatial, temporal or inter-specific species variations.

These variations will cause some (core) species to be abundant as well as being widely distributed, while others remain or become rare (satellite) species. Thus, knowledge of the mechanisms involved in improving the survival rate of the rare species will help in the preservation of the biodiversity of the species.

Computer model

Dennis (1984) conducted a field survey of the Unionid population in the Upper Clinch and Powell rivers in the Tennessee river system. Figures 4.3, 4.4 and 4.5 are plotted from data collected from the survey. Those figures show the freshwater mussels community exhibiting tentative patterns of bimodal distributions. However, is the bimodality shown an artifact of the sampling procedures, as suggested by Raunkiaer

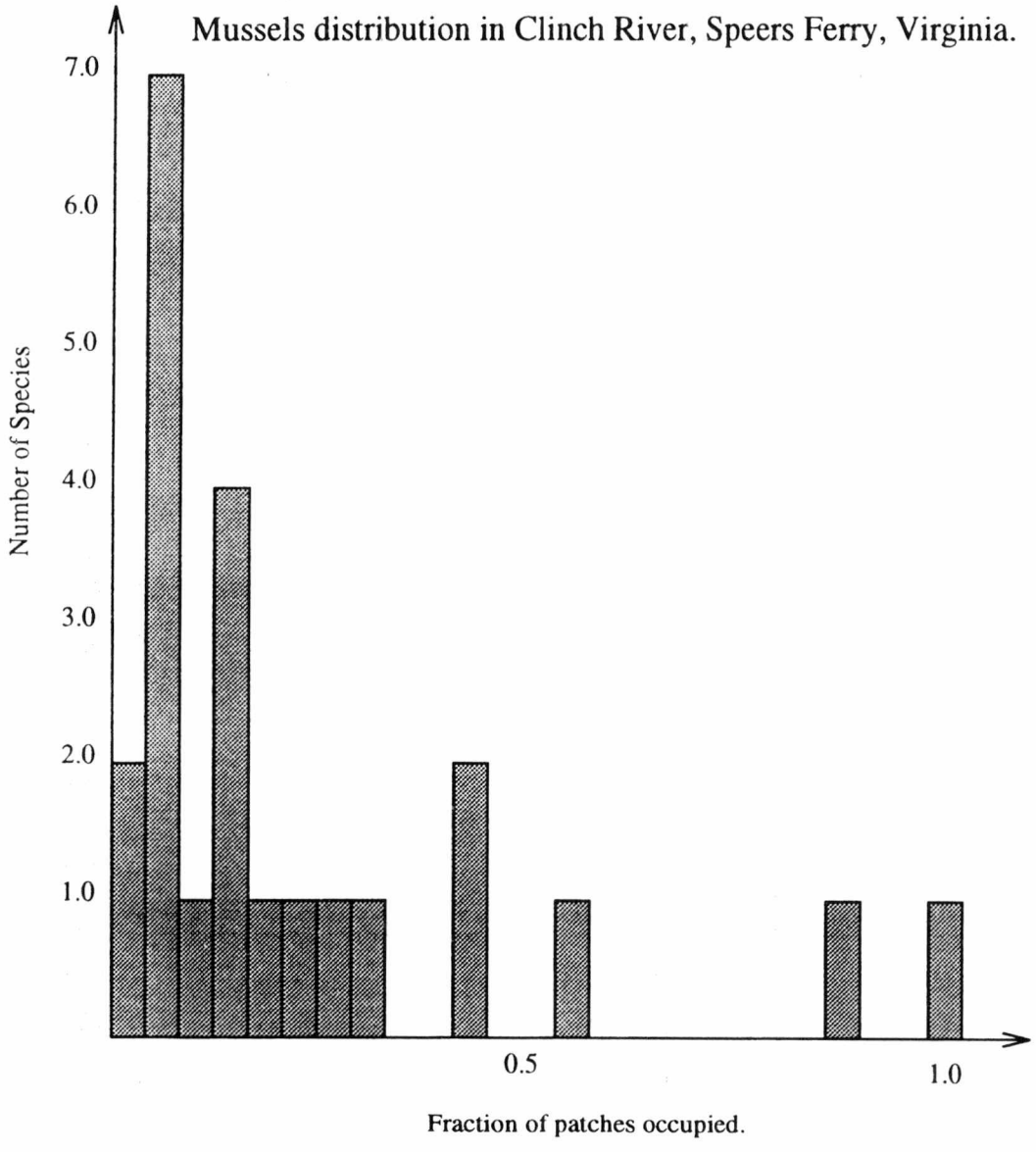

Figure 4.3. Mussels distribution at Clinch River, Speers Ferry, Virginia, from data collected by Dennis (1984).

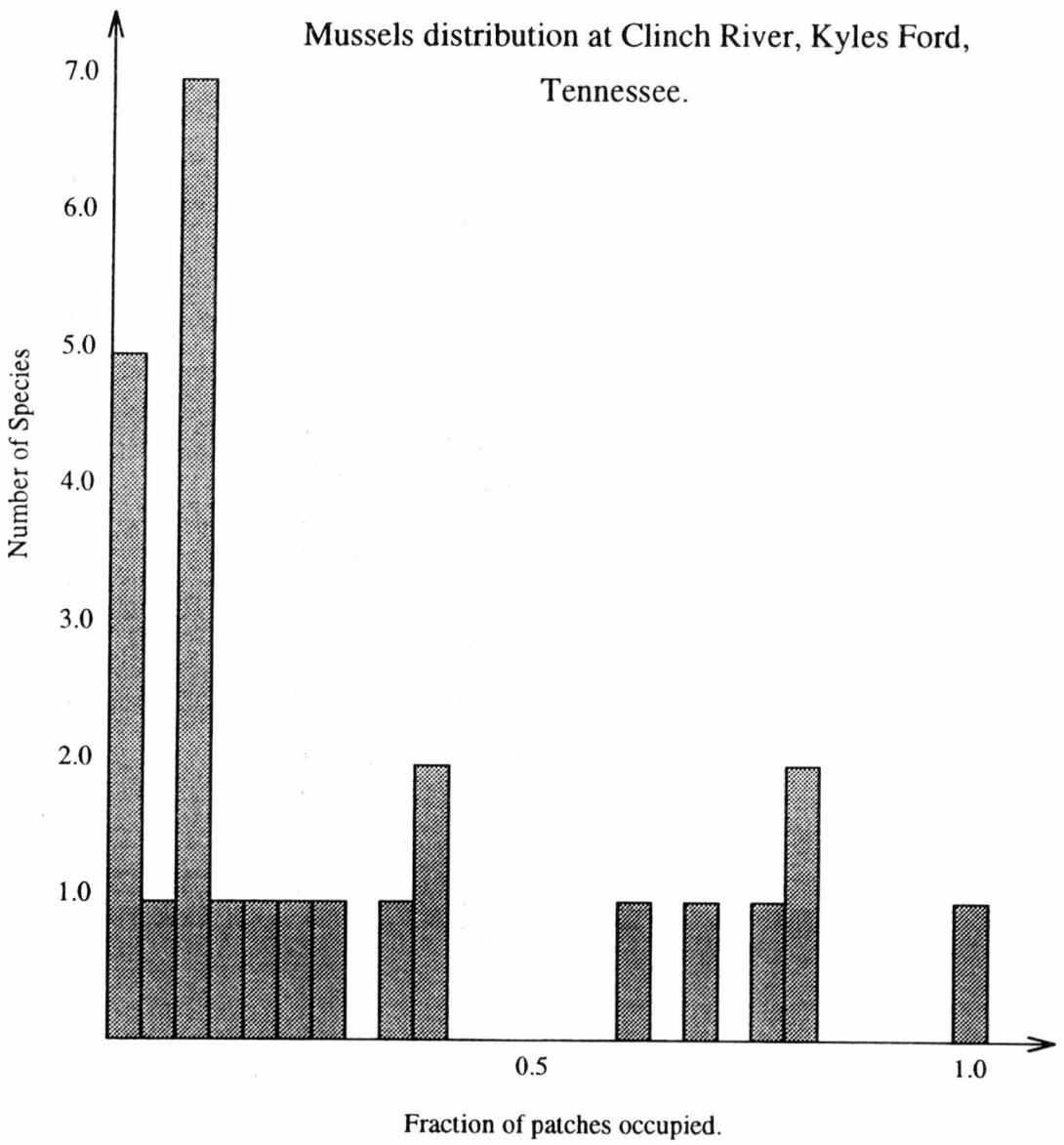

Figure 4.4. Mussels distribution at Clinch River, Kyles Ford, Tennessee, from data collected by Dennis (1984).

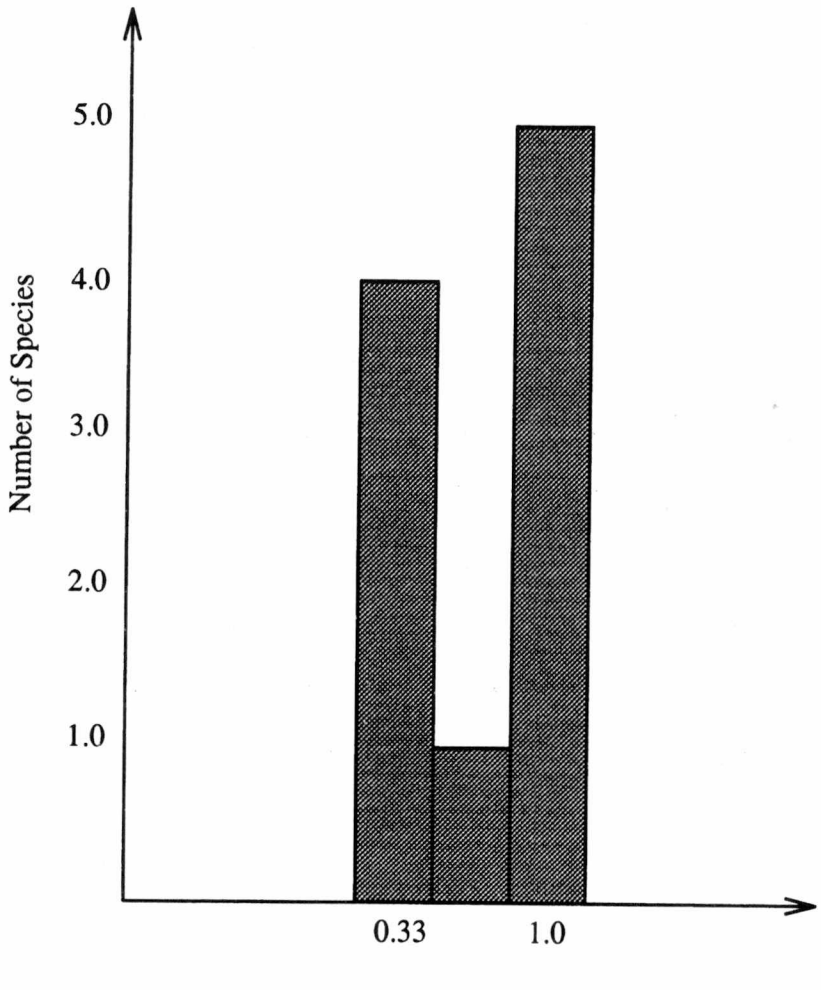

Figure 4.5. Mussels distribution at North Fork and Middle Fork, Holston River, Virginia, from data collected by Dennis (1984).

(1934) and Williams (1950) for similar patterns in other communities or the inherent nature of the mussel community? To attempt to shed light on this question, we use a computer model to explore the nature of community distributional patterns, that result from the assumptions built into the model description of the Unionid life-cycle.

