To the Graduate Council:

I am submitting herewith a thesis written by Jeffrey R. Duncan entitled "Predicting Community Dynamics in the Wake of Invasion: A Case Study of the Zebra Mussel." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Zoology.

Dr. James A. Drake, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

PREDICTING COMMUNITY DYNAMICS IN THE WAKE OF INVASION: A CASE STUDY OF THE ZEBRA MUSSEL

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Jeffrey Robert Duncan
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DEDICATION

This one's for Mom,

for her loving support, nurturing patience, and uncompromising faith that I would succeed.

And for Dad,

for instilling in me the fortitude to never give up and the challenge to excel.

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When giving birth, as I have to a humble yet hopefully significant accomplishment, there are always others without whom gestation, not to mention conception, would have been impossible. In my particular case, these individuals are as numerous as their contributions. Here, I attempt to recognize these individuals with apology to those who I may have been inadvertently omitted.

I would like to begin by thanking my research committee for their insight, guidance, and patience. Dr. James A. Drake has been not only a superlative academic advisor but a valued friend. I can only hope to aspire to his level of intuition and his degree of humility. The kind-hearted wisdom of Dr. Dewey Bunting has been of great value. Thanks for tolerating a Zoology student. Thanks also to Dr. Gerald Vaughan—I have never met a man who knew as much about as many things and was as willing and enthusiastic to share.

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ABSTRACT

The fragile complexity associated with aquatic ecosystems has proven, in past situations, to be vulnerable to effects induced by invaders (e.g., the sea lamprey invasion of the Great Lakes). Unlike many other invasions, the zebra mussel (*Dreissena polymorpha*) threatens to disrupt the natural food webs of North American waters in unprecedented proportion. The full impact of the zebra mussel invasion of North America is yet to be experienced, though it will likely result in wholesale changes in aquatic biodiversity due to the mussel's ability to exploit open niches and out-compete indigenous species. This study provides a synopsis of the invasion and a review of history characteristics of the zebra mussel that contribute to its success as a colonizing species. Finally, a computer simulation model composed of a set of differential equations is proposed to analyze the direct and indirect ecological effects induced by the zebra mussel invasion. The role *Dreissena* plays in altering aquatic primary production, light availability, and nutrient dynamics are considered. Predictions of future ecosystem/community structure are proposed and the plausibility of alternative community states are assessed with consideration given to properties associated with community assembly including interspecific competition and intransitive switching. In addition, the application of non-linear analysis suggests evidence of chaos within ecosystem trajectories, indicating dependence upon initial conditions such that future attempts at inter-ecosystem extrapolation of ecological effects will be challenging.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Zebra mussels encrusting native clam *Photo courtesy of Tennessee Valley Authority*

"Yet, if we wield the sword of extermination as we advance, we have no reason to repine the havoc committed."

—Charles Lyell (1832)

"Wherever the European had trod, death seems to pursue the aboriginal. We may look to the wide extent of the Americas, Polynesia, the Cape of Good Hope, and Australia, and we find the same result."

—Charles Darwin (1839)

"We must make no mistake, we are witnessing one of the great convolutions of the world's flora and fauna."

—Charles Elton (1958)

1. INTRODUCTION

The onslaught of global exploration and expansion in the latter half of the present millennium has been silently accompanied by the pandemic inoculation and homogenization of previously isolated species (Crosby 1986). From microbial pathogens to agricultural pests to encrusting marine and freshwater organisms, exotic species encompassing virtually every taxa and trophic level have altered landscapes and threatened biodiversity. Though biological invasion, an inherently natural process contributing to community structure, has no doubt occurred since the beginning of life itself, the rate at which invasions occur has been markedly accelerated by human activity. While most invasions by novel species are likely unsuccessful or go unnoticed due to

their benign consequences, many have succeeded as colonists and have caused a cascade of ecological effects resulting in profound alterations in species populations, community dynamics, and ecosystem structure (Simberloff 1981). As we near the end of the millennium, another invader, perhaps one of the most catastrophic in recent history, has stepped into the limelight—the zebra mussel.

1.1 THE ZEBRA MUSSEL INVASION

In the summer of 1988, established populations of zebra mussels (*Dreissena polymorpha*), a bivalve mollusk endemic to Europe, were discovered in lakes St. Clair and Erie near Detroit, Michigan (Hebert et al. 1989). By the summer of 1990, colonies had been reported throughout the Great Lakes (Kraft 1993). These invaders are likely the result of veliger-infested ballast water from ocean-going merchant ships taken on at a freshwater port in Europe and subsequently discharged into Lake St. Clair (Mackie et al. 1989). Although the exact source of the invasion is left to speculation, it is known that the species originated near the Caspian Sea. During the eighteenth century, after extensive canals were constructed to facilitate trade between eastern and western Europe, zebra mussels expanded their range into the waterways of western Europe.

Consistent with its native distribution in Eurasia, *Dreissena* has continued to expand its North American range southward from the Great Lakes into the waterways of the lower midwestern and southeastern United States. Most current observations pinpoint populations in the Hudson River Estuary, the Mississippi River as far south as Louisiana, the Cumberland River, and more recently near the headwaters of the Tennessee River (Figure 1.1). Implications of the species' spread into the Tennessee drainage will likely include the extinction of many bivalve species which currently comprise one of the most diverse mussel faunas in the world (Ahlstedt personal communication).

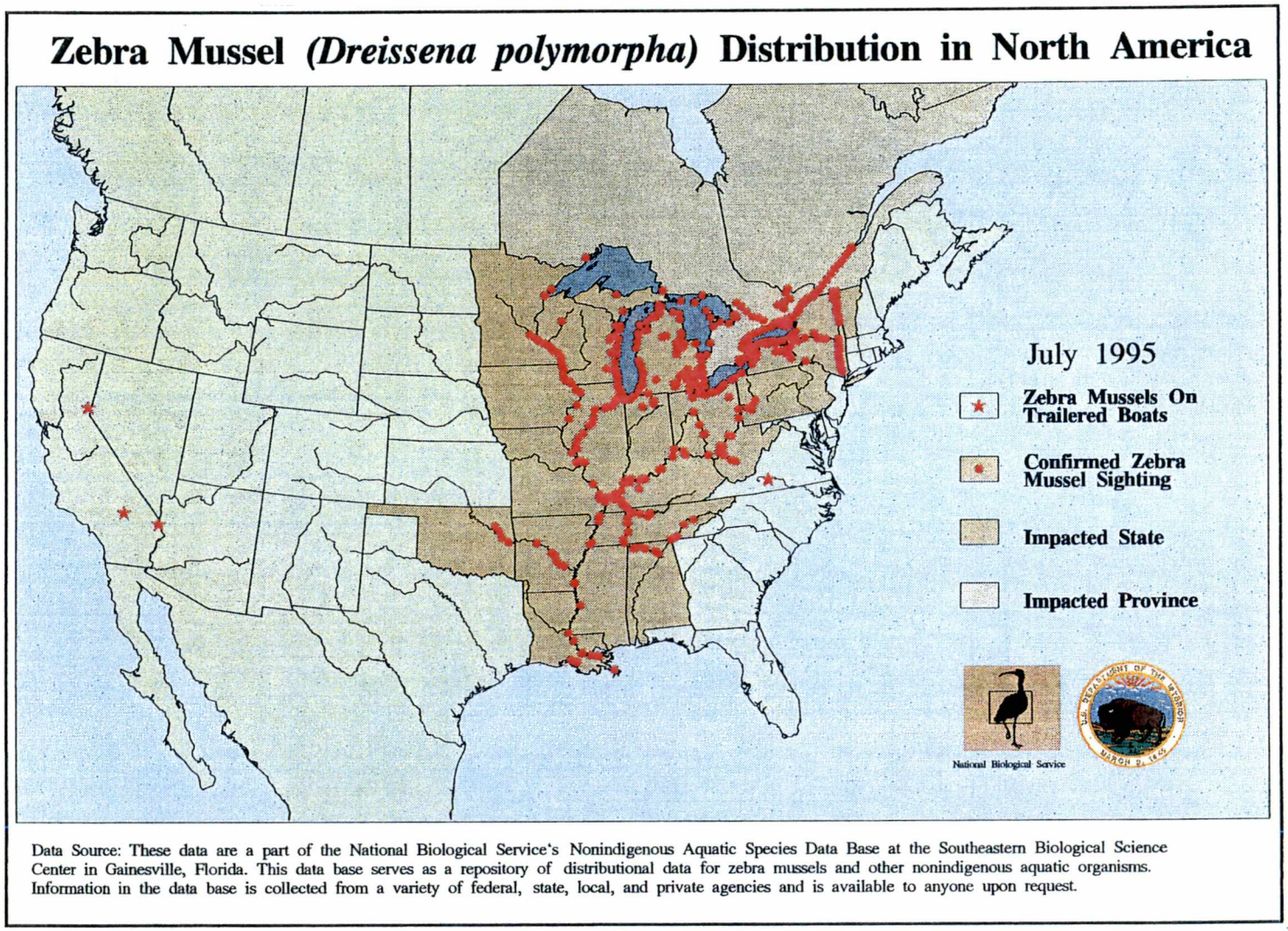

Figure 1.1 Distribution of zebra mussel (*Dreissena polymorpha*) in North America

1.2 OBJECTIVES

The objectives of this thesis are to provide a synthesis of information concerning the extent, velocity, and ecological implications of the zebra mussel invasion. In addition, I provide the results of a first order computer simulation that I developed to investigate and predict a set of plausible alternative community states and their corresponding dynamics. While a high degree of uncertainty necessarily exists within the model's initial parameter values, trends emergent in the behavior of resultant ecosystem trajectories suggest that zebra mussel populations may be susceptible to extreme fluctuations in abundance caused by cascading indirect ecological effects. For example, the ability of zebra mussels to filter large quantities of water may result in increased water clarity enhancing production by periphyton and other light-limited organisms. Further study using a more developed model coupled with field data may offer promise toward appropriate ecological management of this and subsequent biological invasions.

1.3 ORGANIZATION

This thesis is organized into 4 major sections. The remainder of Section 1 contains background information concerning the zebra mussel, its biology, life history, physiology, and the potential economic and ecological consequences it poses. Section 2, Methods, contains a description of the mathematical model that I developed to evaluate the invasion; included in the section is a brief discussion of the use of mathematical models to describe and predict ecosystem behavior and of the sensitivity analysis procedure I used to reduce the level of uncertainty of the model's results. Section 3, Results, presents the outcome of the model run with initial conditions being set at 27 different configurations. Finally, in Section 4, Discussion, I detail some of the implications of the model results with respect to the likely existence of alternative community

states and their implications toward managing the invasion. The Discussion section also serves as a personal forum for suggestion regarding the direction for additional work on the subject.

1.4 SPECIES DESCRIPTION

The zebra mussel (*Dreissena polymorpha*) is easily distinguished as an adult in a variety of ways from other freshwater mussels endemic to North America; its ability to attach to hard substrata is perhaps its most noted characteristic. Retention of a byssus allows the zebra mussel to exploit habitat inaccessible to other species that lose this structure early in their life cycle (Pennak 1978). Attaching to hard surfaces including woody debris, rock, concrete, metals, and hard-bodied benthic animals (e.g., unionid mussels, crustaceans, etc.) is a feat accomplished by no other mussel species extant in North America. This characteristic allows the zebra mussel to fill a previously unoccupied niche—that of a hard surface attacher.

Additionally, shell morphology of the species is rather atypical of native clams. *Dreissena* are generally small (less than 5 cm in length) with a characteristic "D"-shaped shell. Most zebra mussels have a varying degree of alternating light and dark bands, which attribute to its name. The veliger and post-veliger stages of *Dreissena* are not as easily recognized as the adult; although, larval stages are readily identified using standard microscopic techniques.

1.4.1 Taxonomy and Evolution

Nuttall (1990) and Morton (1993) offer in-depth accounts of the evolution of *Dreissena*. Perceiving it in a taxonomic hierarchy (i.e., phylogeny) is crucial to understanding the presumed evolution of any species. *Dreissena* is one of four genera (as described by Nuttall 1990) found within the subfamily Dreisseninae within the family Dreissenidae. Today, only two genera survive, *Mytilopsis* and *Dreissena*. The former, once found in Europe, invaded the Western Hemisphere in the late Oligocene. Since that time, its European counterparts have become extinct

(Nuttall 1990). *Dreissena* presumably arose in the late Miocene of the Paratethys. The present day distribution of both genera is apparently due largely to human activity.