The computer model is based on Roughgarden et al. (1983) concept of a single species, open marine population with space limited recruitment. However, it was necessary to modify the concept in numerous ways to both extend the model to a mussel community and to incorporate the unique life-cycle of the Unionids and their immediate habitats. The computer model is a multi-species age-structured model designed for 35 different species. There are 15 age-classes for each species in the model. The habitats of the mussels are divided into different spatial cells as shown in Figure 4.6. Each cell is an area in the river with uniform physical and chemical properties affecting the mussels. Each cell is then rated based on its suitability to mussel life. A cell with the suitability rating of 0.0 is incapable of supporting mussels life while a rating of 1.0 is optimum to mussel life.

A juvenile mussel dropping into a particular cell will live there its entire life. The mussel community in a given cell does not interact with mussel communities in other cells except during the breeding season. Glochidia from one cell can be carried and spread by fish hosts to other cells, with the

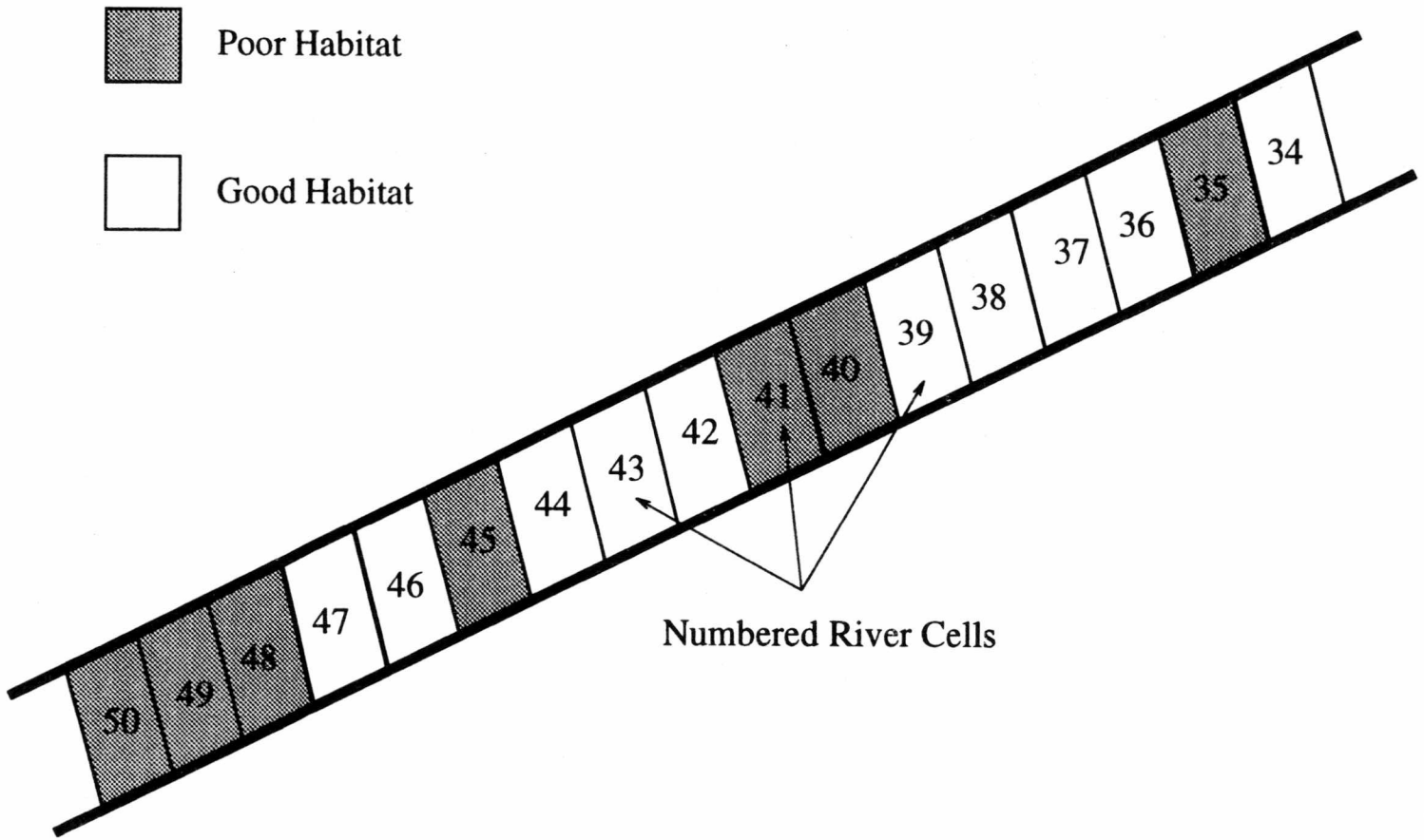

Figure 4.6. Segmentation of a hypothetical river into good and poor habitats.

highest likelihood of settling in the same or immediate neighboring cells. Habitat conditions in a cell do not influence the recruitment process of juvenile mussels, but play a big role in assuring the survival of juveniles after recruitment. The settling of the glochidia in a cell is by lottery, randomly matching cell to glochidia. A limit is placed on the maximum distance the chosen cell is from the home cell of the glochidia, as the movements of fish tend to be limited.

The physiological growth of the mussels is described by a set of deterministic functions which is individually parameterized for each species at each stage of growth. The general equation is:-

$$S_j^i = \alpha_j^i \, MS^i \, \frac{A_j^i}{MA^i} + \beta_j^i \, MS^i$$

where

S_j^i = size of species i mussel in cell j(m^2)

MS^i = maximum size of the species i mussel (m^2)

A_j^i = age of species i mussel in cell j(days)

MA^i = maximum life span of species i mussel (days)

α_j^i, β_j^i = growth coefficient for species i mussel at stage k of growth.

The mussels have three phases in their growth rate; intermediate in the first phase, accelerated in the second phase and slow in the final phase. Unlike humans, mussels

continue to grow in size their entire lives.

Probability of survival per unit time increases as the mussels age and grow in size. However, upon reaching their maximum age, the mussels undergo instantaneous mortality in the model. Besides size and age, the probability of surviving from one age-class to another is significantly affected by the habitat conditions and species type. The equation assumed for survival as a function of age, species and environmental crowdedness is:-

$$PSURV_j^i(A_j^i) = \left[\frac{A_j^i - \eta MA^i}{\lambda MA^i}(PMAX^i - PMIN^i) + PMIN^i\right]\left[1.0 - \exp^{-M^i \frac{F_j}{TA_j}}\right] \nu_j$$

where

$PSURV_j^i$ = probability of survival of species i mussel of age A_j^i in cell j

$PMAX^i$ = maximum probability of survival of species i mussel

$PMIN^i$ = minimum probability of survival of species i mussel

M^i = space-dependent survival coefficient of species i mussel

λ, η = proportionality constants

F_j = free space available in cell j (m^2)

TA_j = total area in cell j (m^2) and

ν_j = scaling coefficient incorporating habitat conditions in cell j and

A_j^i and MA^i are as defined earlier.

To simplify matters in the model, the mussels are allowed to reproduce up to a maximum of 3 times a year. Although each species has its own maturity and fecundity rate, the actual age of reproduction and fecundity rate is influenced heavily by habitat conditions, as well as the individual mussel's size and age. Ellis (1978) suggested that only 1 in 500,000 glochidia survive to reach the juvenile stage. The function is:-

$$JM_{kj}^i = \mu^i AM_k^i \, B^i \, \frac{F_j}{TA_j} \, \delta_j$$

where

JM_{kj}^i = total number of species i juveniles produced by species i mussels from cell k settling in cell j

AM_k^i = total number of sexually mature species i mussels in cell k

B^i = fecundity coefficient of species i mussel and

μ^i = coefficient of availability of species i mussel's fish host

δ_j = scaling coefficient incorporating habitat conditions in cell j

F_j, and TA_j are as defined before.

The probability of selecting cell j for settling by glochidia from home cell k is based on a normal probability distribution function. The function is:-

$$P(Y_i) = \frac{1}{\sqrt{2\pi}} e^{\frac{-Y_i^2}{2}}$$

and

$$X_i = |Y_i|\tau_i$$

where

$P(Y_i)$ = the probability function of species i mussel

Y_i = the scaled distance chosen for species i glochidia. Y_i is assumed to lie between -1.0 and 1.0.

X_i = the actual distance traveled between cell k and cell j for species i glochidia

τ_i = the maximum movement range of the fish host for species i mussel. The movement range of the fish host included foraging range as well as movement for other purposes.

Computer simulations

In the computer simulation, the mussels' habitat is made up of a hypothetical river with 2000 cells. Each cell is 100 m by 100 m. Less favorable patches for mussels are created randomly in the river. A stretch of adjacent cells make up a

patch, with each cell in the patch sharing the same suitability rating. A good patch has a rating of 1.0, while for the less favorable patches, rating ranges from 0.0 to 0.5. The number of cells in a poor patch is randomly selected with an upper limit of 35 cells. The construction of the patches was shown previously in Figure 4.6.

Each simulation was initiated by randomly choosing 4 favorable habitat cells and seeding them with a multi-species of mixed age-class mussels population. Five sets of simulations were performed, sets 1, 2, 3, 4 and 5. Each set tested the effects of a certain parameter of the mussels' characteristic on the mussels' distribution. Each set had 35 different species of mussels. The mussels in the simulation had life-spans ranging from 10 to 60 years.

Each simulation was split into two subsets, subset A and subset B. Subset A had mussels with shorter life-span while subset B had the longer-lived mussels. Communities made up of shorter-lived species attain equilibrium faster than do communities of their longer-lived sisters. Hence the reason for splitting the mussels into two groups that can be simulated separately is that greater efficiency in the simulation is possible. The splitting of the mussels into two groups did not affect the results of the simulation as competition in the form of spatial-crowding is not a big issue, unlike the marine barnacles studied by Roughgarden et al. (1983). Simulation subset A was performed over a 200 year

time interval, while for subset B it was 500 years. The time step used for both sets of simulation was 5 days.

The mussels used in all the simulations range from 4.5 cm^2 to 60 cm^2 in maximum size. The success rate of the glochidia in finding fish hosts range from 150 glochidia per female mussel per breeding season to 900 glochidia per female mussel per breeding season under optimal conditions. Nevertheless, the fecundity rate of mussels can be considerably lower in poorer patches. The dispersal range of the glochidia is from 0.5 km to 5 km. The onset of maturity occurs between 1.8 years to 26.4 years depending on species. The late maturity age set for some mussels is designed to indirectly mimic delayed birth time due to extreme unfavorable conditions.

Five replicate runs were executed for each set of simulation parameters to calculate the mean and varians in each set of simulations. The replicate runs had identical parameters except for the initial pseudo-random number seed. A random number seed was used in cell selection during the breeding season. The parameter values of the mussels in each simulation were varied systematically to determine their significance in the mussel communities.

Results

The results of the simulations are shown in Figures 4.7 through 4.11. Table 4.1 and Figure 4.7 show the parameters

Table 4.1. Mussels life-cycle parameters and prediction of percentage of habitat occupied for simulation 1.

Species	Max. Size (cm^2)	Max. Life-Span (yr)	Glochidia[A] Success Rate	Max. Fish Range[B] (km)	Maturity Age (yr)	Average % of habitat occupied[C]
1	4.5	10	150	1.0	1.8	22
2	4.5	10	600	1.0	2.6	73
3	4.5	10	300	2.0	4.4	100
4	4.5	10	600	2.0	1.8	100
5	4.5	10	150	5.0	2.6	99
6	8.0	15	150	1.0	3.9	7
7	8.0	15	300	2.0	2.1	32
8	15.0	15	300	2.0	2.7	31
9	15.0	15	300	3.0	3.3	100
10	10.0	15	150	5.0	3.9	100
11	10.0	20	300	1.0	5.2	52
12	6.0	20	600	2.0	8.8	90
13	8.0	20	150	3.0	3.6	38
14	6.0	20	900	3.0	5.2	100
15	8.0	20	150	5.0	5.2	41
16	10.0	30	300	1.0	7.8	43
17	10.0	30	600	2.0	9.0	87
18	30.0	30	900	3.0	17.4	94
19	15.0	30	300	4.0	4.2	100
20	20.0	30	300	5.0	7.8	92
21	20.0	40	450	1.0	10.4	58
22	20.0	40	150	3.0	5.6	91
23	15.0	40	300	3.0	8.8	100
24	20.0	40	450	3.0	7.6	92
25	15.0	40	225	5.0	10.4	54
26	10.0	50	900	0.5	13.0	11
27	60.0	50	600	1.0	13.0	31
28	40.0	50	300	1.5	13.0	58
29	4.5	50	525	4.0	9.0	100
30	20.0	50	150	5.0	13.0	41
31	40.0	60	600	1.0	15.6	18
32	50.0	60	300	3.0	6.0	88
33	35.0	60	900	4.0	26.4	62
34	60.0	60	900	5.0	6.0	100
35	60.0	60	600	5.0	15.6	82

[A]=Number of glochidia produced per female mussel per breeding season that succeed in finding fish host.
[B]=Movement range of different species of host hosts for foraging and other purposes.
[C]=Percentage of suitable habitat occupied by the mussels.