Although, epibyssic bivalves of various lineages probably evolved independently during several different periods, the superfamily Dreissenoidea would seem to be the most recent, appearing in the fossil record sometime during the Eocene. Fossil evidence suggests that the superfamily Corbicluoidea (of which another North American exotic, the Asiatic Clam [*Corbicula fluminea*], is a member) arose about the same time from common ancestry (Morton 1993). While the two groups display morphological similarities, their modes of life differ markedly. Corbiculids avoid predation by adopting an infaunal (i.e., sediment-dwelling) existence; conversely, Dreissenids exploit an open niche by adopting an epifaunal (i.e., attached to hard surfaces) strategy, making them more susceptible to predators but apparently decreasing competition.

1.4.2 Genetics

Since the 1960s, genetic studies of invading species have generated a considerable amount of scientific research, speculation, and debate (e.g., Baker and Stebbins 1965, Parsons 1983, Mooney and Drake 1986, and Drake et al. 1989). This type of research is of importance to ecologists for a number of reasons including estimating the number and origins of colonists, predicting future colonizing events and dispersal rates, and understanding developmental processes which of mediate population dynamics.

Hebert et. al. (1989) and Boileau and Hebert (1993) have conducted in depth genetic surveys of *Dreissena* in the Great Lakes as well as in some European populations. The use of allozyme electrophoresis in these studies indicates that *Dreissena* possesses an extremely high degree of genetic diversity in both European and post-invasion North American populations. The fact that nearly 74% of the loci evaluated were polymorphic and that individual heterozygosities averaged 31.6% is extremely uncharacteristic of most colonizing populations of various other species.

Dreissena specimens analyzed from the Great Lakes are among the highest 1% of animal species measured for genetic diversity (Boileau and Hebert 1993). This unprecedented level of genetic variation is indicative that the founding population in the Great Lakes did not undergo a bottleneck as is characteristic of many founding populations of other invasions. Accordingly, it seems likely that a large number of individuals were released simultaneously, or that multiple inoculations occurred within a relatively short time period, thereby precluding significant loss of genetic variation.

Boileau and Hebert (1993) have also suggested that population growth is brought about by local recruitment rather than long-distance dispersal. This notion is supported by the discovery of a fringe population in Oneida Lake, New York, with a relatively lower degree of heterozygosity as compared with more centrally distributed populations. While Boileau and Hebert pose an intriguing explanation of population growth dynamics, their one sample of a single fringe population requires for further study to verify this conclusion. Now that fringe populations have been discovered great distances from the presumed source in lakes Saint Clair and Erie, the potential to test their hypothesis exists. A more extensive allozyme survey encompassing sample sites from across the southeastern United States would appear useful.

In their survey, Boileau and Hebert (1993) discovered three alleles present in North American *Dreissena* that were absent in European studies, indicating that the actual source population in Europe may be traceable. Again, more extensive study is needed, but discovery of this information could play a vital role in policy-making and serve to reduce the risk of future invasions.

1.4.3 Life History, Population Dynamics, and Dispersal

The life cycle of *Dreissena* is unique relative to endemic North American bivalves. This has likely been essential in its conquest of the Great Lakes and will continue to benefit the species as it proliferates throughout the rest of the continent. The uniqueness of its life cycle is two-fold:

having a free-swimming larval stage and the ability to attach to hard surfaces as an adult. These two characteristics permit the zebra mussel to overcome major ecological filters which typically restrict invaders (e.g., dispersal and interspecific competition). Therefore, the species is afforded the ability to exploit a niche inaccessible to any other freshwater bivalve extant in North America. Appreciating the mechanisms behind the recent success of *Dreissena* requires exploring how the species lives.

The zebra mussel is a diecious species with external fertilization occurring when gametes are released into the water column (Mackie et al. 1989, Sprung 1993). Depending on size of the individual and on ambient conditions, females may release up to 1 million eggs per spawning event. While this is certainly an extreme case, it nonetheless illustrates the enormity of the species' reproductive capacity, a property which further enhances its invasive tenacity. After fertilization, development progresses rapidly from a zygote suspended in the water column to a larval stage which is capable of swimming within less than one day (Sprung 1993).

Unlike other native unionids, its larval stage, known as a veliger, is non-parasitic and therefore not dependent upon a fish host for dispersal (Pennak 1989). The mussel may remain in its rudimentary veliger stage for as long as two weeks, depending in part upon ambient conditions, swimming or being moved significant distances by current. Settlement occurs as morphological changes (i.e., shell development) reduce bouyancy (Sprung 1993). Mortality is high during this process since the majority of settling veligers lose their buoyancy in the absence of suitable attachment substrata, settling in silty or muddy bottom areas where they are unable to siphon properly and subsequently starve.

Once the zebra mussel has successfully settled on suitable habitat, it is generally classified as a post-veliger, lacking a fully developed shell but possessing the ability to produce byssal threads for attachment. When its shell is fully developed, the mussel is known as a juvenile. It remains

in its juvenile state through its first year until it grows to maturity with the ability to reproduce. The life span of a zebra mussel may be as long as 7–8 years if environmental conditions are favorable.

Density of zebra mussel colonies may vary with temperature and eutrophication and have been recorded in excess of 200,000 individuals/m^2. In addition, adult mussels have evolved a strategy of coping with unfavorable environmental conditions known as byssall-pelagic transport (Carlton 1993). This trait allows the mussel to detach itself from its substrate and float, supported by buoyant byssal threads, to a more suitable location. Passive detachment and relocation may also occur as the result of severe wave action due to storm events (Carlton 1993).

While *Dreissena* lacks any major competitors in its recently expanded range, predation by invertebrates, fish, waterfowl, and parasites likely affect *Dreissena*, although the extent to which population structure is influenced remains unclear. For example, Piesk (1974) notes that smaller mussels can be consumed by crayfish at a rate greater than 100 mussels per day per crayfish. Since this form of predation is age-specific (i.e., crayfish prey primarily on younger mussels), the effect on *Dreissena* colonies would be the potential alteration of age-structure within populations.

Indeed, there are a host of predators that consume zebra mussels, potentially regulating colony densities (Smit et al. 1993), age-structure, and possibly reproduction, though little is known concerning the extent these predators will have in regulating zebra mussel populations in North America. What is certain is that the presence of *Dreissena* in the food web will stimulate direct and indirect effects that will likely propagate throughout entire ecosystems.

1.4.4 Distribution Constraints

Like any organism, the zebra mussel may successfully colonize only where environmental conditions are appropriate. Six environmental parameters are crucial for the prolonged persistence of *Dreissena* populations. These include temperature, pH, dissolved oxygen concentration, water hardness, the availability of attachment substrata, and food availability. While all of these conditions are of importance to zebra mussel survival, the degree to which each affects growth and development may be dependent upon which stage of the organism's life cycle is in question. For instance, the availability of attachment substrata may be of no consequence to an already attached adult mussel, and food availability may be of no immediate concern to a developing embryo not yet capable of feeding. The importance of a specific environmental constraint as well as the tolerance limits for each is briefly discussed in the following subsection.

1.4.4.1 Physiological considerations

Progression of the zebra mussel life cycle is largely temperature dependent. External fertilization occurs when water temperatures are between 12° and 24°C with 18°C being optimal for growth and development (Sprung 1987). In locations where water temperatures do not drop below 10°C, reproduction may be continuous throughout the year (Nichols 1993). While water temperature appears critical for reproductive success, the tolerance limits are greatly broadened if one merely considers the conditions at which individuals can survive. Adult mussels can persist in temperatures from near freezing to over 30°C. The resistance to a broadened range of temperatures appears to be age-dependent with veligers and juveniles being more susceptible to the extremes.

1.4.4.2 Water chemistry

Calcium ion concentration (i.e., water hardness) is critical for growth and development of all organisms. This may be particularly true for zebra mussels which require calcium for shell

development. Calcium levels below 60–70 mg/L result in an increase in larval mortality (Sprung 1987). While this finding indicates that calcium hardness critical to reproduction and larval development, the spread of zebra mussels to new areas may not be significantly affected by the lack of calcium. Recruitment of individuals through anthropogenic transport of mussels can offset the immediate need for reproduction. Further, as has been observed with the Asiatic clam, which survives in waters relatively low in calcium, efficiency of uptake when concentrations are low may be as important as absolute concentration.

While not as tight a constraint, dissolved oxygen (DO) is another important factor. The level of DO must remain above 20% at 18°C for proper growth and development to occur. Below this level, veliger crippling and slow growth of adults may occur.

1.4.4.3 Substrata availability

Availability of appropriate attachment substrata is an environmental feature that is imperative to settling mussels. As planktonic veligers grow to approximately 220 μm, they undergo a series of morphological changes including the shell development. These changes facilitate the beginning of the settlement and attachment process. The presence of hard substrata, conducive to byssal thread attachment, is an important factor that regulates mortality during this vulnerable stage. Most veligers (~99%) do not survive settlement due to the lack of suitable hard surfaces (Sprung 1993); instead, they settle into the silt- and mud-laden bottom where they are unable to attach and siphon properly.

1.4.4.4 Food supply

As with any organism, adequate food supply is vital to long-term persistence of *Dreissena* populations. Phytoplankton density may be an important factor governing the onset of spawning. While little field data specific to *Dreissena* exist, there is extensive evidence that various marine bivalves postpone reproduction until an ample food supply is present (Nichols 1993). Various

in vivo studies of *Dreissena* have revealed that female gonad volume and fecundity are maximized when seston is abundant, approximately 1–2 mg/L ash-free dry weight (Neumann 1993). In addition, Neumann (1993) has observed through laboratory studies that fertilization may be delayed until water temperature is 15–20°C, significantly higher than 12°C which is normal. This latter point suggests that a positive relationship between temperature and food availability with respect to the onset of reproduction.

Throughout development, larval *Dreissena* remain dependent on a rich food source. While little is known concerning the filtering rate of veligers, Sprung (1993) hypothesizes that it is probably not unlike that of other bivalves such as *Mytilus* whose veliger stage siphons between 10 and 40 μL/H, depending upon the size of the individual. Selected particle size is known and ranges from 1–4 μm. Based on this constraint, the diet of larval *Dreissena* may consist of bacteria, cyanobacteria, small green alga, and fine particulate matter (Sprung 1993).

Considerably more information is known regarding the feeding habits of adult *Dreissena* (Dorgelo 1993). Studies have shown that the growth of individual mollusks increases with eutrophication, and nothing in the literature suggests that zebra mussels are an exception. One important consideration pointed out by Dorgelo (1993), however, is that of food quality may have profound influences on size increase regardless of the trophic state of the system. For example, larval oysters increase in size more rapidly when fed algae species with under-developed cell walls. While this would intuitively seem the same for *Dreissena*, empirical studies have yet to confirm this.

It can be asserted, however, that an increase in diet diversity is beneficial to bivalves in general; this notion is fitting since the more species that exist in the diet the greater the chance of encountering species more easily digested. Particle sizes selected by adult zebra mussels range in size from 15–45 μm with particles not in this range generally being excluded (Dorgelo 1993).

On average, assimilation is 50% for bacteria and 20% for alga. Undigested particles are released as pseudofeces containing intact viable algal and bacterial cells.

1.4.4.5 Limitations in the Tennessee Valley

The Tennessee Valley Authority (TVA) reviewed the vulnerability of zebra mussel infestations within the Tennessee River system, including its major tributaries (Rucker and Urban 1994). Limiting factors evaluated by TVA were water quality characteristics (i.e., temperature, calcium carbonate hardness, and calcium hardness), mechanism of inoculation (e.g., natural dispersion, barge transport, and recreational transport), and habitat availability. Table 1.1 presents the set of limiting assumptions proposed in the TVA report. Because the present state of the Tennessee River system can be characterized as a series of manmade impoundments, the system's response to the zebra mussel invasion may differ profoundly from other situations in North America and Europe where experiences with natural lakes and rivers have resulted in the majority of documented observations. The combination of commercial barge traffic, recreational uses, moderate year-round temperatures, winter drawdowns, and hypoxic or anoxic hypolimnetic conditions during the summer assert a level of complexity to zebra mussel life history and population dynamics that is unprecedented in the literature.