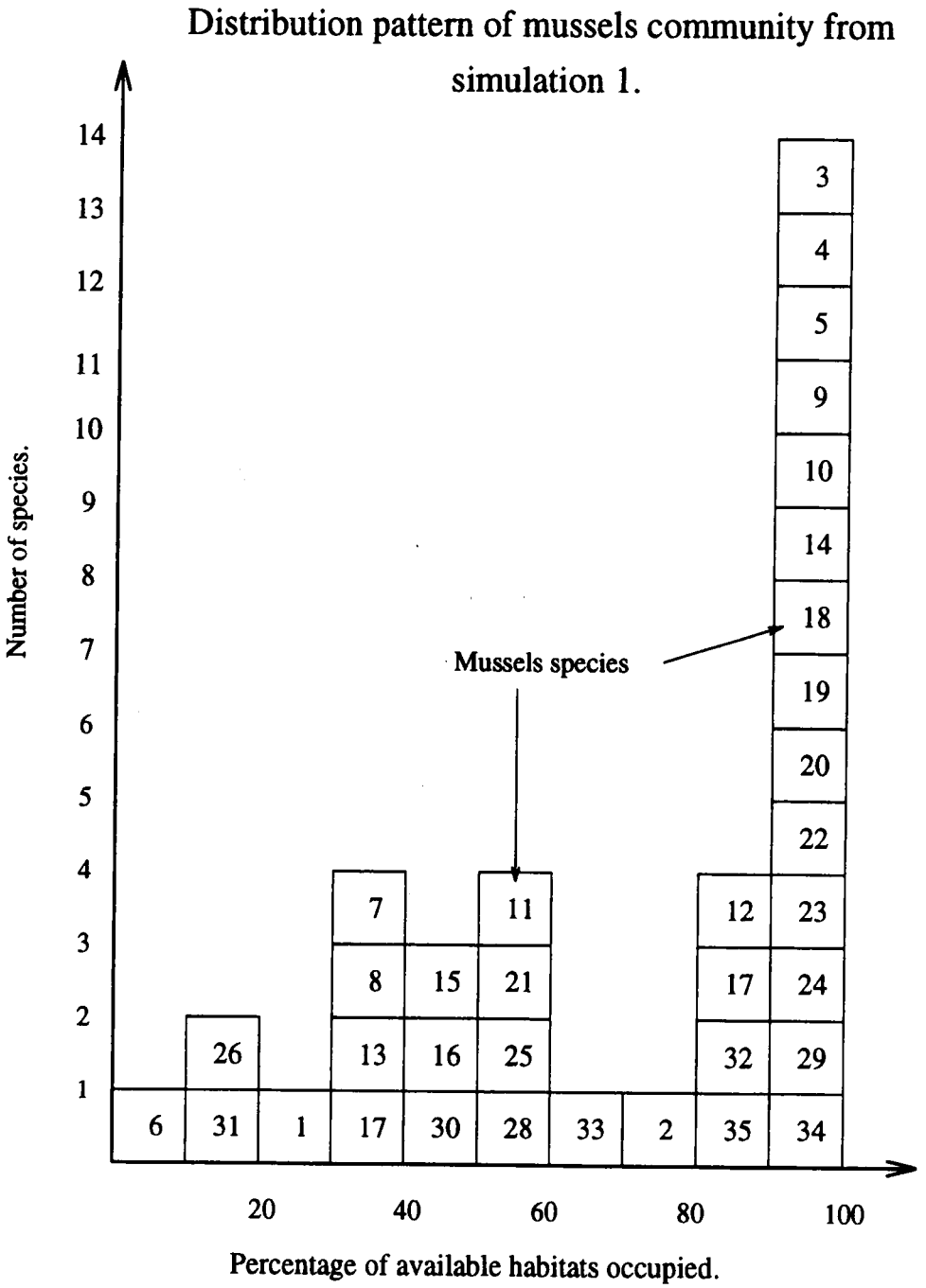

Figure 4.7. Results of simulation 1.

and the results for the baseline case called simulation set 1. Figures 4.8 through 4.11 show the results of different variations on the baseline case.

The mussels' maximum life-spans ranged from 10 to 60 years with 5 species for each life-span. Thus the mussels can be grouped informally into subgroups based on their life-spans. The baseline values for the mussels' characteristics are chosen 'semi-randomly', i.e.; subject to some constraints in the chosen values. As an example, each subgroup of mussels must have fish hosts with the minimum and maximum movement ranges of 1 km and 5 km respectively. The movement range of the fish hosts includes foraging range as well as movement for other purposes. Also, the earliest each subgroup of mussels can attain maturity is at 14% of the maximum life-span of that group. The minimum success rate of the glochidia in finding fish host is 150 glochidia/female mussel/breeding season, while the maximum success rate is 900 glochidia/female mussel/breeding season in the subgroup.

Figure 4.7 shows the results of the baseline simulation while Table 4.1 shows the mussels characteristics. The distribution of the mussels appears to be skewed to the right. It also shows there are 14 species of mussels which can be found in almost all the suitable habitats. Those 14 species shared the characteristics of having glochidia with high success rate in finding fish hosts, or fish hosts with large movement range or both features.

Thus to determine which of the characteristics is the primary cause of the mussels' wide distribution, we reduced the success rate of the glochidia to 150 glochidia/female mussel/breeding season for all of the above mentioned 14 species in simulation 2. Besides that we also changed the glochidia success rate to 150 glochidia/female mussel/breeding season for intermediate species, species 2, 3 and 33, to ascertain if the mussel community would then produce a bimodal distribution pattern. The rest of the parameters remained unchanged as noted on Table 4.2. Figure 4.8 exhibits some apparent form of bimodality from the results of simulation 2. But a closer examination of the numerical results proved that simulations 1 and 2 distributions are not statistically different. We tested the differences in the two simulations using Kolmogorov-Smirnov two-sample test. The results showed the unsigned difference, D, is 0.1428 compared to 0.3891 and 0.3246 for $D_{0.01}$ and $D_{0.05}$ respectively. Thus we can conclude, in general, that reducing the success rate of the glochidia does not affect the mussels' distribution significantly.

However, an exception occurs for species 14, 18, 33 and 34, where the impact is much heavier than expected. A possible explanation for the aberrant feature of those four species could be due to the four species' glochidia having an extremely high success rate previously. Further testing is necessary to verify this observation. The results of simulation 1 also appear to imply that the age of maturity

Table 4.2. Mussels life-cycle parameters and prediction of percentage of habitat occupied for simulation 2.

Species	Max. Size (cm^2)	Max. Life-Span (yr)	Glochidia[A] Success Rate	Max. Fish Range[B] (km)	Maturity Age (yr)	Average % of habitat occupied[C]
1	4.5	10	150	1.0	1.8	24
2	4.5	10	150*	1.0	2.6	68
3	4.5	10	150*	2.0	4.4	88
4	4.5	10	150*	2.0	1.8	92
5	4.5	10	150	5.0	2.6	100
6	8.0	15	150	1.0	3.9	8
7	8.0	15	300	2.0	2.1	32
8	15.0	15	300	2.0	2.7	28
9	15.0	15	150*	3.0	3.3	100
10	10.0	15	150	5.0	3.9	100
11	10.0	20	300	1.0	5.2	67
12	6.0	20	600	2.0	8.8	99
13	8.0	20	150	3.0	3.6	38
14	6.0	20	150*	3.0	5.2	24
15	8.0	20	150	5.0	5.2	61
16	10.0	30	300	1.0	7.8	34
17	10.0	30	600	2.0	9.0	95
18	30.0	30	150*	3.0	17.4	23
19	15.0	30	150*	4.0	4.2	100
20	20.0	30	150*	5.0	7.8	91
21	20.0	40	450	1.0	10.4	56
22	20.0	40	150	3.0	5.6	92
23	15.0	40	150*	3.0	8.8	82
24	20.0	40	150*	3.0	7.6	89
25	15.0	40	225	5.0	10.4	53
26	10.0	50	900	0.5	13.0	14
27	60.0	50	600	1.0	13.0	35
28	40.0	50	300	1.5	13.0	65
29	4.5	50	150*	4.0	9.0	90
30	20.0	50	150	5.0	13.0	41
31	40.0	60	600	1.0	15.6	18
32	50.0	60	300	3.0	6.0	88
33	35.0	60	150*	4.0	26.4	14
34	60.0	60	150*	5.0	6.0	19
35	60.0	60	600	5.0	15.6	84

[A]=Number of glochidia produced per female mussel per breeding season that succeed in finding fish host.
[B]=Movement range of different species of fish hosts for foraging and other purposes.
[C]=Percentage of suitable habitat occupied by the mussels.
*=New changes made to the mussels' characteristics.

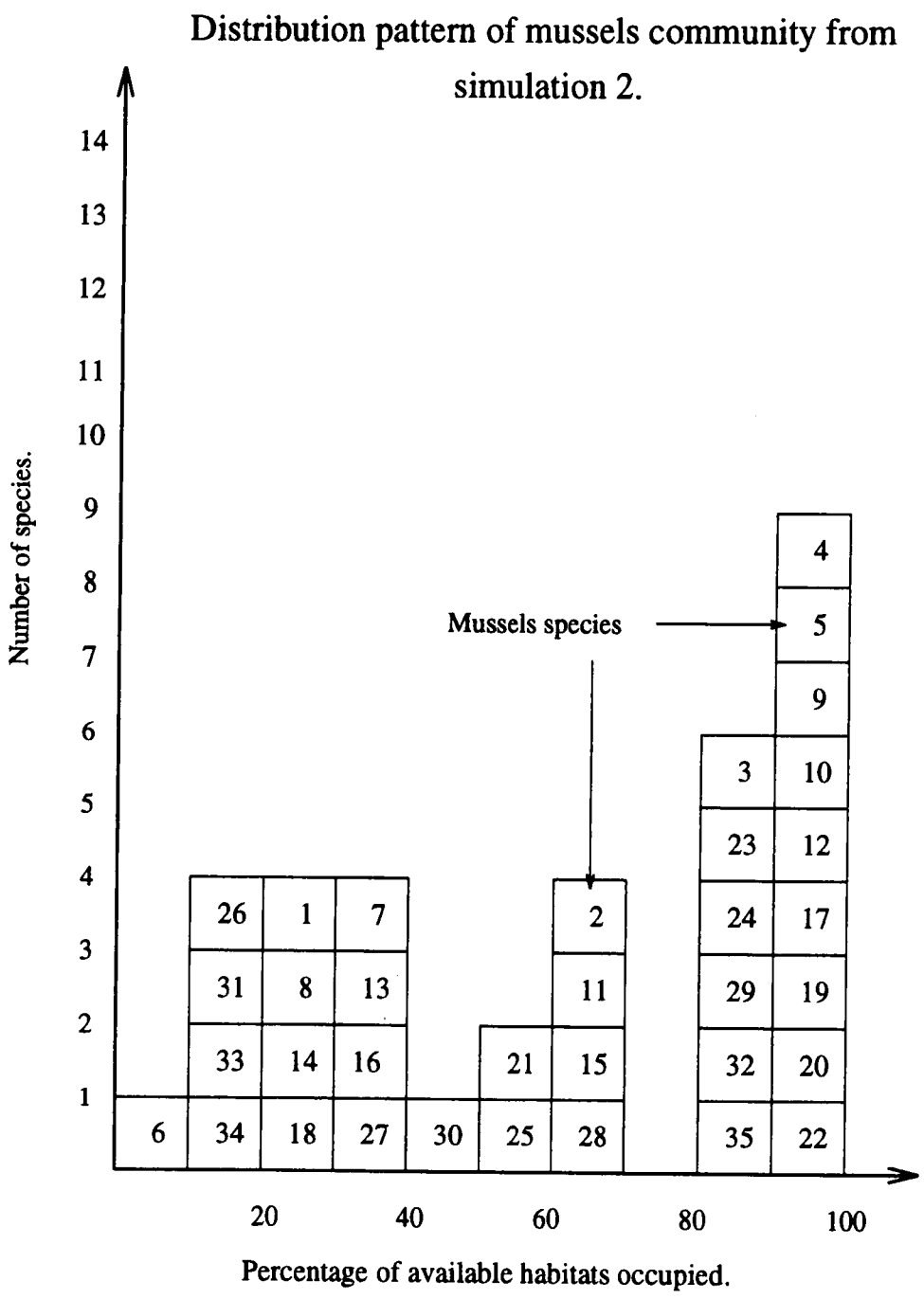

Figure 4.8. Results of simulation 2.

does not impact heavily the mussels' distribution.

In simulation 1, species 14 mussels attain maturity much later than species 13 but species 14's glochidia are six times more successful than species 13's, which resulted in species 14 being more widely distributed then species 13. A similar observation is seen on species 22 and 23. Thus in simulation 3, we changed the age of maturity of the mussels to test the observation.

Changes were made to delay the attainment of maturity in the 14 prolific species of mussels mentioned earlier in simulation 1 for simulation 3. Table 4.3 tabulates the changes made and Figure 4.9 graphically shows the result of this simulation. The distribution is skewed to the right and looks almost identical to Figure 4.7. The Kolmogorov-Smirnov test performed on the results of simulations 1 and 3 suggests the two distributions are the same. The unsigned difference, D is 0.1714 while $D_{0.05}$ is 0.3246. Thus changing the age of maturity does not affect the mussels' distribution seriously.

Suspecting the size of the movement range of the fish host to be responsible for the mussels' distributional patterns, we reduced the movement range of the fish hosts to 1 km for 11 of the 14 abundant species. Furthermore, we also changed all fish hosts with 5 km movement range to 1 km. Table 4.4 shows the changes made for simulation 4. The results of the simulation are displayed in Figure 4.10. The mussels' distribution is now skewed to the left, opposite to

Table 4.3. Mussels life-cycle parameters and prediction of percentage of habitat occupied for simulation 3.

Species	Max. Size (cm^2)	Max. Life-Span (yr)	Glochidia[A] Success Rate	Max. Fish Range[B] (km)	Maturity Age (yr)	Average % of habitat occupied[C]
1	4.5	10	150	1.0	1.8	23
2	4.5	10	600	1.0	2.6	79
3	4.5	10	300	2.0	2.6*	100
4	4.5	10	600	2.0	2.6*	100
5	4.5	10	150	5.0	2.6	91
6	8.0	15	150	1.0	3.9	7
7	8.0	15	300	2.0	2.1	25
8	15.0	15	300	2.0	2.7	31
9	15.0	15	300	3.0	3.9*	94
10	10.0	15	150	5.0	3.9	100
11	10.0	20	300	1.0	5.2	66
12	6.0	20	600	2.0	8.8	92
13	8.0	20	150	3.0	3.6	37
14	6.0	20	900	3.0	8.8*	98
15	8.0	20	150	5.0	5.2	35
16	10.0	30	300	1.0	7.8	32
17	10.0	30	600	2.0	9.0	93
18	30.0	30	900	3.0	17.4	94
19	15.0	30	300	4.0	17.4*	89
20	20.0	30	300	5.0	17.4*	91
21	20.0	40	450	1.0	10.4	59
22	20.0	40	150	3.0	10.4*	89
23	15.0	40	300	3.0	10.4*	98
24	20.0	40	450	3.0	10.4*	94
25	15.0	40	225	5.0	10.4	56
26	10.0	50	900	0.5	13.0	13
27	60.0	50	600	1.0	13.0	37
28	40.0	50	300	1.5	13.0	58
29	4.5	50	525	4.0	13.0*	100
30	20.0	50	150	5.0	13.0	41
31	40.0	60	600	1.0	15.6	24
32	50.0	60	300	3.0	6.0	79
33	35.0	60	900	4.0	26.4	63
34	60.0	60	900	5.0	26.4*	89
35	60.0	60	600	5.0	15.6	86

[A]=Number of glochidia produced per female mussel per breeding season that succeed in finding fish host.
[B]=Movement range of different species of fish hosts for foraging and other purposes.
[C]=Percentage of suitable habitat occupied by the mussels.
*=New changes made to the mussels' characteristics.

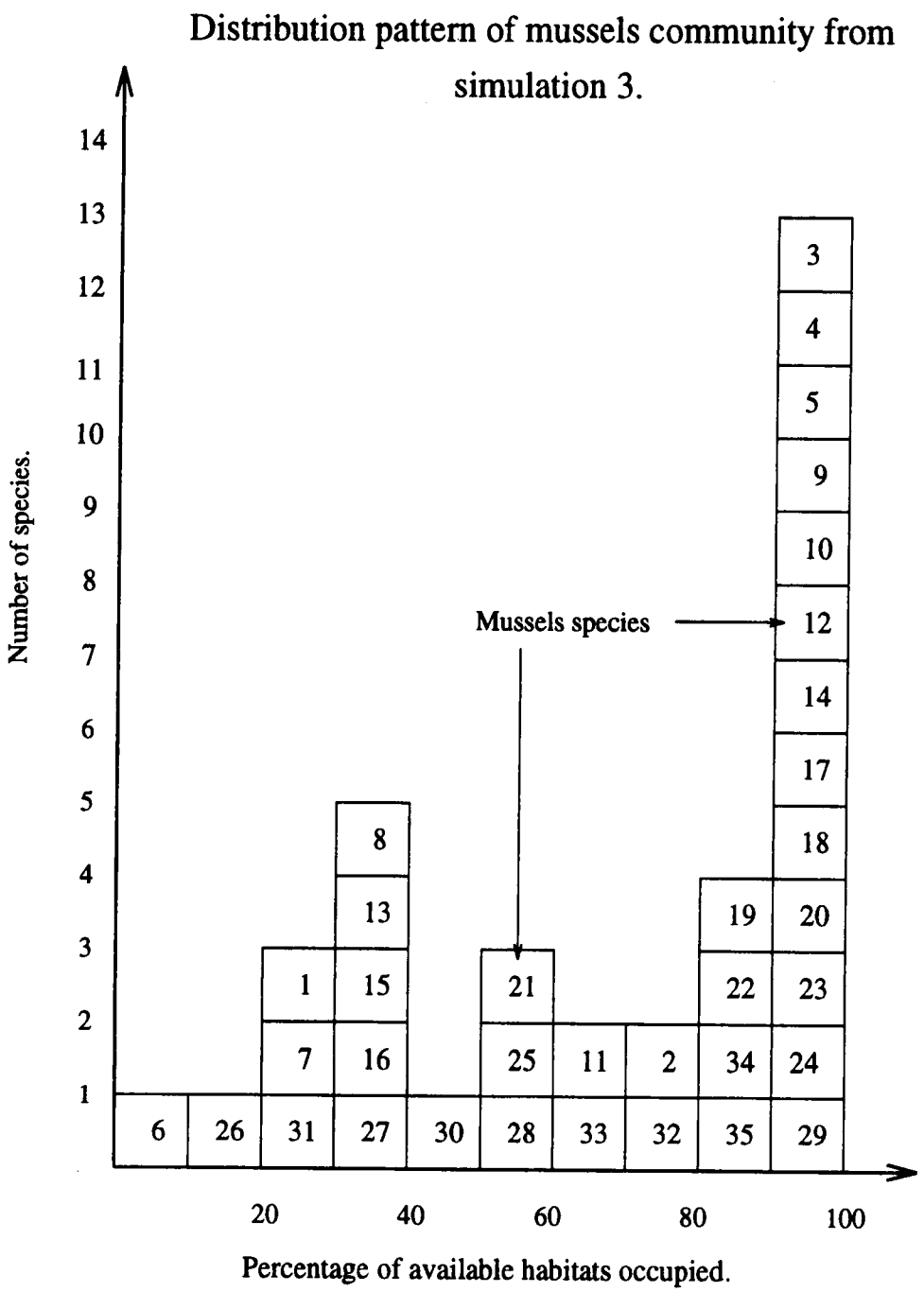

Figure 4.9. Results of simulation 3.

Table 4.4. Mussels life-cycle parameters and prediction of percentage of habitat occupied for simulation 4.

Species	Max. Size (cm^2)	Max. Life-Span (yr)	Glochidia[A] Success Rate	Max. Fish Range[B] (km)	Maturity Age (yr)	Average % of habitat occupied[C]
1	4.5	10	150	1.0	1.8	25
2	4.5	10	600	1.0	2.6	71
3	4.5	10	300	1.0*	4.4	19
4	4.5	10	600	1.0*	1.8	85
5	4.5	10	150	1.0*	2.6	17
6	8.0	15	150	1.0	3.9	8
7	8.0	15	300	2.0	2.1	34
8	15.0	15	300	2.0	2.7	36
9	15.0	15	300	1.0*	3.3	17
10	10.0	15	150	1.0*	3.9	11
11	10.0	20	300	1.0	5.2	60
12	6.0	20	600	2.0	8.8	92
13	8.0	20	150	3.0	3.6	39
14	6.0	20	900	1.0*	5.2	72
15	8.0	20	150	1.0*	5.2	14
16	10.0	30	300	1.0	7.8	43
17	10.0	30	600	2.0	9.0	87
18	30.0	30	900	1.0*	17.4	51
19	15.0	30	300	1.0*	4.2	42
20	20.0	30	300	5.0	7.8	91
21	20.0	40	450	1.0	10.4	63
22	20.0	40	150	1.0*	5.6	29
23	15.0	40	300	1.0*	8.8	37
24	20.0	40	450	1.0*	7.6	51
25	15.0	40	225	1.0*	10.4	26
26	10.0	50	900	0.5	13.0	11
27	60.0	50	600	1.0	13.0	28
28	40.0	50	300	1.5	13.0	61
29	4.5	50	525	1.0*	9.0	28
30	20.0	50	150	1.0*	13.0	8
31	40.0	60	600	1.0	15.6	25
32	50.0	60	300	3.0	6.0	88
33	35.0	60	900	4.0	26.4	59
34	60.0	60	900	1.0*	6.0	48
35	60.0	60	600	5.0	15.6	85

[A]=Number of glochidia produced per female mussel per breeding season that succeed in finding fish host.
[B]=Movement range of different species of fish hosts for foraging and other purposes.
[C]=Percentage of suitable habitat occupied by the mussels.
*=New changes made to the mussels' characteristics.