1.5 CONSEQUENCES: ECONOMIC AND ECOLOGICAL

Potential ecological as well as industrial hazards are posed by the zebra mussel invasion. The species' ability to secrete bysall fibers similar to those of barnacles affords them the adaptive advantage of attachment to hard surfaces including shells of endemic species and industrial water exchange systems. This ability, coupled with mussel's tendency to develop dense aggregations (up to 200,000 individuals/m^2) (Mackie et al. 1989) allows it to literally smother individuals of other species and partially or completely occlude water exchange manifolds at various industrial

Table 1.1 Limiting factors for zebra mussel infestation in the Tennessee Valley[1]

Limiting Factor	Parameter	Criteria
Water Quality	Temperature	<-2°C and >40°C = No survival; 0-8°C and 28-30°C = Poor growth; 9-12°C and 25-27°C = Moderate growth; 13-17°C and 21-24°C = Good growth; 18-20°C = Best growth
	Alkalinity (calcium)	0-17 mg/l = No survival; 18-35 mg/l = Poor growth; 36-87 mg/l = Moderate growth; 88-122 mg/l = Good growth; >122 mg/l = Best growth
	Hardness (calcium)	0-22 mg/l = No survival; 23-41 mg/l = Poor growth; 42-90 mg/l = Moderate growth; 91-125 mg/l = Good growth; >125 mg/l = Best growth
Inoculation	Primary method	Natural dispersion via current; Transport on large commercial vessels
	Secondary method	Transport on recreational vessels
Habitat	Winter Drawdown	Dessication
	Summer Hypolimnion	Hypoxia

[1] Summarized from Rucker and Urban 1994.

and/or public facilities. In addition, Kraft (1993) and Strayer (personal communication) have reported navigational buoys becoming partially submerged due to the sheer weight of colonizing *Dreissena*, thereby creating a potential hazard to navigation. While a variety of control technologies currently exist, and more are presently being developed (Duncan et al. 1993), the cost of these control efforts is likely to exceed $5 billion in the Great Lakes region alone by the end of the century.

While the majority of this expense will be targeted at reducing the invasion's impacts to industry (i.e., control and maintenance), there is little chance that the zebra mussel can be eliminated from North American waters. Clearly, the ecological implications of the invasion will likely be profound due primarily to the magnitude of the species' fecundity as well as its tenacity as a competitor.

As is typical of bivalves, *Dreissena* feeds by siphoning water across its gills where phytoplankton as well as other suspended particles are captured by its mucus coating. From there the food-laden mucus is transported via ciliary action to the mouth where assimilation begins (Pennak 1989; Ten Winkle and Davids 1982; Jorgensen et al. 1984; Sprung and Rose 1988). The siphoning rate of an individual adult zebra mussel has been measured in excess of 1 L/d (Mackie et al. 1989) and up to 4 L/d by some accounts. This rate, the zebra mussel's ability to persist in dense aggregations, and its practice of encrusting other species will no doubt, at a minimum, induce wholesale shifts in community composition and likely a net reduction in biodiversity.

Perhaps the greatest threat to biodiversity exists in the Tennessee River system where the species has recently colonized. Historically, the upper Tennessee River watershed has been home to one of the most speciose mussel faunas in the world. For several years, recruitment among many species has dwindled. The cause of this decline is speculative, but flow regimes altered by Tennessee Valley Authority (TVA) impoundments, urbanization, and pollution are among the

suspects. To date, approximately 30 species found only in the Tennessee River are listed as federally threatened or endangered, and many others are believed to have recently become extinct. For many of the species that continue to exist in small numbers, the anthropogenically accelerated spread of the zebra mussel will likely prove devastating—forever altering the structure and function of the Tennessee River ecosystem. Should the zebra mussel spread throughout the Tennessee watershed, many remaining mussel species will be guaranteed a rapid demise.

1.6 ALTERNATIVE STATES: THE ZEBRA MUSSEL/ECOSYSTEM INTERACTION

While much attention (and research funding) has been devoted to the control of local infestations, little has been accomplished with regard to the community-/ecosystem-level effects of the zebra mussel (e.g., Nalepa and Schloesser 1993). Apparently, this lack of vigor in studying the zebra mussel from a more theoretical community perspective stems from the failure of funding agencies to see beyond the "quick fix". In this case, it is doubtful that a quick solution will be the answer. Clearly, acute economic concerns are the driving force surrounding zebra mussel research, as well they should be, but in the process of protecting our capital investments, we must not forget the importance of expanding our knowledge of ecological processes and the ways in which we influence them!

The zebra mussel invasion of North America is an ecological event that is unprecedented in recent history. The impacts the species will have on the natural systems may extend far beyond the inconvenience and corresponding loss of revenue it imposes on utility companies. As noted by Drake (1990, 1991), species composition within a microcosm-community is dependent upon the history of how the community assembled.

The zebra mussel, being well adapted as both an invader and a competitor, is clearly capable of driving many native species extinct, forever changing the structure of the invaded community.

The rippling effects that may be associated with such a structural shift in community structure are likely profound and may encompass an array of possible outcomes ranging from to minor species substitutions to near chaotic fluctuations in community dynamics through time. A community's response to a foreign species is difficult if not impossible to predict. Being able to predict such an outcome is likely dependent upon one's knowledge of the history of the system (i.e., the system's assembly trajectory) (Drake et al. 1996) (Figure 1.2). Despite this, the application of ecosystem modeling may serve to identify a finite set of potential community trajectories, thereby reducing the field to a manageable set of predictable dynamics.

1.7 ECOLOGICAL MODELING

> *"It ain't so much the things we don't know that gets us in trouble; it's the things we know, that ain't so."*
>
> *— Artimus Ward*

Despite the projected negative consequences of the zebra mussel invasion, the situation presents an unprecedented opportunity to further our understanding of the mechanisms of species invasion and community assembly. Only in the latter half of the current century have biological invasions gained notoriety among scientists (Skellam 1952, Elton 1958, Baker and Stebbins 1965, Parsons 1983, Mooney and Drake 1986, Drake et. al. 1989). Although much knowledge has been gained in the past 30 years, many questions concerning invasions and their relationship to community structure and dynamics have yet to be answered. For example, it remains difficult to predict which species may become a successful invader in a given ecosystem and which will not; this uncertainty is due in part to our inadequate understanding of the basic elements that provide structure in natural communities (Drake 1990, 1991; Drake et al. 1996). Because zebra mussels are new to North

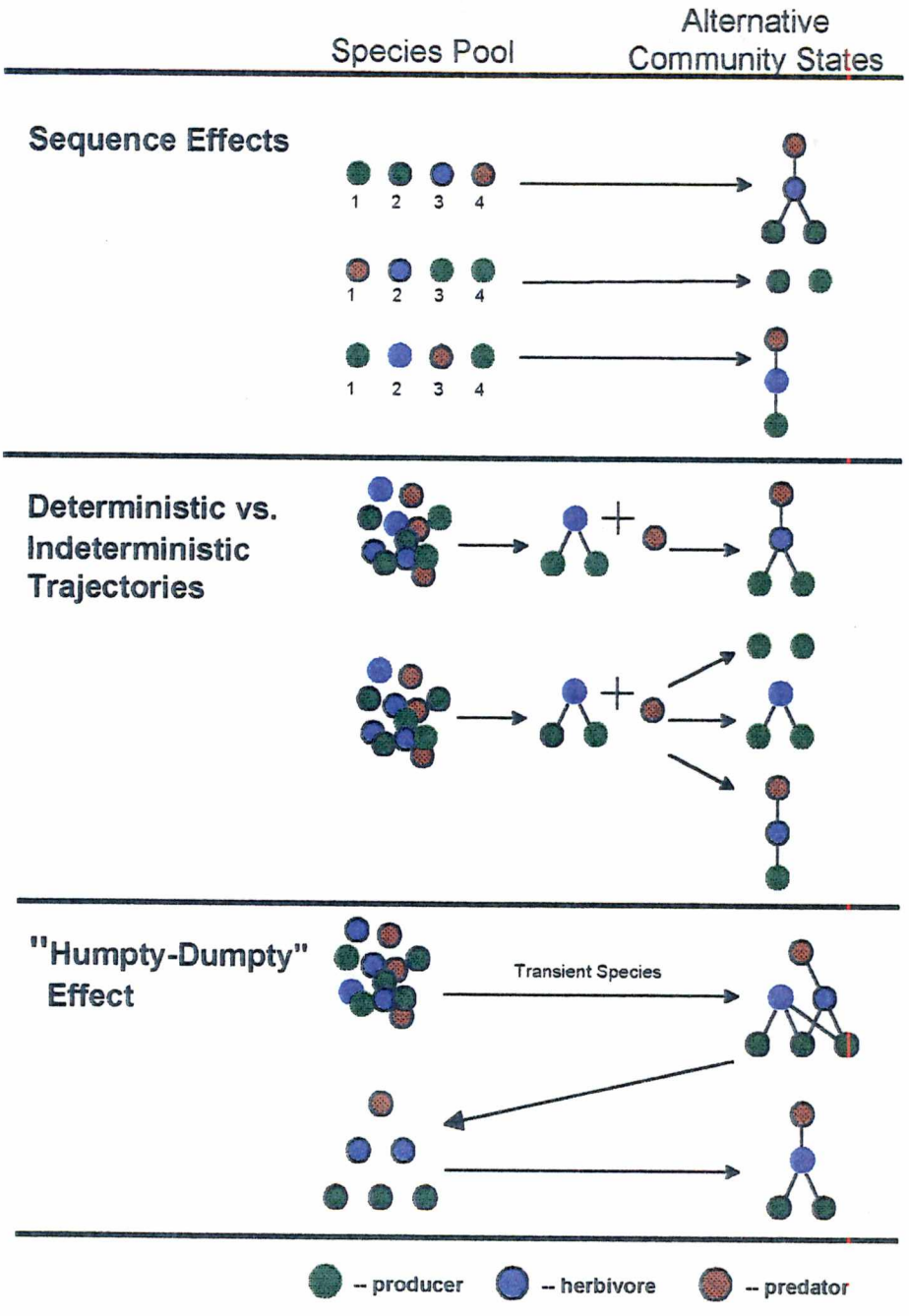

Figure 1.2 Potential community assembly trajectories and alternative states (Adapted from Drake et al. 1996).

America, their spread has been thoroughly documented and much information exists about the systems they invade prior to the invasion; therefore, the opportunity for comprehensive study abounds. Analysis of biological and limnological data from infested systems may offer some degree of predictive ability as to ecological effect of species invasions. Further, applying existing information to computer simulation models of ecological populations and processes may offer additional insight and even predictability on the nature and outcome of invasions and the basic elements of community structure (Swartzman and Kaluzny 1987).

In examining a species' potential colonizing ability, it is perhaps best to evaluate the species based on a set of criteria which may include such factors as life history, mode of spread, human influences, and community interactions. (Early studies of invasive potential have neglected consideration of the latter, thereby diminishing their predictive power [Baker and Stebbins 1965, Baker 1986, Ehrlich 1986]). Current research on the zebra mussel invasion focuses primarily on the organismal biology and control strategies. While this is obviously a valuable and required undertaking, its reductionistic nature ignores the interconnected nature of ecological systems, leaving us naked of predictive ability.

More than a century ago, Forbes (1887) put forth the notion that one cannot fully understand an organism without also considering other species and the environment with which it interacts. Perhaps it is more appropriate at this early stage of the invasion to adopt a more holistic approach in creating a template that can offer the insight of predictability to those studying biology and control. Mathematical computer simulation models have, in other situations, proven useful in predicting the outcome and velocity of various ecological events (Monod 1950, Swartzman and Kaluzny 1987, Di Toro et al. 1971, DeAngelis et al. 1985, Drake et al. 1993, Jorgensen 1976, Okubo 1980). I developed such a model using characteristics such as life history traits, mode of spread, and siphoning rates (Mackie et al. 1989, Stanczykowska 1977, Morton 1969) to predict a set of plausible

alternative community states. It is hoped that this model will aid in our ability to foresee the future ecological impacts of this and similar invasions—foresight that may ultimately help us combat the invasion or, at a minimum, in reduce its ecological and economic consequences.

2. METHODS

2.1 THE MATHEMATICAL MODEL

A worst case scenario of the invasion depicts the zebra mussel as a sort of aquatic plague, ultimately wreaking ecological havoc on every ecosystem it encounters. Indeed, there may be some merit to this notion, but the magnitude of the effect and exactly which species and which ecosystem processes/functions will be affected is unknown. The goal of this model is to analyze the various processes and trophic interactions, examining how they change in the presence of *Dreissena*, thereby narrowing the scope of possible consequences and offering more realistic predictions regarding the invasion.