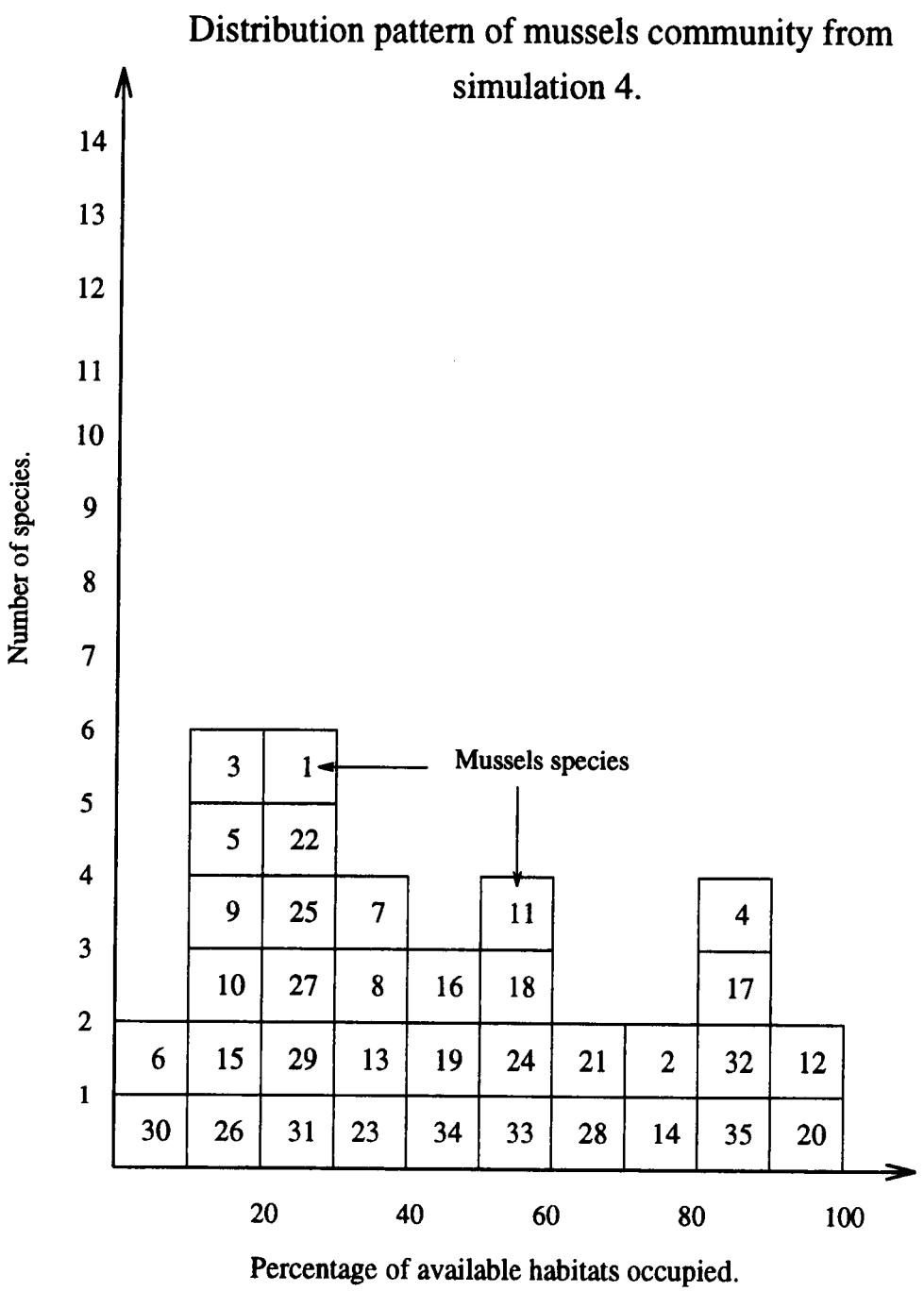

Figure 4.10. Results of simulation 4.

what had been the case in previous simulations. This indicates the size of the fish hosts' movement range is very much responsible for the distribution pattern produced. This is confirmed by the Kolmogorov-Smirnov test. The unsigned D is 0.3714, which is greater then 0.3214 for $D_{0.05}$.

The reduction in fish hosts' movement range caused many previously abundant species in simulation 1, such as species 3, 5, 9, 10, 22 and 29, to become 'rare', found in less then 30% of the total available habitats. It is not shown here, but reducing the fish hosts movement range to 0.5 km can cause the mussels to become extinct, unless the mussels have glochidia with success rate of 600 or more. Even then, the mussels are still found in less then 30% of the habitats.

For the last simulation, simulation 5, we tried to produce a 'true' bimodal distribution by selectively changing the fish hosts movement range for some species of mussels. Table 4.5 noted the changes made and Figure 4.11 presents the graphical result. It shows a clear division of core-satellite species distributions. Thus it seems the size of the fish hosts movement range plays a key role in determining the distribution patterns of the mussels community.

Discussion and conclusion

Overall, the most important factor governing the distribution of the mussels appears to be the size of the movement range of their fish hosts. Fish hosts with large

Table 4.5. Mussels life-cycle parameters and prediction of percentage of habitat occupied for simulation 5.

Species	Max. Size (cm^2)	Max. Life-Span (yr)	Glochidia[A] Success Rate	Max. Fish Range[B] (km)	Maturity Age (yr)	Average % of habitat occupied[C]
1	4.5	10	150	1.0	1.8	18
2	4.5	10	600	1.0	2.6	76
3	4.5	10	300	1.0*	4.4	17
4	4.5	10	600	1.0*	1.8	83
5	4.5	10	150	1.0*	2.6	15
6	8.0	15	150	1.0	3.9	7
7	8.0	15	300	2.0	2.1	32
8	15.0	15	300	2.0	2.7	31
9	15.0	15	300	1.0*	3.3	17
10	10.0	15	150	1.0*	3.9	12
11	10.0	20	300	3.0*	5.2	100
12	6.0	20	600	2.0	8.8	89
13	8.0	20	150	3.0	3.6	39
14	6.0	20	900	1.0*	5.2	79
15	8.0	20	150	1.0*	5.2	10
16	10.0	30	300	2.0*	7.8	86
17	10.0	30	600	2.0	9.0	86
18	30.0	30	900	3.0	17.4	94
19	15.0	30	300	3.0*	4.2	90
20	20.0	30	300	5.0	7.8	92
21	20.0	40	450	2.0*	10.4	80
22	20.0	40	150	1.0*	5.6	27
23	15.0	40	300	1.0*	8.8	37
24	20.0	40	450	3.0	7.6	94
25	15.0	40	225	1.0*	10.4	25
26	10.0	50	900	0.5	13.0	11
27	60.0	50	600	1.0	13.0	31
28	40.0	50	300	3.0*	13.0	71
29	4.5	50	525	1.0*	9.0	28
30	20.0	50	150	1.0*	13.0	8
31	40.0	60	600	1.0	15.6	20
32	50.0	60	300	3.0	6.0	86
33	35.0	60	900	5.0*	26.4	88
34	60.0	60	900	4.0*	6.0	89
35	60.0	60	600	5.0	15.6	84

[A]=Number of glochidia produced per female mussel per breeding season that succeed in finding fish host.
[B]=Movement range of different species of fish hosts for foraging and other purposes.
[C]=Percentage of suitable habitat occupied by the mussels.
*=New changes made to the mussels' characteristics.

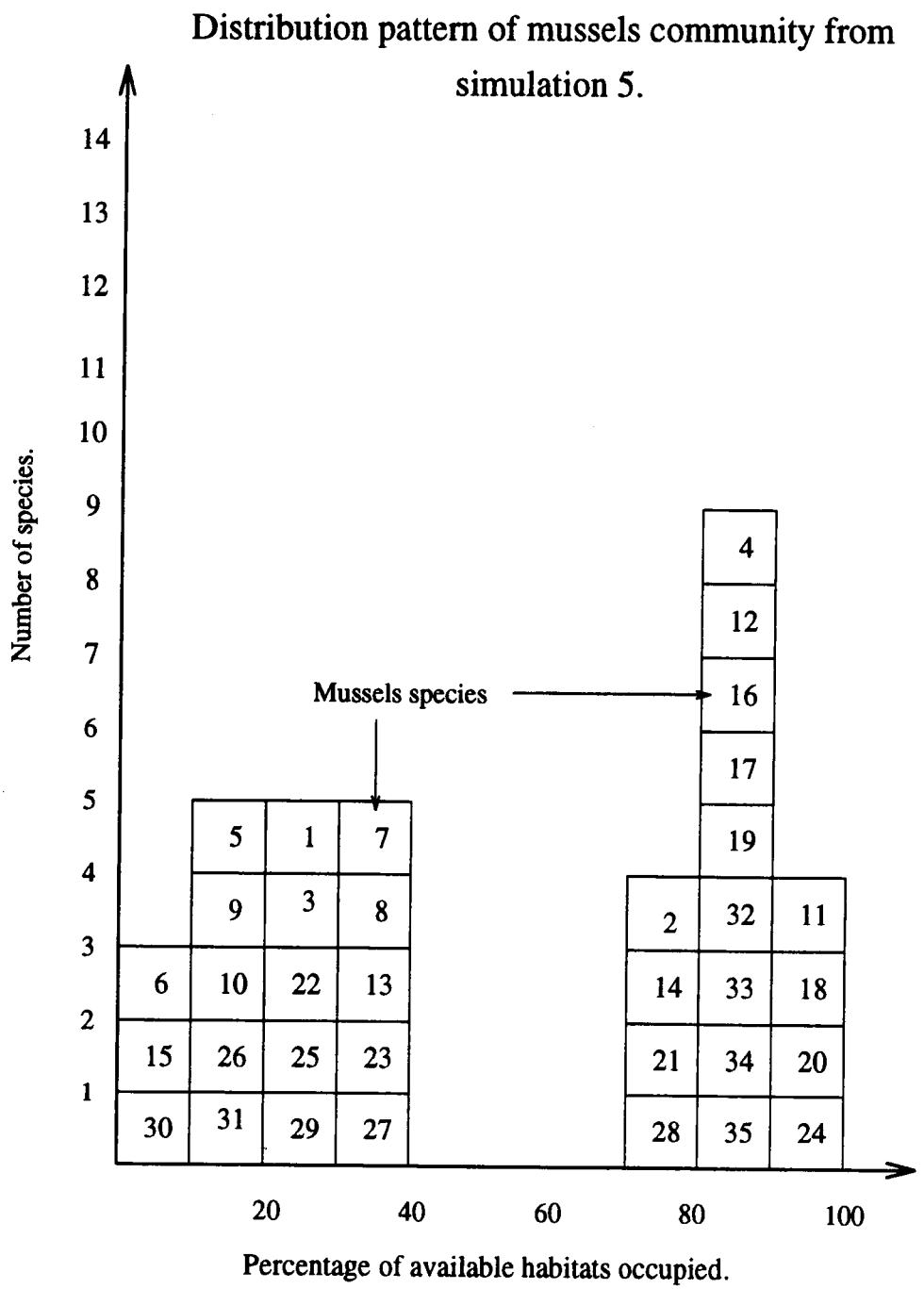

Figure 4.11. Results of simulation 5.

movement range distribute the mussels widely. Mussels that are widely distributed also tend to be abundant in numbers, fitting aptly the description of core species as proposed by Hanski (1982 and 1993). In general in the simulations, mussels which have fish host movement range of at least 2 km in radius are widely distributed as shown in simulation 1. Those mussels also tend to be very abundant in numbers and can be called core-species. For mussels with fish host movement ranges of 1 km or less in radius, the success rate of the glochidia in finding fish hosts will determine if the mussels become rare or intermediate in distribution as indicated in simulation 4.

When the success rate of finding fish hosts is at least 300 glochidia/female mussels/breeding season, the mussels will have an intermediate distribution pattern. In cases when the success rate of finding fish hosts is less then 300 glochidia/female mussel /breeding season the mussels will exhibit satellite species characteristics, i.e.; it will be rare in numbers as well as distribution. However the success rate of the glochidia by itself is not of primary importance, as its effects are not significant when the fish hosts movement range is large enough, as demonstrated in simulation 2.

The age of maturity is another factor that does not impact the distribution patterns of the mussels directly. However it does have a secondary influence when the success

rate of the glochidia is low and the fish hosts movement range is small as well. In such cases, maturing late will cause the mussel's distribution to shrink significantly as seen in species 1, 3 and 5 in simulation 4.

Since space limitation is not a constraint for the mussel communities, the sizes of the individual mussels have very little influence over the distributional patterns of the mussels. However, it is observed that the individual characteristics of the mussels that make up a community do exert an effect on the overall distributional patterns of the mussels community. Selectively choosing the mussels' species that make up a community, we can induce the distributional pattern we want.

Large movement ranges in the fish hosts do not always assure that the mussels species will be abundant and widely distributed. It can nevertheless ensure that the distribution of the mussels will be intermediate at least, as exhibited in Table 4.1 for species 15, 25, 30 and 35. Thus the general rule mentioned earlier regarding core species is still valid. Core species of mussels always have fish hosts with large movement ranges but the reverse is not always true.

In cases where movement ranges of the fish hosts are similar for different species of mussels, the success rate of the glochidia in finding fish hosts will be the deciding factor in determining how widely distributed the mussels are going to be. Hence we can conclude that there are two

characteristics that identify a mussel as a core species; fish hosts with large movement range and high success rate of glochidia.

The results of simulation 5 do resemble slightly the field data collected by Dennis (1984) and displayed in Figures 4.3, 4.4 and 4.5. To reproduce the bimodal distribution in simulation 5, we had to curtail the movement ranges of the fish hosts. Hence we reiterate that the availability of fish hosts and their movement ranges will ultimately determine the distributional patterns of the mussels. This observation concurs with hypotheses proposed by Stein (1971) and Fuller (1974) on why the Unionids are slowly heading for extinction.

Hence the results from this research suggest that rejuvenation of various mussels communities might be achieved by making more fish hosts available, artificially or otherwise. But for recolonization purposes, as well as to spread the mussels populations significantly, the fish hosts must be allowed direct access to those habitats of concern, i.e. enlarging their foraging ranges. Furthermore, this research also suggests using only core species of mussels for recolonization purposes. Lastly, it appears that the removal of core species can enhance the population of satellite species. In closing, the authors feel that more field data and non-destructive field tests by other researchers are necessary to enhance the computer model and to establish the claims.

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PART V

PARALLEL ALGORITHM FOR AN AGE-STRUCTURED POPULATION MODEL

Introduction

The United Nations held its first Conference on the Environment in Stockholm in 1972. Then, environmental problems were perceived as the problems of the wealthy industrialized nations of the world. However this is no longer true, as the environmental problems of today tend to transcend international borders, national laws and regional customs. Some examples of these problems are the growing spread of deserts, the gradual global warming, the growth of the human populations, and the exhaustion of ecological communities.

Mathematical and computer models are currently the tools of choice employed to study environmental problems. In particular, these models are applied to study or predict changes in the ecosystems due to anthropogenic activities. The use of these models have given researchers numerous insights into the mechanisms at work in the ecosystems, as well as proving to be useful in ecological risk assessment studies. The use of computer models in those studies is helpful in guiding management decisions aimed at protecting ecosystems, or components of these ecosystems, such as species populations (EPA, 1992).

However, in applying modeling to practical ecological problems, the degree of realism and detail that can be incorporated into the model is of great importance. Therefore, in such cases simulation models would appear to be more useful than mathematical models that are simple enough to be solved analytically. The impressive improvements in computational speed and memory in personal computers and workstations achieved in the 1980's, have in general allowed researchers to build some fairly complex and sophisticated simulation models. Nevertheless, those models still lack a high degree of realism, and incorporation of more details in the models is needed. Incomplete empirical information, such as knowledge about the ecosystem and species populations and the mechanisms that control them, are the main factors that have limited the development of simulation models.

In cases where more empirical information is available, limits on computer memory may constrain the amount of information that can be included in the simulation models. Besides that, computational speed can also become an issue in detailed simulation models, as computational time increases with the complexity of the model. This can quickly and easily become a dominating constraint, especially in cases where multiple runs of the model are required. These limitations in general have resulted in a restriction on the multiplicity of species, the size of the spatial dimension and/or spatial heterogeneity being studied in the simulation models.

A possible solution for the computer limitations is the parallel computational approach. The basic idea behind parallel computing is to link as many processors together as needed to reduce the computational time. This is accomplished by removing the bottlenecks occurring in the sequential programs by allowing many parts of the simulation to be worked on simultaneously. As an example, if one processor can solve a problem in 60 minutes, then two processors will do it in 30 mins and four processors in 15 minutes, provided the problem can be evenly divided between the processors.

However the usefulness of the parallel approach will depend largely on how well it fits the particular problem. Intuitively some types of problems are more suited for parallelization then others. For example, the effects of habitat fragmentation on elk and bison in a landscape ecology have been studied by Berry et al. (1994). Another example is the drainage basin analysis by Mower (1994), where the drainage basin is divided into grid cells. Each cell has its own slope, aspect and cell drainage direction, and is assigned to a single processor. Simultaneous computation on all the grid cells is then conducted.

In this paper, we study the Unionid mussel communities in the United States of America. We report on an application of a parallelization on this particular ecological problem and compare sequential and parallel codes. An evaluation of the benefits and weaknesses of the parallelization is included.

A model of a freshwater mussel population

(a) Life-cycle of the Unionids

The Unionid mussels were originally highly diverse in the North America river systems, but many of these mussels have gone extinct while others are declining rapidly in population numbers (Stansbery and Clench, 1974; Bates and Dennis, 1978; Ahlstedt, 1984). The purpose of the model is to understand the reasons for the declines, which are hypothesized to be attributed to anthropogenic changes in river habitats.

The life cycle of the mussel is shown in Figure 5.1. The Unionids are freshwater mussels with life-spans ranging from 9-60 years (Stein, 1971; Lewandowski and Stanczykowska, 1975; Burky, 1983; Jirka, 1986). They are sessile creatures and are parasitic on fish in the larval stage of their life cycle. The sperm are released into the water and carried by the water currents to the female mussels for fertilization and incubation (Edgar, 1965). After that, the female mussels release the larvae into the water, often triggered by the close approach of a fish.

The larvae, called glochidia, are parasitic on fish and are dispersed by the fish host away from the location of the parents. Different species of mussels have different species of fish as host (Fuller, 1974). Density-dependent competition may occur among glochidia for fish hosts (Stein, 1971; Fuller, 1974).

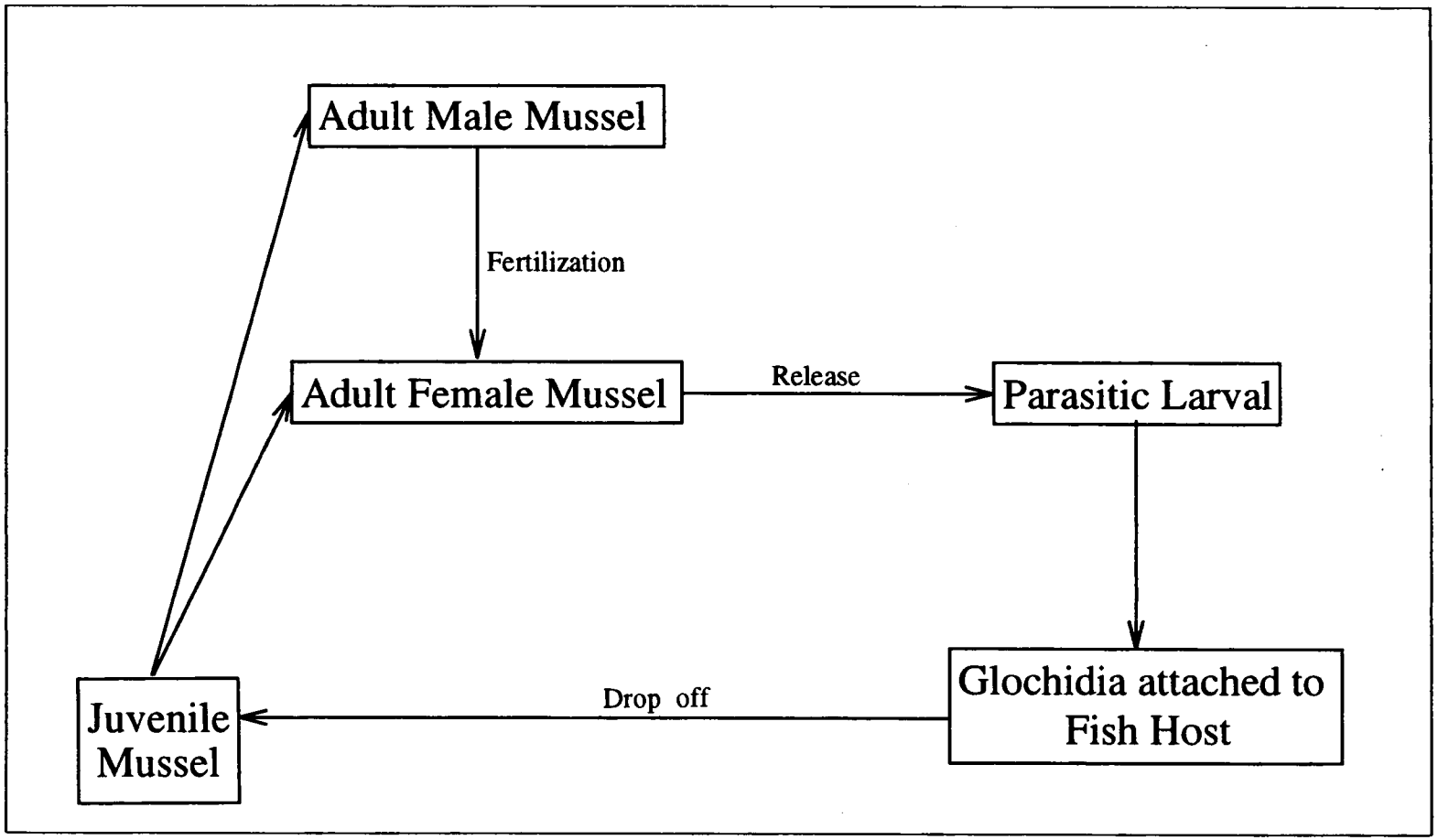


Figure 5.1. Life-cycle of the Unionids.

(b) The simulation model

The mathematical model used in this study is based on the Roughgarden et al.(1985) concept of a single open marine population with space-limited recruitment. However several major modifications were necessary to simulate the life cycle of the Unionids. The present simulation model uses an age-structured modeling approach, a generalization of the Leslie matrix model to include density dependence and spatial dispersal.

The model simulates the whole population of a particular mussel community in the river system, composed of age class cohorts. The river system is modeled as a set of contiguous spatial cells with varying habitat suitability index to the mussels. The mussel metapopulation in each cell has 15 different age classes, and there can be a maximum of 35 different species in the model. Deterministic equations describe the physiological growth and the probability of survival of the mussels. Reproduction occurs upon reaching sexual maturity and occurs at the same time each year for the mussels. The dispersal of the glochidia is assumed to occur through the random movements of the fish hosts. The glochidia are assumed to be transported away from the spatial cell of the parent, and to settle at locations with decreasing probability as the distance increases.

The number of cells in a river system can range from several hundreds to thousands, depending on the variability of

habitats and the size of the river system. The characteristics of each cell are parameterized by five variables. As mentioned earlier, each cell can have up to 35 different species of mussels, and each species can have up to 15 different age classes. Thus the number of variables can easily run into thousands or tens of thousands. Computing and assessing those variables can be very time consuming, which makes this ecological problem a likely candidate for parallelization. Refer to Lee and DeAngelis (1996) for further details of the computer model.