As previously stated, a mathematical model was constructed to evaluate potential cascading ecological effects caused when zebra mussels successfully colonize an ecosystem. This first-order model was developed as a simplified representation of an aquatic system. The objective of the model is to provide a foundation for further investigation of the zebra mussel invasion using ecological computer simulations. The system represented here contains six inter-dependent components (i.e., nutrients, phytoplankton, periphyton/marcophytes, zooplankton, fish, and zebra mussels) (Figure 2.1). For the purposes of this exercise, zooplankton and vertebrate species (e.g., fish and waterfowl) have been ignored. While these groups likely affect the magnitude and velocity of ecosystem dynamics, their exclusion was intended to simplify the scope of this initial modeling activity. In the model, the dynamics of each component are represented by a differential equation which is mathematically coupled to other components of the model upon which they depend.

2.1.1 Nutrients Pathways

Chemical nutrients represent the sole abiotic component of the model. It is assumed that nutrients are freely available is the system and may be either dissolved, suspended, or present in

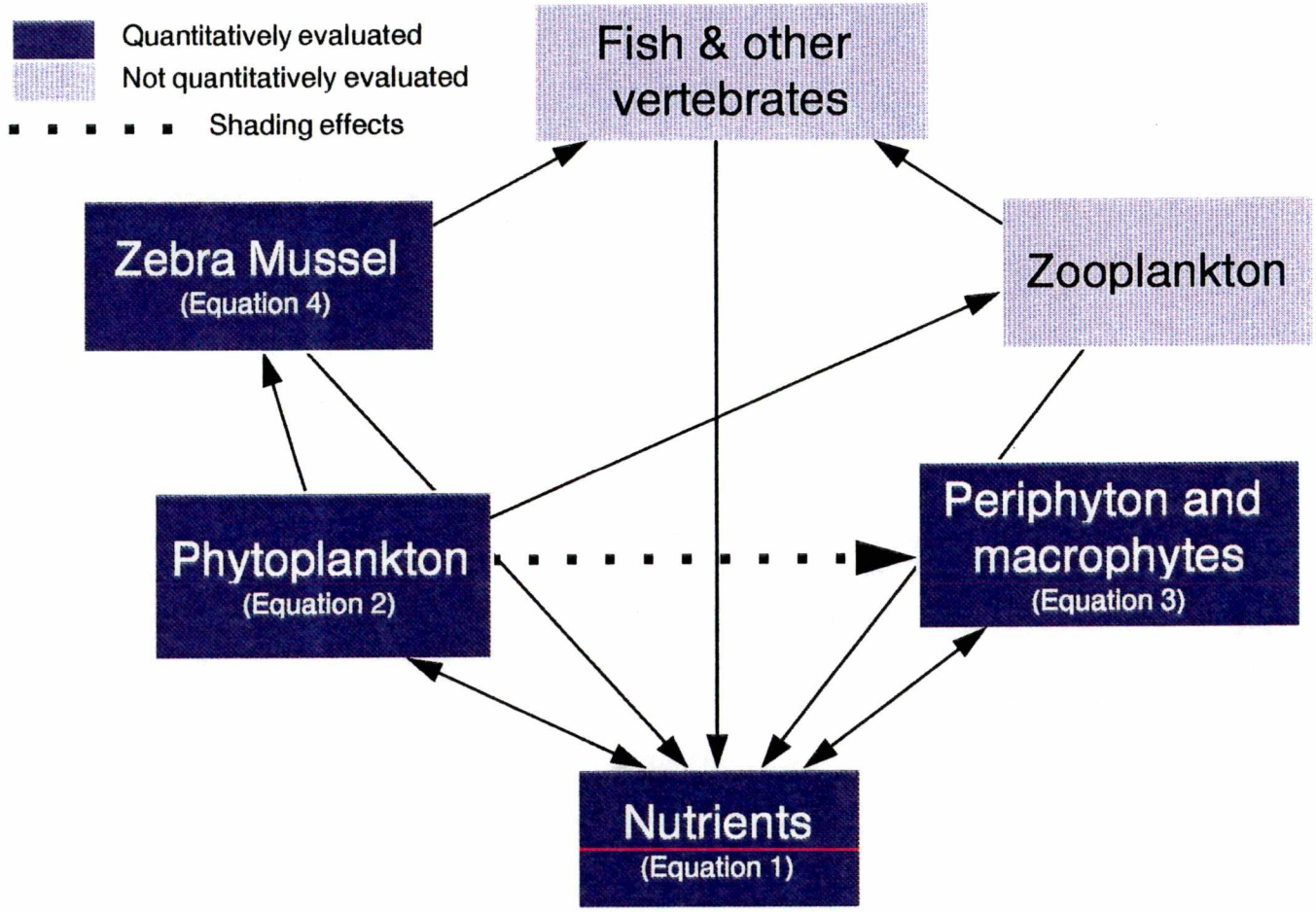

Figure 2.1 Conceptual Community Model

detritus. Because phosphorus is considered to be a limiting nutrient (Imboden 1974, Schindler 1977, Wetzel 1983), at least in lentic systems, the model is simplified to represent only one nutrient. Phosphorus flux through the system is represented by Eq. 1:

$$\frac{dN}{dt} = N_{pool} + (\gamma \cdot [Ph_{death} + P_{death} + Z_{death}]) - [Ph_{increase} + P_{increase}] \qquad \text{(Eq. 1)}$$

where

N_{pool} = limiting nutrient concentration (e.g., mg PO_4/L),

γ = scaling factor to account to the proportion of nutrients returning to N_{pool},

Ph_{death} = decrease in phytoplankton biomass (mg/d),

P_{death} = decrease in periphyton biomass (mg/d),

Z_{death} = decrease in zebra mussel biomass (mg/d),

$Ph_{increase}$ = increase in phytoplankton biomass (mg/d),

$P_{increase}$ = increase in periphyton biomass (mg/d).

Nutrients persist in the system either in the form of nutrients maintained in the nutrient pool (i.e., available nutrients) or by nutrients sequestered in biota (i.e., primary producers and zebra mussels). Flux through the system is governed by the amount of nutrients returning to the nutrient pool in the form of dead biota (i.e., Ph_{death}, P_{death}, Z_{death}) and by nutrients leaving the nutrient pool in the form of biotic reproduction (i.e., $Ph_{increase}$, $P_{increase}$). A scaling factor (γ) was applied to account for nutrients lost from the system.

2.1.2 Primary Producers

Population dynamics of two groups of primary producers are represented as separate compartments of the model: phytoplankton (Eq. 2), and periphyton and other attached vegetation (Eq. 3). Density-dependence is assumed for each compartment, and both phytoplankton and

periphyton are linked to nutrients. In Eqs. 2 and 3, the population growth terms were calculated to assume Michaelis-Menton nutrient uptake dynamics (Edelstein-Keshet 1988) meaning that primary production is directly proportional to nutrient availability (i.e., greatest productivity occurs at $0.5K_{max}$). Although the present application of the model assumes that nutrients are in virtually unlimited supply (i.e., a eutrophic system), future evaluations of the model should include an evaluation of nutrient dynamics when nutrients are in varying degrees of abundance (i.e., mesotrohic and oligotrophic systems). Linking nutrients to the growth terms for primary producers allows for the evaluation of community dynamics in the model under varying trophic states, or in this case, assuming eutrophic conditions (e.g., Carpenter and Kitchell 1984, Kitchell et al. 1979).

Population dynamics for the aggregate of the phytoplankton community are estimated by Eq. 2.

$$\frac{dPh}{dt} = \left[\left[\frac{(r_{phytoplankton} \cdot N)}{1+N}\right] + [1-\phi] - [d_{Ph} + (\Theta \cdot ZM)]\right] \cdot Ph \qquad \text{(Eq. 2)}$$

where

$r_{phytoplankton}$ = intrinsic growth rate of phytoplankton (mg/d),

N = nutrient concentration (mg/l),

Ph = phytoplankton biomass (mg/l),

ϕ = zebra mussel grazing efficiency (unitless),

d_{Ph} = intrinsic dead rate of phytoplankton (mg/d),

Θ = effect of zebra mussel on phytoplankton loss (unitless),

ZM = zebra mussel biomass (mg/L).

Grazing pressure on phytoplankton by zebra mussels is represented by the *zebra mussel grazing efficiency* (ϕ) term. Since it is unrealistic that zebra mussels could maintain a 100% grazing efficiency causing the extinction of all individuals and all species of the phytoplankton community

(e.g., Porter 1977, Beddington et al. 1978), inclusion of this parameter is to allow for the persistence of phytoplankton at some base level even when zebra mussels are highly abundant.

Population dynamics for the aggregate of obligate-attached primary producers (i.e., periphyton and macrophytes) is estimated using Eq. 3.

$$\frac{dP}{dt} = \left[\left[\frac{(r_{periphyton} \cdot N)}{1+N}\right] - d_P\right] \cdot P - [Ph \cdot \beta] \qquad \text{(Eq. 3)}$$

where

P = periphyton biomass (mg/l),

$r_{periphyton}$ = intrinsic growth rate of periphyton (mg/d),

N = nutrient concentration (mg/l),

β = shading coefficient (unitless),

d_P = intrinsic death rate of periphyton (mg/d).

Studies have demonstrated that phytoplankton can interfere with productivity of attached photosynthetic communities (Leob et al. 1983). The *shading coefficient* (ß) is intended to represent the inhibition of periphyton/macrophyte growth as a function of water clarity (i.e., the effect of phytoplankton on periphyton). While empirical data are scarce, it has been hypothesized that the zebra mussel has been accountable for significant increase in water clarity in Lake Erie. Since attached vegetation is arguably light limited, an increase in water clarity may to some degree, allow for higher productivity within the epiphytic community. The impact of such a phenomenon may cause profound shifts in abundances of attached and planktonic producers; such shifts would likely

lead to cascading dynamics to other trophic levels within the system (e.g., Schoener 1974, Grover 1990).

2.1.3 Zebra Mussels

Despite the prolific and fucund nature of zebra mussels, the model assumes that population change among the zebra mussel population is closely bound to the abundance of phytoplankton (Sprung and Rose 1988). Therefore, the rate of change within the zebra mussel population can be represented by Eq. 4.

$$\frac{dZM}{dt} = \left[\left(r_{zebra\ mussel} + [\alpha \cdot Ph]\right) - d_{zebra\ mussel}\right] \cdot ZM \qquad \text{(Eq. 4)}$$

where

ZM = zebra mussel biomass (mg/L),

$r_{zebra\ mussel}$ = intrinsic rate of increase for the zebra mussel (mg/d),

α = scaling factor to account the proportion of phytoplankton biomass contributing to zebra mussel biomass (unitless),

Ph = phytoplankton biomass (mg/L),

$d_{zebra\ mussel}$ = intrinsic rate of decrease for the zebra mussel (mg/d).

A scaling factor (α) is applied to the growth rate of zebra mussels to represent relative efficiency phytoplankton biomass conversion to zebra mussels biomass (i.e., the amount of phytoplankton biomass transferred to a zebra mussel biomass).

2.1.4 Other Consumers and Predators

It is likely that consumers such as zooplankton, fish, and waterfowl play crucial roles in defining the dynamics of zebra mussel–invaded ecosystems; however, the current version of the model does not include these components. To maintain simplicity of the model, inclusion of these parameters is beyond the scope of this evaluation, but the contribution of these components should be accounted for in future simulations.

2.2 PARAMETERIZATION

Because sufficient data are lacking for many of the model parameters, initial parameter values were often assumed according to informed judgement. Table 2.1 contains values and their justifications for parameters which were held constant. Since the primary objective of this project was to construct a model that can be used to evaluate the feasibility of alternative community states and presence of nonlinear dynamics, clearly more empirical information is needed to hone its precision and validate its findings. While models of this nature are characteristically sensitive to initial conditions, some degree of uncertainty among the model's trajectories can be eliminated by applying more precise, empirically derived parameter values.