Parallelization of the computer code

(a) Motivations for parallelizations

The mussels are sessile organisms, but they are usually found at densities low enough to suggest very little inter- or intra-specific competition occurs in the population most of the time. Hence, we can assume interactions among the individual mussels are almost non existent, especially when there is an abundance of food and space, except during the breeding season. This lack of interactions is a primary factor making possible the construction of a parallel algorithm for the mussel model. Intuitively, we would assign each age class of each species in each cell (called age class cohort) to a processor. There are some similarities in this approach to the assignment used by Ramachandramurthi et al. (1996) in their parallel algorithm of physiologically

structured population models. However, this approach is less suitable for the mussel model. This is because conservatively there can be 525,000 (15X35X1000) age class cohorts in a population, which would require an assignment of 130 age class cohorts to a single processor, a multi layering of data on the processors. But more importantly, to account for density dependent interactions for a population within a cell there may be inter-processor communications. Besides, the number of age class cohorts are dynamic through time. Thus a constant reassignment of age class cohorts to processors may be needed to utilize the processors efficiently.

A better alternative would be the assignment of a community of mussels to a processor. We define a community of mussels here, as a group of mussels regardless of species or age, living together within a spatial boundary (a spatial cell). This division is called cell-to-processor assignment. This form of parallelization is much more efficient as it minimizes expensive inter-processor communication. This is convenient, as mussel communities from different cells in the model do not interact with each other except during the breeding season, just as in nature. Also, the number of cells remains constant throughout the simulation run. Hence there is no necessity for reassignment of processors during the simulation run, unlike the allocation of age class cohorts to processors.

Furthermore the mussels exist in a variety of habitats and each type of habitat exerts its own distinct influence on the mussels. However the influence of the habitats is localized, and with cells/habitats-to-processors assignment, the processors do not need to communicate with each other to assess the habitats' impacts on the mussels, while still allowing the limited effects of density-dependent interactions within a mussel community to take place.

The parallel algorithm used here is designed for a MasPar MP-2 machine. We will briefly describe some of the key features of the MasPar MP-2 in next section, followed by details of the parallel algorithm. A sequential algorithm using FORTRAN 77 running in the Unix environment is used as a benchmark for comparison with the parallel algorithm. The sequential algorithm also serve as a starting point in the development of the parallel algorithm.

(b) MasPar MP-2

There are two different approaches towards parallel computing today. They involve either linking loosely a few (fewer than 32) powerful processors or connecting tightly many (more then 1000) less powerful processors together. The MasPar MP-2 uses the second approach and is the computer used in this study. The MP-2 consists of a Front End (FE) workstation and a Data Parallel Unit (DPU). The DPU is made up of an Array Control Unit (ACU) and the processor elements

(PE). MP-2 has 4096 processors in its PE array and each of these PEs is a RISC processor with 64KB of memory (MasPar, 1992). The ACU has 512KB of memory. By default the MP-2 will allocate 16KB of PE and 128KB of ACU memory to each user unless specified otherwise. The function of the ACU is to control the PE array.

The MP-2 is a Single Instruction Multiple Data (SIMD) machine. A SIMD machine sends identical instructions synchronously to all of its processors. Thus each processor will evaluate the same type of data at the same time. The MP-2 has two programming languages, the MasPar Fortran (MPF) and the MasPar Language (MPL). MPF is an implementation of the Fortran 90 programming language with data parallel controls. The MPL is based on the C language. This study uses the MPF language.

(c) Parallel algorithm

The concept of the parallel algorithm is as follows. The river is divided into cells as shown in Figure 5.2. In each cell, it is assumed the characteristics affecting the mussels are uniform throughout the cell. However, the properties of each cell are unique to that individual cell. It is assumed that a mussel in cell *i* will not migrate to any other cells due to the sessile nature of these organisms. But glochidia released by a mussel in cell *i* can settle in any other suitable cell, including cell *i*. The distance the

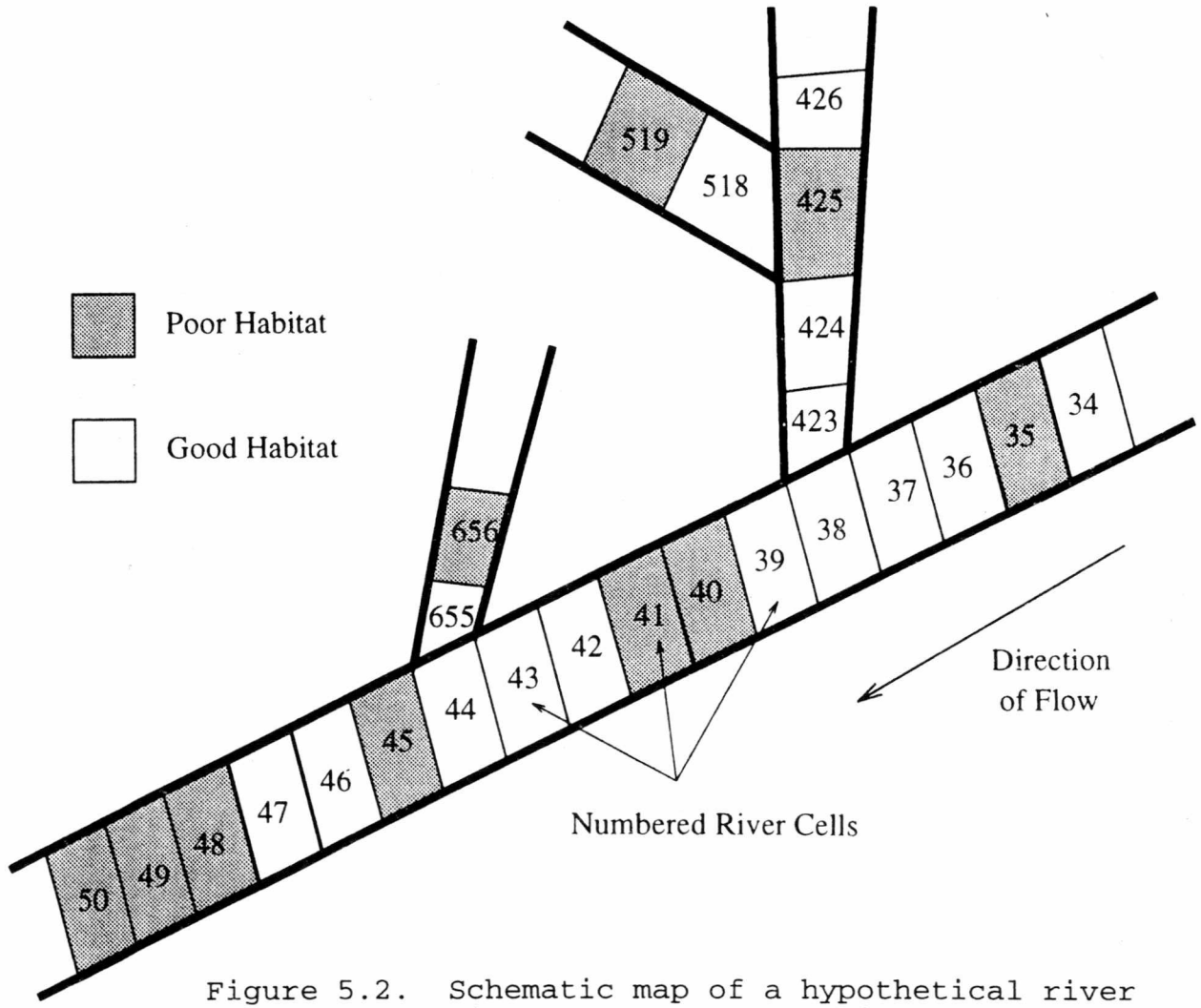
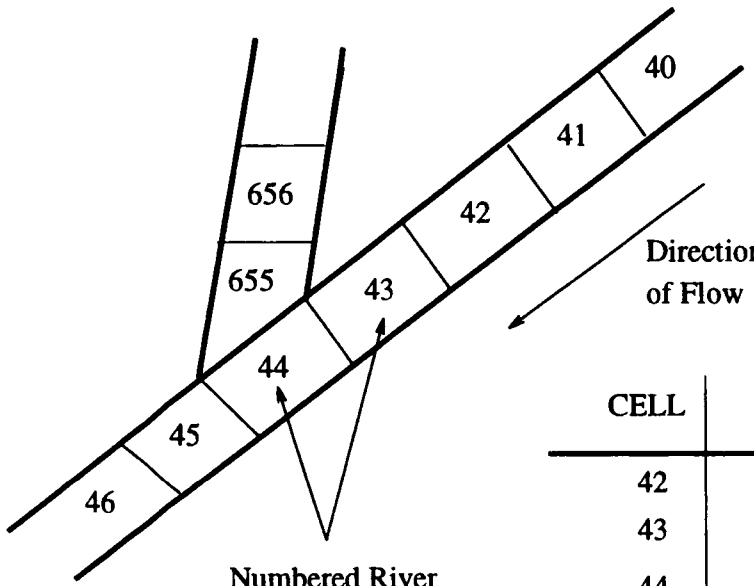


Figure 5.2. Schematic map of a hypothetical river with good and poor habitats.

glochidia/juvenile travels is determined by its fish host. We use a random normal distribution probability function to determine the distance and direction of settlement. (The random normal distribution generator subroutine is taken from Numerical Recipes in Fortran by Press et al. (1994)). However limits are placed on the possible maximum distance travelled as different fish species have different size movement range, affecting the possible maximum distance travelled by the glochidia.

The algorithm parallelized the river cells. Each cell with its local mussel community is assigned to a micro-processor. The main river branch is numbered sequentially first, followed by the tributaries. This form of numbering system allows easy addition of tributaries to the river scheme later on. The position of each cell in the river is referenced by relating the cell to its immediate upstream, downstream and tributary neighbors by pointers IUP, IDOWN and IFORK respectively. Figure 5.3 shows how the pointers are assigned. For cells with no tributary neighbor, pointer IFORK points to zero. For the uppermost cell in the river, the IUP pointer will point to zero. Similarly in the lowermost cell in the river, IDOWN pointer will also point to zero. Each cell is allowed to have only one tributary. When two tributaries flow into the same cell (cell i), then one of the tributaries should be moved to an immediate upstream or downstream cell, or cell i should be split into two separate cells with one



CELL	IUP	IDOWN	IFORK
42	41	43	0
43	42	44	0
44	43	45	655
45	44	46	0
.		.	
.		.	
.		.	
655	656	44	0
656	0	655	0

Figure 5.3. Allocation of cells.

tributary each. The cell size and shape are allowed to vary significantly.

The simulation is initialized with each processor storing the individual characteristics of all the mussel species. These characteristic data are kept in two-dimensional arrays. The first dimension is species-type and is mapped to the local MEMORY of the individual PEs, while cell number in the second dimension is assigned to the individual PE itself. In effect, we reduce the two-dimension array into local vectors in the separate PEs.

We compute the dynamics of the mussels in all cells simultaneously in each time step. The subroutines CALSIZE, CALCULATION and CALPROB are responsible for calculating the growth in mass of each mussel cohort, the availability of free-space in the cells and the probability of survival from one age class to another respectively. We use the INTERFACE procedure to allow all the PEs to call each subroutine simultaneously. Communication between processors is kept to a minimum, as the mussel community in cell *i* does not interact with other mussel communities in other cells at this stage. Inter-processors communication is costly and should be eliminated when possible.

Regardless, the individual processors still have to communicate with each other during the dispersion/settling period of the glochidia/juvenile. We minimize this communication by allowing up to only 5 discrete reproductive

events to occur in a each year, as opposed to one continuous breeding season per year.

The individual PEs compute how many glochidia are produced by each adult mussel living in its cell. Glochidia produced by the same mother are then grouped into a cohort. However only a certain percentage of each individual cohort will survive to become juvenile mussels. The juvenile cohorts are then assigned a random direction and distance of travel. Inter-processor communication comes into play when the juvenile cohorts are moved to their new homes. Given a direction and a target distance, for every step the juvenile cohort takes, the juvenile cohort will query if the new cell has a tributary. If not, the juvenile cohort will continue on its way. But should the new cell have a tributary then a decision has to be made as to change the original direction and go into the tributary or not. Using this approach, there is no need to explicitly model the fish host movements in the algorithm, but the model still retains a certain degree of flexibility in juvenile cohorts movements. The numbering system for the river cell explained earlier ensures the distance for inter-processors travel is minimized, as the probability of glochidia settling in the main river branch is significantly higher than in the tributaries.