2.3 SENSITIVITY ANALYSIS

Once the computer-based version of the model was constructed, several of its parameters were found to be more sensitive than others. Ideally, to reduce the degree of uncertainty of the model, all parameter values should be varied by ordinate degrees to consider the variation in model behavior given uncertain parameterization. Because of time requirements and the complexity associated with interpreting simulation results, I chose three parameters each of which to assign three initial values. Selection of critical parameters was based on a criterion consisting of 3 major components; this

Table 2.1 Summary of intial parameterization

Parameter	Definition	Range of Values	Justification
N_{pool}	Available nutrient concentration	10000	Large values eliminated potential nutrient limitation.
Ph	Phytoplankton biomass	1	Initial biomass 2 orders of magnitude greater the consumer.
$r_{Phytoplankton}$	Phytoplankton intrinsic growth rate	0.55	Approximate median value for various phytoplankton species. Extracted from Reynolds (1984).
$d_{Phytoplankton}$	Phytoplankton death rate	0.001	Estimated.*
Θ	Effect of zebra mussel on phytoplankton loss	.0005	Estimated.*
ϕ	Zebra mussel grazing efficiency	0.1, 0.0001, 0.0000001	Estimated.* Sensitivity analysis.
P	Periphyton biomass	1	Initial biomass 2 orders of magnitude greater the consumer.
$r_{Periphyton}$	Periphyton intrinsic growth rate	0.55	Consistent with $r_{Phytoplankton}$.
$d_{Periphyton}$	Periphyton death rate	0.001	Estimated.*
β	Shading coefficient	1, 10, 1000	Estimated.* Sensitivity analysis.
ZM	Zebra mussel biomass	0.01	Initial biomass 2 orders of magnitude less than consumer representing colonization of eutrophic system.
$r_{zebra\ mussel}$	Zebra mussel intrensic growth rate	0.001, 0.0005, 0.0001	Estimated.* Sensitivity analysis.
$d_{zebra\ mussel}$	Zebra mussel death rate	0.001	Estimated.*
α	Effect of phytoplankton on zebra mussel growth rate	0.0001	Estimated.*

Shaded rows indicate parameters evaluated in sensitivity analysis.
*Compare with Jørgensen et al. 1991.

criterion included the following conditions: (1) the existence of little or no empirical data defining the parameter in terms appropriate for evaluating the feasibility of model assumptions, (2) natural variation in data should they exist or be quantified in the future, and (3) the intangibility of measuring parameter values empirically.

Parameters chosen for sensitivity analysis based on one or more of these criterion components were zebra mussel grazing efficiency (ϕ), the shading coefficient (ß), and intrinsic growth rate for zebra mussels (r_{zm}). Each of these parameters was assigned three values (Table 2.1), that were intended to bridge the range of actual values. Computer simulations run using three values for each of 3 model parameters resulted in 3^3 (27) possible initial configurations of the model.

The computer-based model was constructed using Stella II© Version 3.05. Simulations were conducted using an IBM-compatible Pentium© desktop computer. Each simulation was run through 2000 iterations to ensure that equilibrium was reached by each trajectory. In some cases, parameter combination created instability, thereby causing the system to collapse before equilibrium could be reached. Results in relative biomass for phytoplankton, periphyton/macrophytes, and zebra mussels were recorded and graphed for each simulation that could be tracked through 2000 generations.

2.4 NONLINEAR ANALYSIS

Data resulting from the sensitivity analysis were quantitatively evaluated for the possible presence of exotic nonlinearity. Trajectories qualitatively suggesting evidence of nonlinearity were evaluated quantitatively for chaotic behavior by calculating Lyapunov exponents using Chaos Data Analyzer© (CDA). In general, chaos is characterized by sensitivity to initial conditions, where minute changes in a model parameter are magnified leading to little predictive ability. Several measures of deterministic chaos can be calculated by CDA including Lyapunov exponents. The Lyapunov exponent is a measure of the divergence of local trajectories (e.g., the difference in a

given trajectory at times x-1, x, and x+1) and provides a single line of evidence concerning the presence of chaos (Millonas 1996). The time-series is said to be consistent with chaos if at least one Lyapunov exponent is positive. If data are periodic, all exponents must be negative. Lyapunov exponents that equal zero indicate that the trajectory is near a bifurcation suggesting that a shift from one community state to another may occur.

3. RESULTS

Data from the sensitivity analysis procedure and from the analysis of chaotic dynamics are presented. Subsection 3.1 characterizes the results of alternative community states created be varying initial values of ϕ, ß, and r_{zm}. Subsection 3.2 lists results of the calculation of Lyapunov exponents.

3.1 SENSITIVITY ANALYSIS

Alternative community states, represented as time-series fluctuations in zebra mussel, phytoplankton, and periphyton/macrophyte biomass, are shown in Figures 3.1 through 3.27 in the Appendix. To analyze these graphs, it is necessary to observe two distinct classes of results: the relative trajectories of the producers (i.e., phytoplankton and periphyton/macrophytes) and of the consumer (i.e., zebra mussels).

Table 3.1 qualitatively summarizes the behavior of producer trajectories. Four categories of results were possible including phytoplankton dominance, periphyton/macrophyte dominance, codominance (i.e., both categories of consumers appear to persist in relatively equal biomass), and community instability (i.e., the model crashed due to the generation of unrealistically large numbers). Under possible combinations of the selected parameter values, there were no instances when phytoplankton became solely dominant. Codominance occurred in nine simulations (Figs. 3.1, 3.2, 3.3, 3.10, 3.11, 3.12, 3.19, 3.20, and 3.21), always when the zebra mussel growth rate was low. Periphyton/macrophytes were dominant in 12 simulations (Figs. 3.4, 3.5, 3.7, 3.8, 3.13, 3.14, 3.16, 3.17, 3.22, 3.23, 3.25, and 3.26) when the zebra mussel growth rate was moderate or high and when grazing efficiency was low or moderate. The system became unstable and crashed when

Table 3.1 Summary of primary producer dominance

Zebra Mussel Growth Rate	Grazing Efficiency	Shading Coefficient		
		Low	Moderate	High
	Low	c	c	c
Low	Moderate	c	c	c
	High	c	c	c
	Low	na	na	na
Moderate	Moderate	p	p	p
	High	p	p	p
	Low	na	na	p
	Moderate	p	p	na
High	High	p	p	p

c Phytoplankton and periphyton/macrophyte codominance.
p Periphyton/macrophytes dominant.
na System instability leading to collapse.

grazing efficiency was high and the zebra mussel growth rate was either moderate or high (Figs. 3.6, 3.9, 3.15, 3.18, 3.24, and 3.27).

Table 3.2 qualitatively summarizes the behavior of zebra mussel trajectories. Four categories of results were possible based on the degree of variation in zebra mussel biomass through time. These categories were stable (i.e., zebra mussel biomass fluctuates early but becomes damped well before the simulation terminates), variable (i.e., zebra mussel biomass maintains a degree of fluctuation throughout the simulation), highly variable (i.e., zebra mussel biomass undergoes radical fluctuation throughout the simulations) and community instability (i.e., the model crashed due to the generation of unrealistically large numbers). Trajectories that appeared variable or highly variable were considered candidates for possessing chaotic dynamics and are further evaluated in Subsect. 3.2.

Under possible combinations of the selected parameter values, stability occurred in nine simulations (Figs. 3.1, 3.2, 3.3, 3.5, 3.8, 3.11, 3.16, 3.19, 3.20, and 3.21). Seven simulations were categorized as variable (Figs. 3.7, 3.12, 3.13, 3.16, 3.22, 3.23, and 3.25) and four simulations as highly variable (Figs. 3.4, 3.14, 3.17, and 3.26). Again, the system became unstable and crashed when grazing efficiency was high and the zebra mussel growth rate was either moderate or high (Figs. 3.6, 3.9, 3.15, 3.18, 3.24, and 3.27). Emergent pattern in stability was difficult to detect, but generally stability decreased as a function of increasing zebra mussel growth rate (r_{zm}) and of the shading coefficient (ß).

3.2 DETERMINISTIC CHAOS

Lyapunov exponents were calculated for all zebra mussel trajectories persisting through 2000 time steps. Table 3.3 contains the results of these calculations. Exponents greater than zero indicate that chaotic dynamics exist. Lyapunov exponents exceeded 1 for all simulations evaluated. All

Table 3.2 Summary of zebra mussel biomass trajectory

Zebra Mussel Growth Rate	Grazing Efficiency	Shading Coefficient		
		Low	Moderate	High
	Low	s	s	s
Low	Moderate	s	s	s
	High	s	s	s
	Low	na	na	na
Moderate	Moderate	s	h	v
	High	h	v	v
	Low	na	na	na
	Moderate	s	h	h
High	High	v	v	v

s Stable population.
v Population moderately variable.
h Population highly variable.
na System instability leading to collapse.

Table 3.3 Summary of Lyapunov exponents

Zebra Mussel Growth Rate	Grazing Efficiency	Shading Coefficient		
		Low	Moderate	High
Low	Low	0.230	0.095	0.133
	Moderate	0.226	0.397	0.356
	High	0.214	0.347	0.312
Moderate	Low	na	na	na
	Moderate	0.007	0.195	0.326
	High	0.144	0.579	0.613
High	Low	na	na	na
	Moderate	1.348	0.112	0.320
	High	0.445	0.435	0.456

na System instability leading to collapse.

analyses of trajectories indicate that indeed chaotic dynamics are likely to exist within the time-series produced by the present model configurations. Analysis using additional nonlinear diagnostics would be required to confirm or refute these findings, and new techniques are presently being developed, evaluated, and tested to improve the diagnosis of chaos (e.g., nonlinear forecasting). However, there is presently no consensus among theoreticians regarding which techniques are best (e.g., Millonas 1996).

4. DISCUSSION

4.1 SENSITIVITY ANALYSIS

This investigation proposes and evaluates a first-order simulation model containing four primary components (nutrients, phytoplankton, periphyton/macrophytes, and zebra mussels). A sensitivity analysis of the model was conducted to address the degree of uncertainty surrounding essential parameter values. Since few empirical values were available, the sensitivity analysis was intended to demonstrate which, if any, parameters affected the simulation results most significantly. If it could be shown that modeled results were not sensitive to initial conditions of a given parameter, then the range of uncertainty within the given parameter could be ignored. Conversely, when changes in initial parameter values induce noticeably variant behavior in the simulation outcome, that parameter is critical to the simulation and requires additional empirical study to reduce its inherent uncertainty.

Three parameters were evaluated (ϕ, ß, r_{zm}) in the sensitivity analysis. Results were reported in terms of nutrients, phytoplankton, periphyton/macrophytes, and zebra mussel biomasses. Interpretation of the data yielded classes of results, dominance among primary producer biomasses (i.e., phytoplankton and periphyton/macrophytes), variability within the zebra mussel population, and system instability (i.e., system collapse). Dynamics among primary producers were characterized as being dominated by periphyton/macrophytes or codominance among both classes of primary producers. The dynamics of the zebra mussel component were characterized according to the variability of the time-series. Zebra mussel trajectories were categorized as either stable, variable, highly variable, or unstable.

4.1.1 Zebra Mussel Intrinsic Growth Rate

Dominance among primary producers was driven by the variation in the rate of increase in the zebra mussel compartment of the model (i.e., r_{zm}). Codominance only resulted when r_{zm} was low, with periphyton/macrophyte being dominant when r_{zm} was moderate to high. Pattern in the variability among the zebra mussel population of the alternative community states was not as distinct. Generally, variability increased as a function of r_{zm}, although it is likely that an interaction existed between r_{zm} and grazing efficiency (i.e., ϕ). The system became collapsed when the zebra mussel rate of increase was moderate to high and when grazing efficiency was low. Instability likely occurred under these conditions because the zebra mussel population reached unrealistically large values (e.g., biomass $>10^{18}$mg/L), essentially a state of exponential growth.

The overall pattern attributable to r_{zm} is indicative of the critical nature of this parameter in predicting community dynamics. While there is a growing pool of information regarding the fecundity of zebra mussels, at present empirical data linking zebra mussel growth rates to phytoplankton densities is scarce. However, evidence does suggest that the zebra mussel invasion may be inhibited by oligotrophic conditions While zebra mussels have been reported in Lake Superior, it is believed that the nutrient-poor nature of the lake has prevented the species from proliferating there.

4.1.2 Zebra Mussel Grazing Efficiency

The grazing efficiency parameter (i.e., ϕ) represents the zebra mussels foraging capacity. When grazing efficiency is low, phytoplankton are less affected by zebra mussel predation. Likewise, when ϕ is high, phytoplankton biomass approaches zero. Interpretation of the simulation results reveal that ϕ may be a critical parameter, although to a slightly lesser degree than r_{zm}. States of periphyton/macrophyte dominance and primary producer codominance exist for all values of this

parameter. Similarly, all forms of zebra mussel population behavior occur throughout the entire range of this parameter. However, there does appear to be an interaction between r_{zm} and ϕ.

As previously mentioned (Subsect. 4.1.1), the system becomes unstable when r_{zm} is moderate to high but only when ϕ is low; this serves as further evidence that instability in the system is indicative of exponential growth of zebra mussel population, which ultimately induces collapse. When a relatively high density of phytoplankton is allowed to persist in the system, as is the case when ϕ is low, zebra mussels are afforded a less variable food supply. Although this food supply may appear limiting, it remains more constant through time, damping the variable in resources which leads to virtually unlimited growth.

4.1.3 Phytoplankton Shading Effect

Limited evidence is available in the literature that suggests periphyton and macrophytes are light limited. Interference competition between pelagic and attached primary producers was represented by the shading coefficient (ß). It was hypothesized that phytoplankton might inhibit periphyton and macrophyte production. While the model was originally calibrated to show this effect (i.e., zebra mussel biomass and growth rate = 0), there is no clear pattern in the results that would suggest this phenomenon affects community dynamics with zebra mussels present in the model. The one exception is that zebra mussel biomass remains stable when shading is low and grazing efficiency is moderate, even under the highest r_{zm} scenario. Despite this exception, these data suggest that shading does not play a major role in mediating zebra mussel–infested communities.

4.2 NONLINEAR DYNAMICS

Analysis of Lyapunov exponents revealed that all zebra mussel trajectories were consistent with the presence of deterministic chaos; this phenomenon suggests that even under the very simplified

assumptions of the present model, ecosystem-level dynamics associated with the zebra mussel are sensitive to initial conditions. The results of the present analysis lead to several conclusions:

- Predicting future states of invaded ecosystems with confidence will be difficult at best
- A variety of potential community outcomes exist ranging from co-existence to extinction
- Effects of the invasion will likely vary from location to location due to the sensitivity to initial conditions
- Because of variability among ecosystems (i.e., initial conditions), extrapolation from one system to another will lack validity.

4.3 WHERE DO WE GO FROM HERE?

Clearly, additional study on predicting ecological effects caused by biological invasions is warranted. The present investigation scratches the surface for the zebra mussel invasion itself. Further evaluation of the present model followed by the incorporation of additional parameters (e.g., zooplankton, fish, habitat availability, etc.), further sensitivity analysis, and validation of parameter values through field studies is perhaps the next logical step toward predicting the effects of biological invasions. In addition, continued research with respect to nonlinear dynamics, specifically concerning nonlinear forecasting, is crucial to our ability to predict the future of ecological systems.

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APPENDIX

Figures 3.1–3.27

Figure 3.1 Simulation of alternative community trajectories with low gzm, low B, and low rzm.

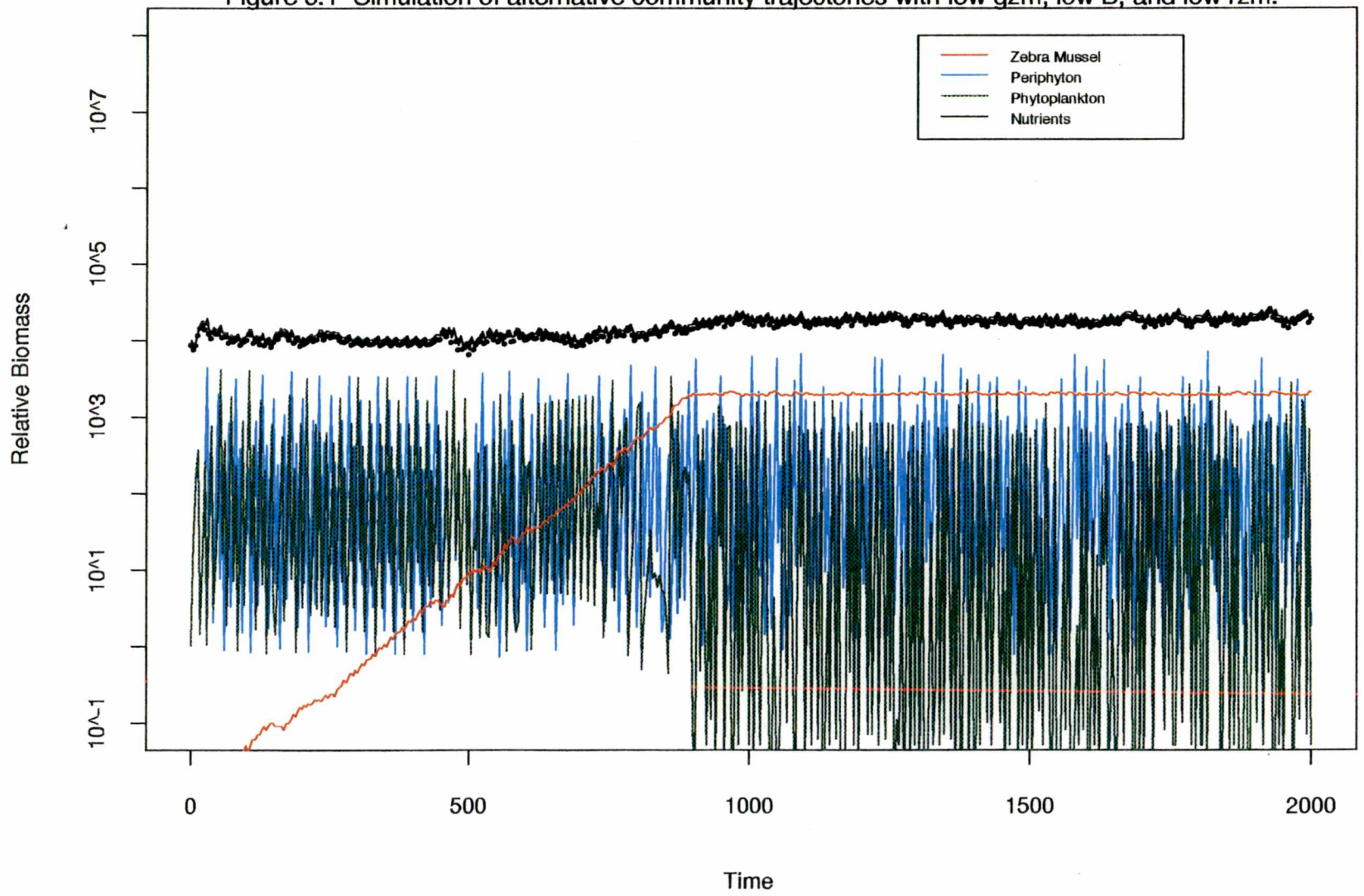


Figure 3.2 Simulation of alternative community trajectories with moderate gzm, low B, and low rzm.

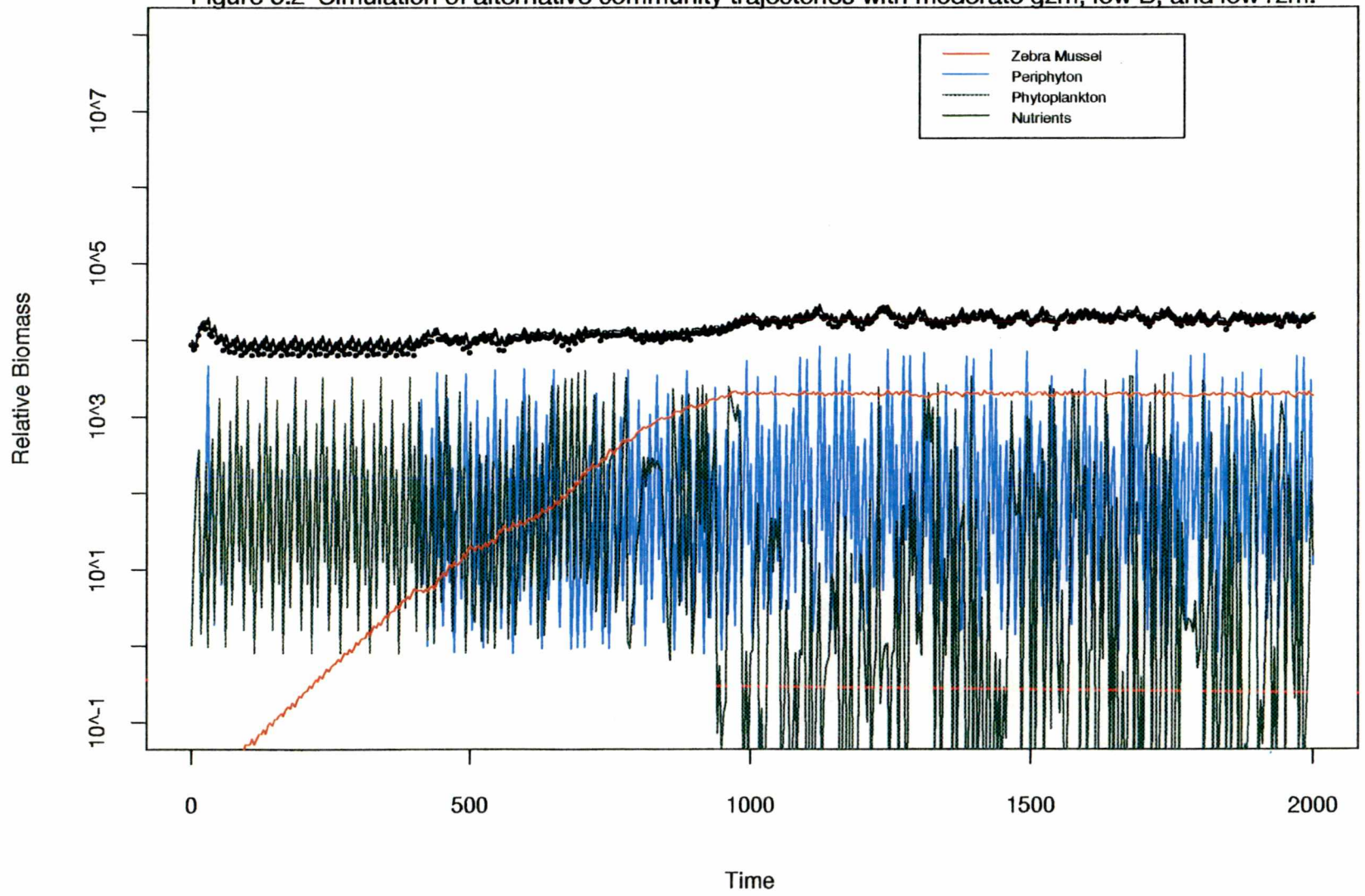


Figure 3.3 Simulation of alternative community trajectories with high gzm, low B, and low rzm.

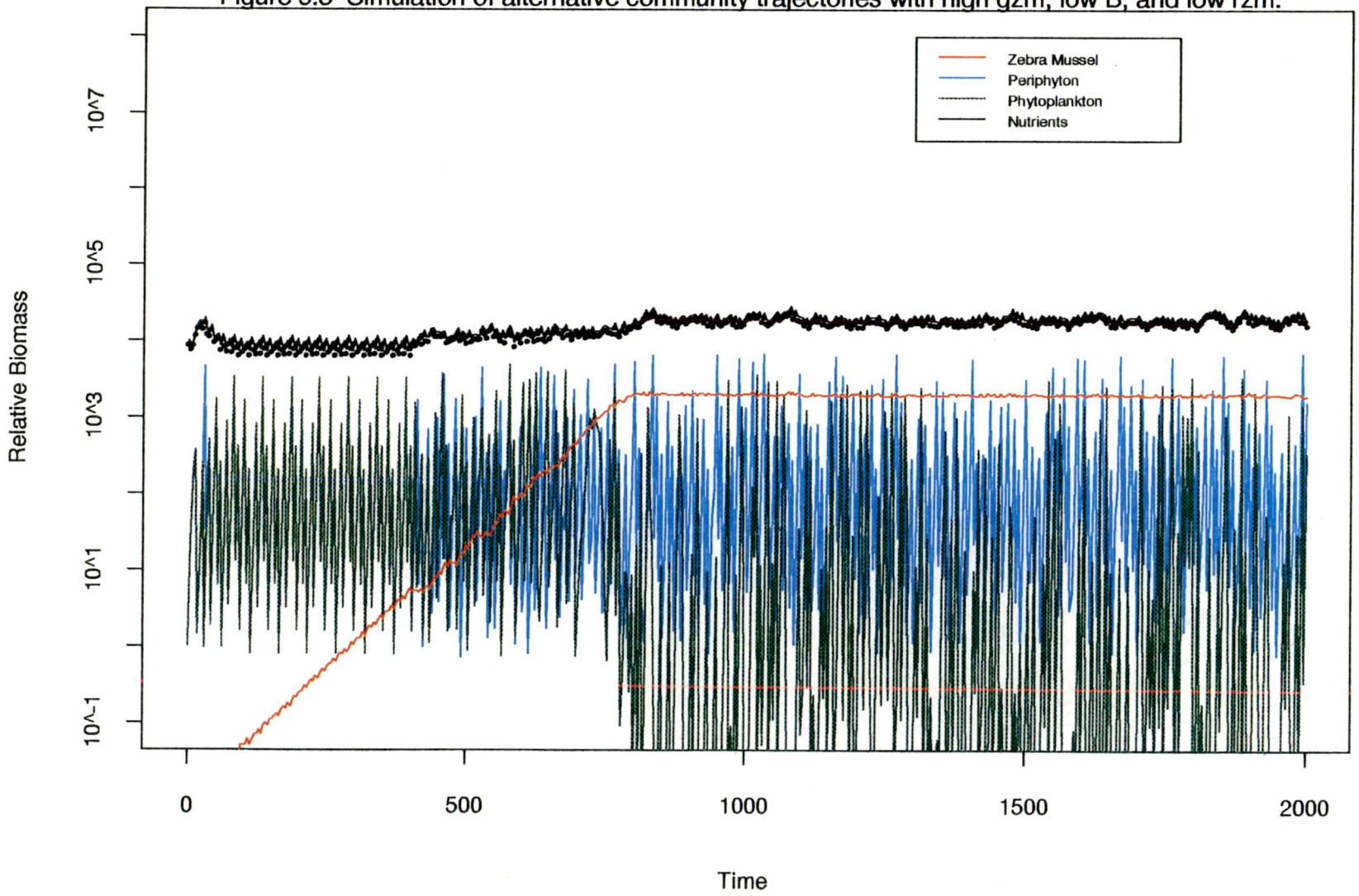


Figure 3.4 Simulation of alternative community trajectories with low gzm, low B, and moderate rzm.