Output of the simulation is performed sequentially by the FE. The output is somewhat time consuming, as several data arrays residing in the PEs have to be passed to the FE.

Furthermore, the output is in text format; a binary output is faster and should be considered for extremely detailed output.

Results

As expected, the parallel algorithm (PALM) is much faster then the sequential algorithm (SEAL) written in Fortran 77. The performance characteristics of PALM were measured and compared with SEAL. Table 5.1 shows the results of the comparison.

Performing a simulation with 18 species and 2050 cells for 100 years with 10 outputs requires 2192 seconds with PALM. SEAL takes 8606 seconds for the same data set. In both cases the time step used was 5 days, and the number of reproductive events was three times per year for all species of mussels. Clearly, we achieved a four-fold speedup using PALM instead of SEAL. Almasi and Gottlieb (1989) termed speedup as the ratio of time taken by one processor to the time taken by n processors to solve the same problem.

Table 5.1. Comparison of the sequential and parallel algorithms.

Algorithm	Computer	Number of Processors	Number of Species	Number of Cells	Exec. time (secs)
Sequential	SPARC 5	1	18	2050	8606
Parallel	MasPar MP-2	4096	18	2050	2192

We also compared the performance of the two algorithms using a data set of only 1 species with 2050, 4096 and 4097 cells respectively. The runs were for 100 years with a time step of 5 days. The number of reproductive time was still 3 times per year. Table 5.2 shows the results of the comparison. PALM requires 127, 133 and 317 seconds for data set with 2050, 4096 and 4097 cells, respectively. Despite almost doubling the number of cells from 2050 to 4096, the program does not require a significantly longer execution period. However the expansion of cells from 4096 to 4097 causes the time to more then doubled. This is not surprising, as the MasPar MP-2 has 4096 processors. An increase of even one additional cell beyond 4096 would require data storage and processing at more then one level on the individual processors.

In SEAL, the time require for 2050 cells is 338 seconds, while for 4096 and 4097 cells the time is 680 and 685 seconds respectively. In SEAL doubling the number of cells causes an almost proportional increase in computational time.

Besides that, in PALM when the number of species is increased from 1 to 18 there is an almost linear increase in the computational time. But in the sequential code, the increment in computational time is non-linear. The validity of this observation is still questionable, as further testing is required to verify it.

In general from comparison of the two different algorithms, we can conclude that PALM is vastly superior to

Table 5.2. Simulation time for the sequential and parallel algorithms.

Algorithm	Computer	Number of Processors	Number of Species	Number of Cells	Exec. time (secs)
Sequential	SPARC 5	1	1	2050	338
			1	4096	680
			1	4097	685
Parallel	MasPar MP-2	4096	1	2050	127
			1	4096	133
			1	4097	317

SEAL in terms of computational speed. However to fully utilize the capabilities of PALM, the number of cells should only be increase in blocks of 4096.

Discussion and conclusion

The basic appeal of SIMD computers is their ability to apply operational instructions synchronously over multiple spatial cells; but this is also one of their weaknesses. This synchronization required all PEs to perform the same task at the same time. This is a problem in our study when the mussel density is not evenly distributed over the cells. Some cells have a high density of mussels while others has a low density or no mussels. Hence during the growth dynamics computation, PEs whose cells have all non-empty age class cohorts will require more time to complete their tasks

compared to other PEs. In addition, during the initial reproductive phase, PEs with cells having a large population of mussels will need more time for the production and assignment of juvenile mussel cohorts compared to PEs with cells having a sparse population. Meanwhile empty cells' PEs will be idle during this time. This is a load-balancing problem for the parallel algorithm in the SIMD environment. This problem might be partially alleviated by recasting the entire collections of procedures in a Multiple Instruction Multiple Data (MIMD) environment. A MIMD machine does not require such strict synchronization of instructions and so the PEs utilization will be more efficient. PEs whose cells have a small population will no longer have to be idle while waiting for other PEs to finish their computation. However synchronization during the dispersal period will most probably be needed, as information regarding existing mussels density in target cell is required.

The more PEs that are active simultaneously, the greater will be the efficiency of a SIMD machine over a sequential machine (Leighton, 1992). To achieve this, some modification of the existing parallel algorithm is necessary. One approach is to allocate only cells capable of supporting mussel life to the PE array. Unsuitable cells (incapable of supporting life) logistics information will be kept in FE for facilitation of the dispersal of the juvenile mussels. Thus not all cells will be automatically assigned to a processor. This can

partially ease the load balancing problem by eradicating empty cells from the PE array. This method will be especially useful in cases where there are more then 4096 cells. Thus PEs that are initially assigned unsuitable cells, which are idle, can be reassigned. This eliminates the need for "stacking" more then one cell to a processor, provided the total number of suitable cells does not exceed 4096. Figure 5.4 shows how the PEs are apportioned for the two different approaches.

Another possible solution to the load-balancing problem is to have a dynamic assignment of cells to PEs. After a certain number of time steps, an evaluation of the mussel density in each cell is performed. Subsequently, cells with very high density of mussels will be split into two or more cells, with the mussel population evenly divided between the newly created cells. Then an automatic renumbering of cells, followed by reassignment of cells to processors, is executed. This will probably give a more even distribution of mussel density among the PEs. However the evaluation step is likely to be costly, as there will be a lot of inter-processor communication during this period. Furthermore, this load-balancing procedure has to be repeated every so often. Thus, it must be determined in the long run if the dynamic assignment of cells to PEs is really cost-effective.

Besides that, the lack of efficiency during the dispersal/settling time will continue to plague the parallel

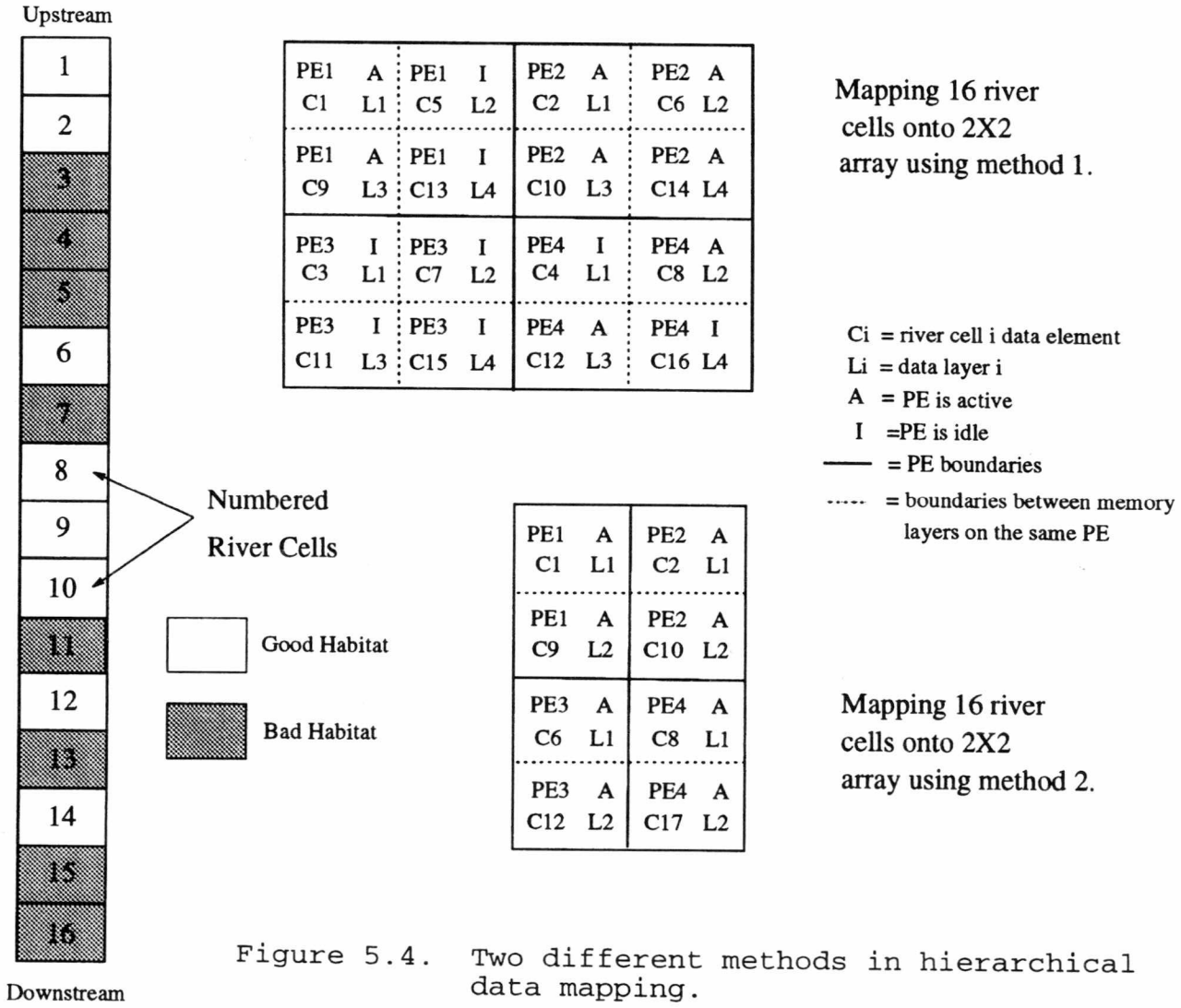


Figure 5.4. Two different methods in hierarchical data mapping.

algorithm. Communication between processors is necessary at this stage and cannot be avoided. The current method of sequentially numbering the main river branch followed by the tributaries can minimize the cost of inter-processor communication by seeking to reduce the distance between the processors. But the movements of the juvenile cohorts are still evaluated sequentially one at a time. An alternative approach might be to group all juvenile cohorts with the same direction and distance of travel together and move them simultaneously. The disadvantage of this methodology is the restriction of any future change of direction once movements have commenced. This makes the moving of juvenile cohorts more rigid than we prefer.

Much of the inter-processor communication performed here is through a *global router*. A *global router* allows the PEs to directly access each other and the communication time is independent of the distance involved between the PEs. The router works on a "first come first serve basis".

Communication through XNET is faster than with a global router. However to use XNET, the assignment of cells to processors will be much more complicated then at present. For the XNET to work properly, the cells nearest to each other must be grouped together and at the same data level in cases when the number of cells exceed 4096. It will require all tributary cells to be near their main river cell, and we can allow each cell to have more than one tributary neighbor. The

drawback of this is the difficulty involved with the mapping of cells to processors. Using this approach, an intimate knowledge of the physical location of the river cells in relation to each other is necessary apriori to implementation. This makes the algorithm hard to use as well as not being portable from machine to machine. Furthermore, an addition of even one tributary (depending on the location) into the original river system later can cause a complete remapping of all the cells to the processors. Thus, overall, this approach is not very user friendly.

In the parallel algorithm, limitation of memory for spatial dimension or heterogeneity is not a problem. The parallel algorithm for a river with 4096 cells and using single precision currently required only 6300B. The MasPar MP-2 can support up to 64KB on the DPU by using the **mplimit** command. Hence in theory we can increase the number of cells to 40,000. This can allow a considerable refinement on the cells. Smaller cells with greater degree of uniformity is possible. However if possible, cells increments should be in blocks of 4096 to allow efficient use of the processors. A scheme with 4097 cells will required 12,600B of memory just as one with 8192 cells.

Finally, it must be noted here, complete parallelization of the mussel problem is not likely. This is because the problem is not in reality a parallel problem but rather a problem with features of parallelization in it.

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