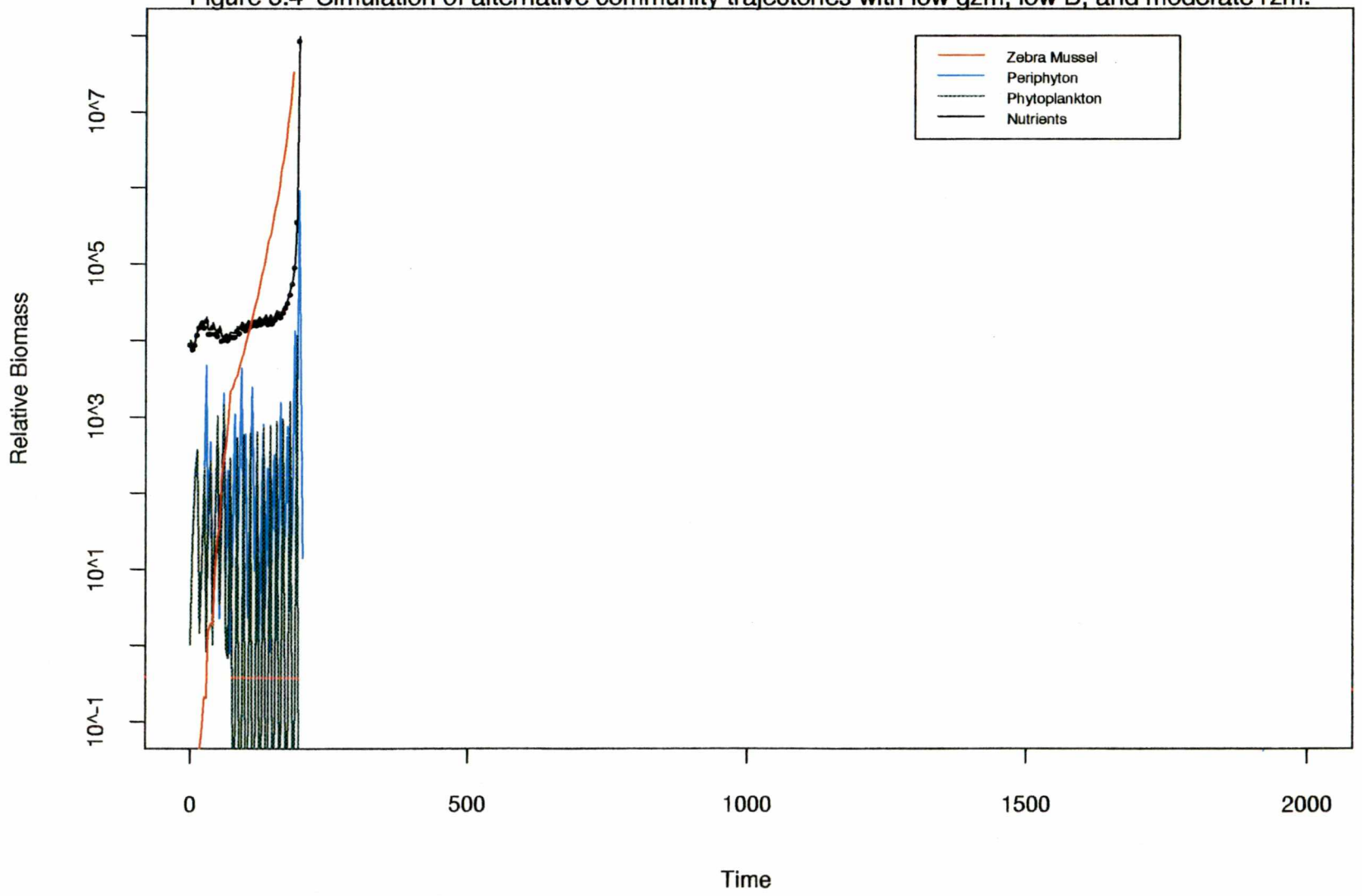


Figure 3.5 Simulation of alternative community trajectories with moderate gzm, low B, and moderate rzm.

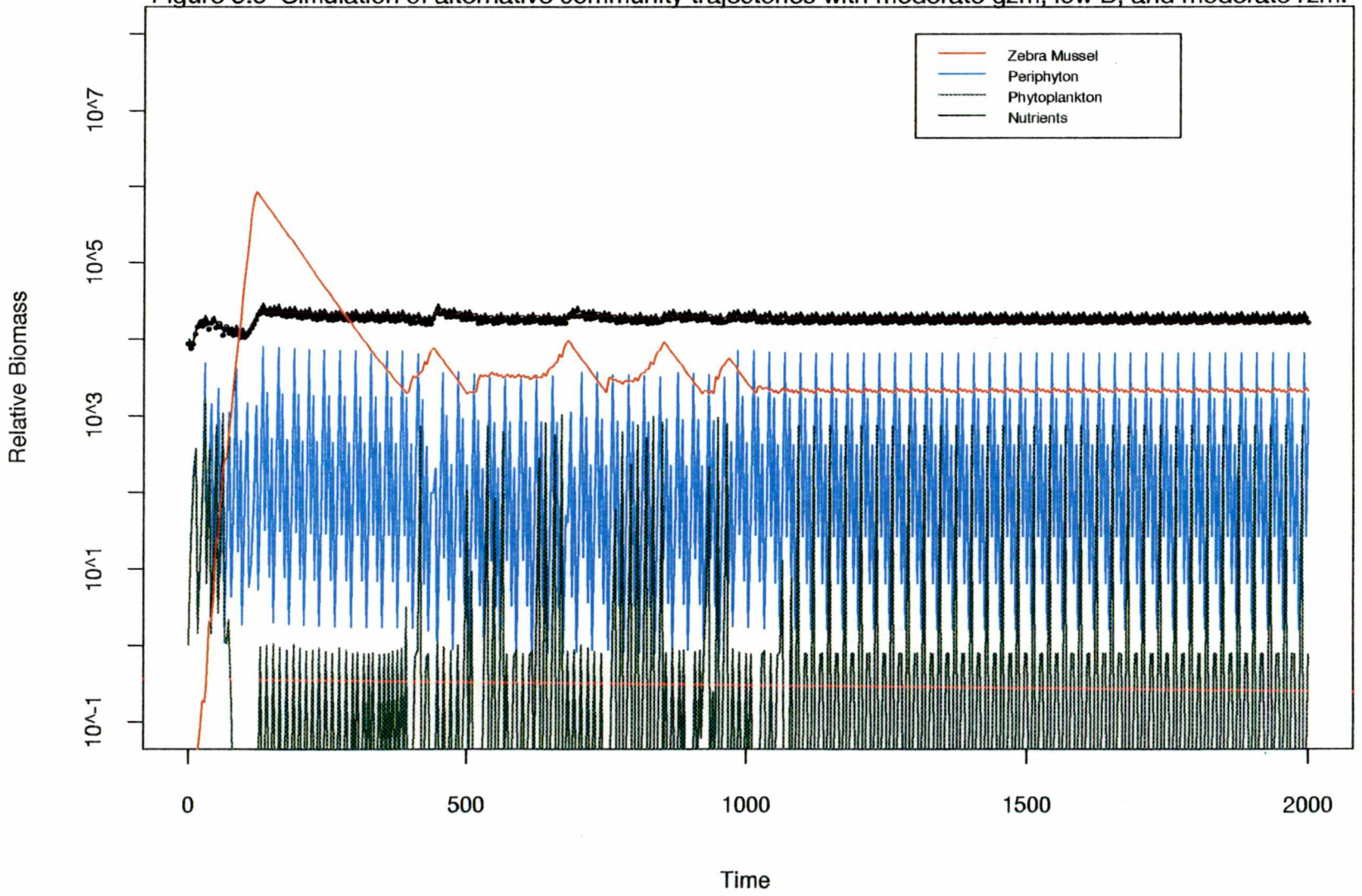


Figure 3.6 Simulation of alternative community trajectories with high gzm, low B, and moderate rzm.

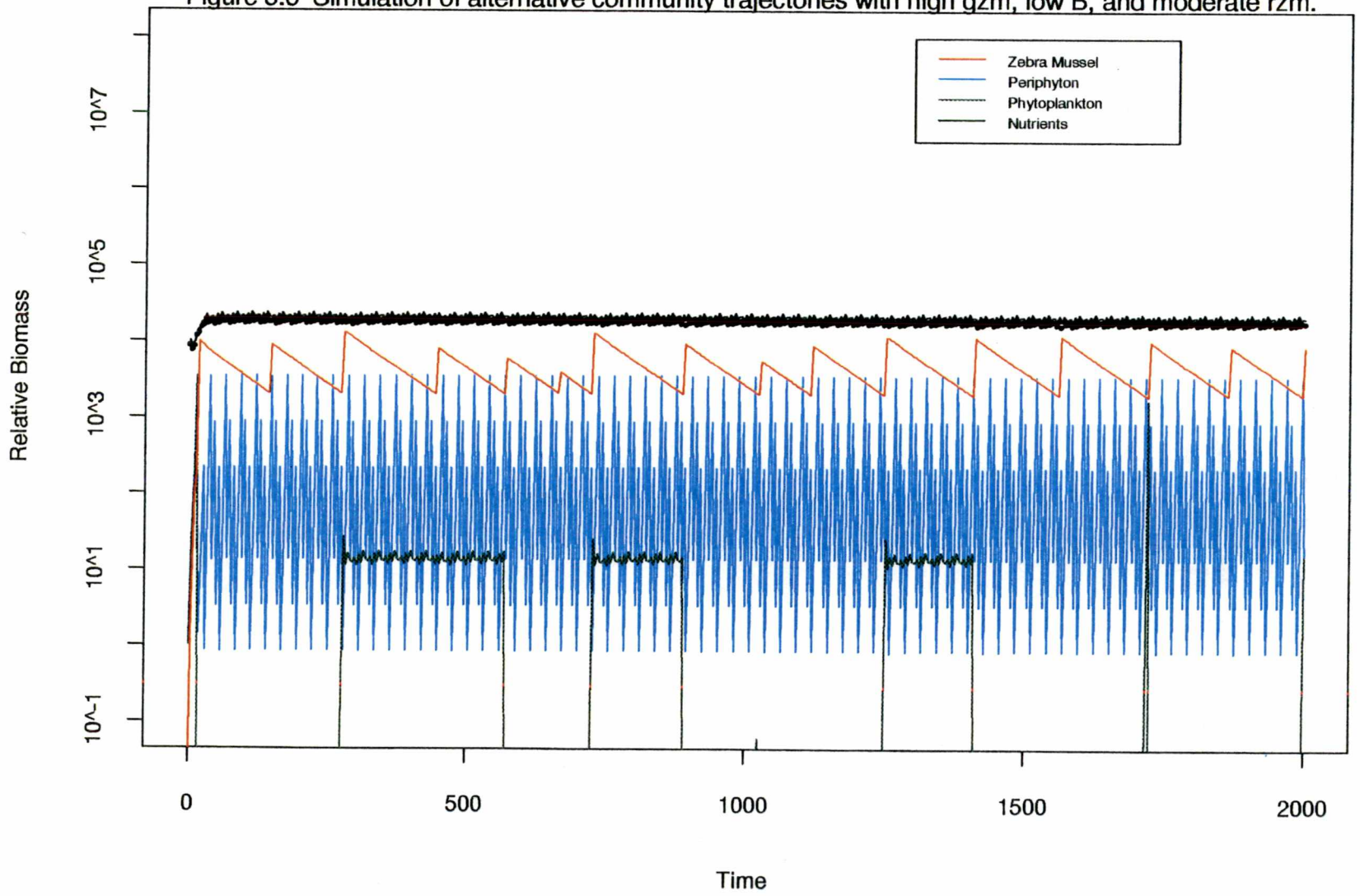


Figure 3.7 Simulation of alternative community trajectories with low gzm, low B, and high rzm.

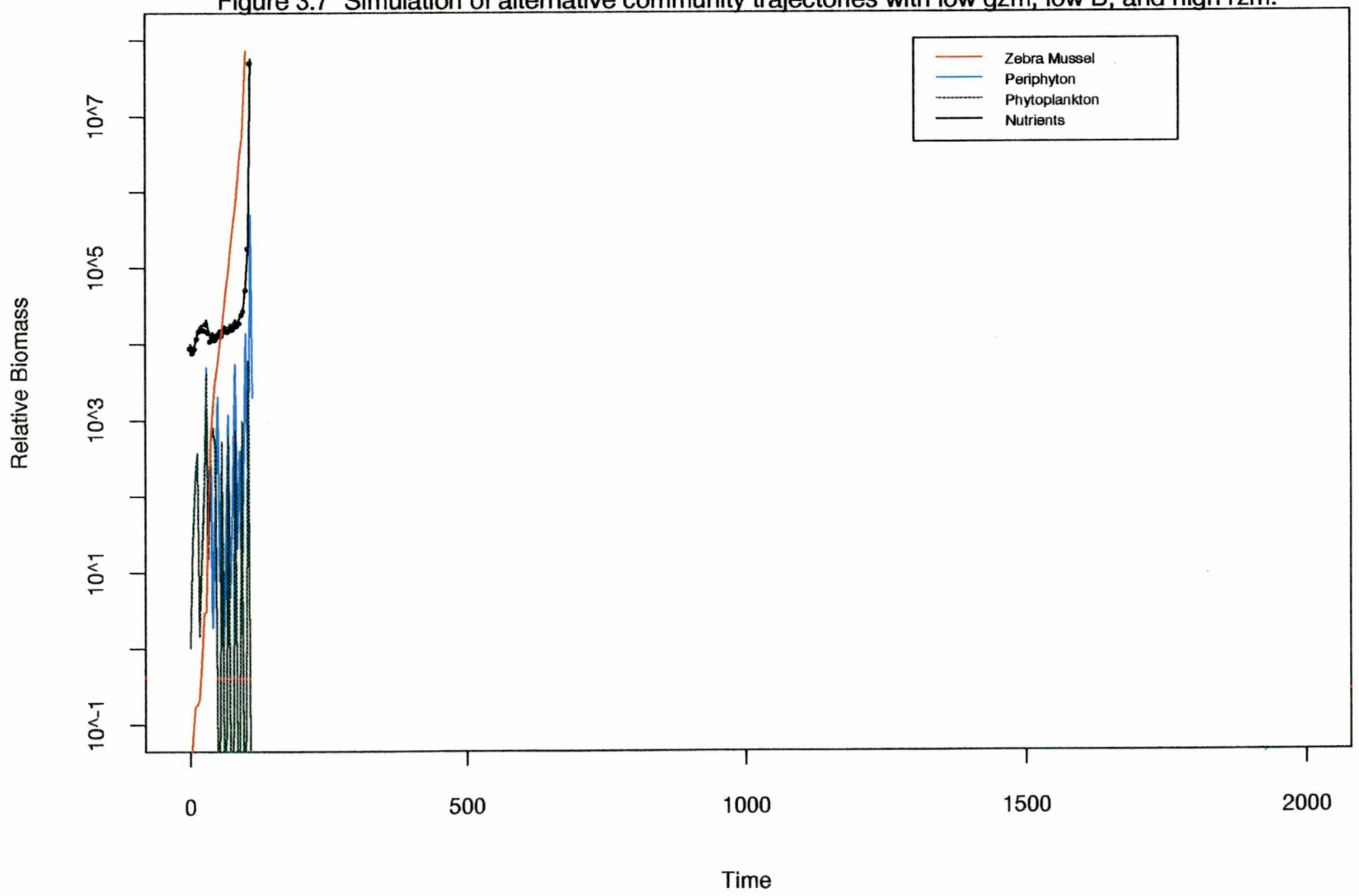


Figure 3.8 Simulation of alternative community trajectories with moderate gzm, low B, and high rzm.

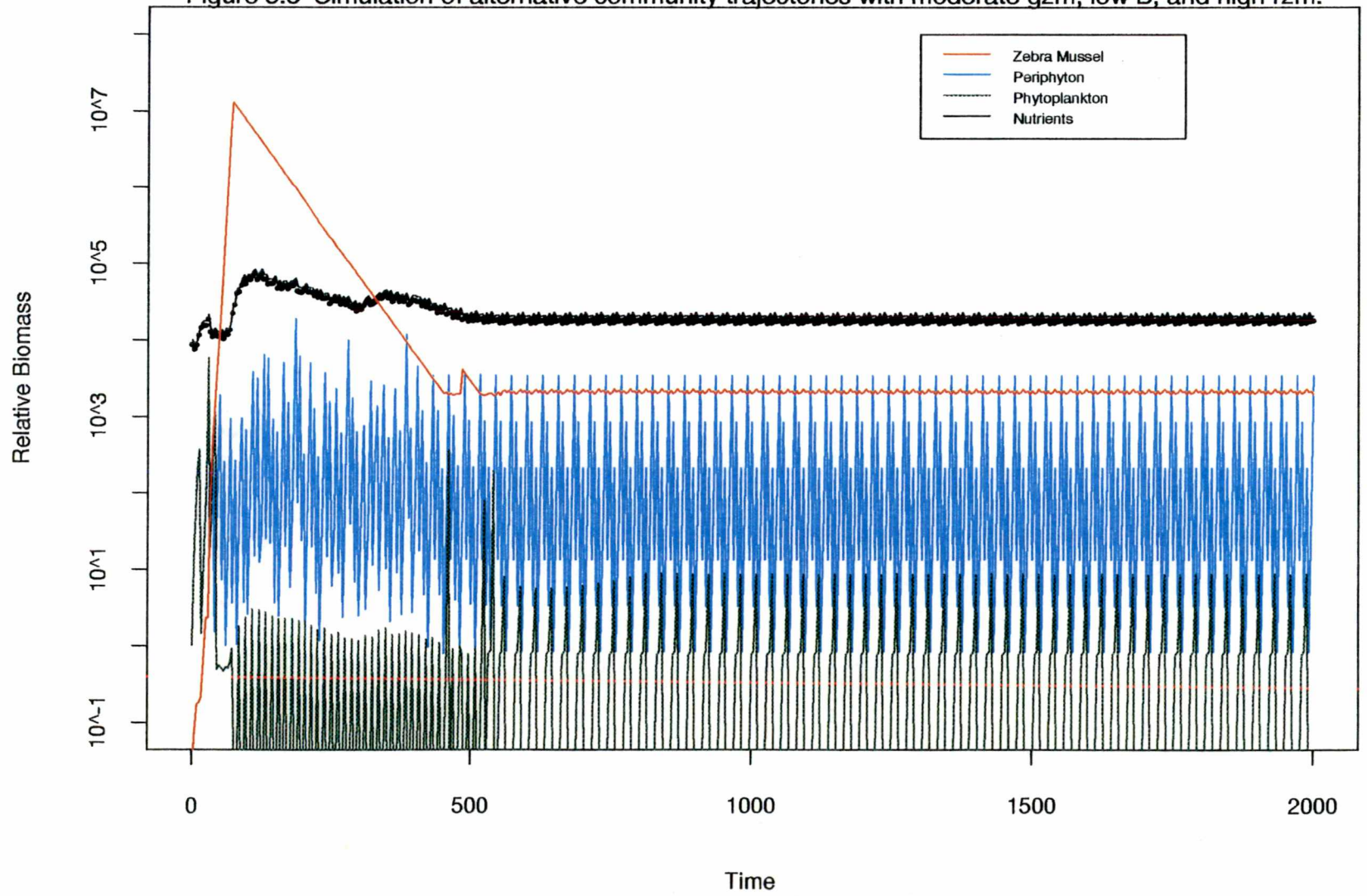


Figure 3.9 Simulation of alternative community trajectories with high gzm, low B, and high rzm.

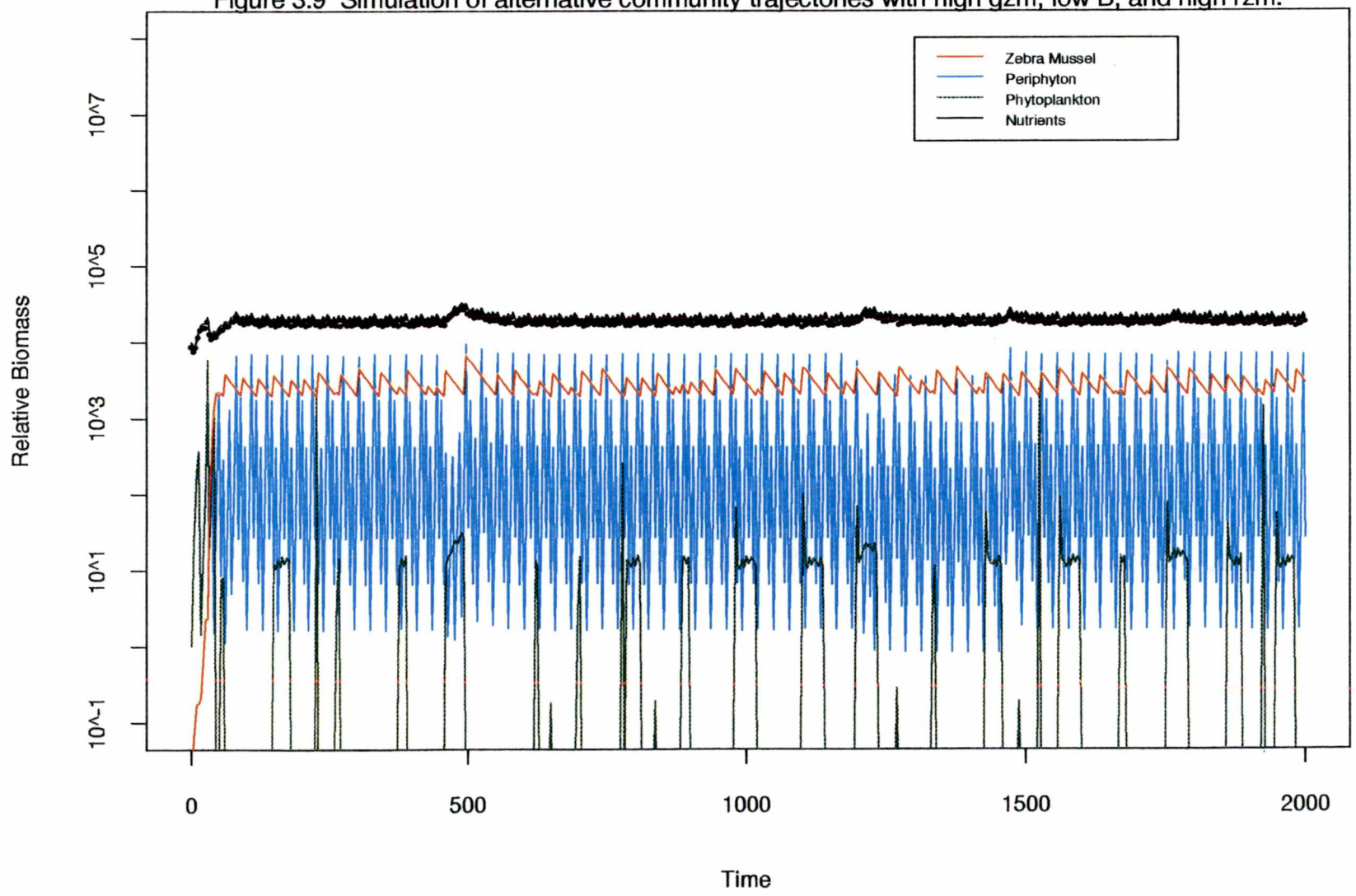


Figure 3.10 Simulation of alternative community trajectories with low gzm, moderate B, and low rzm.

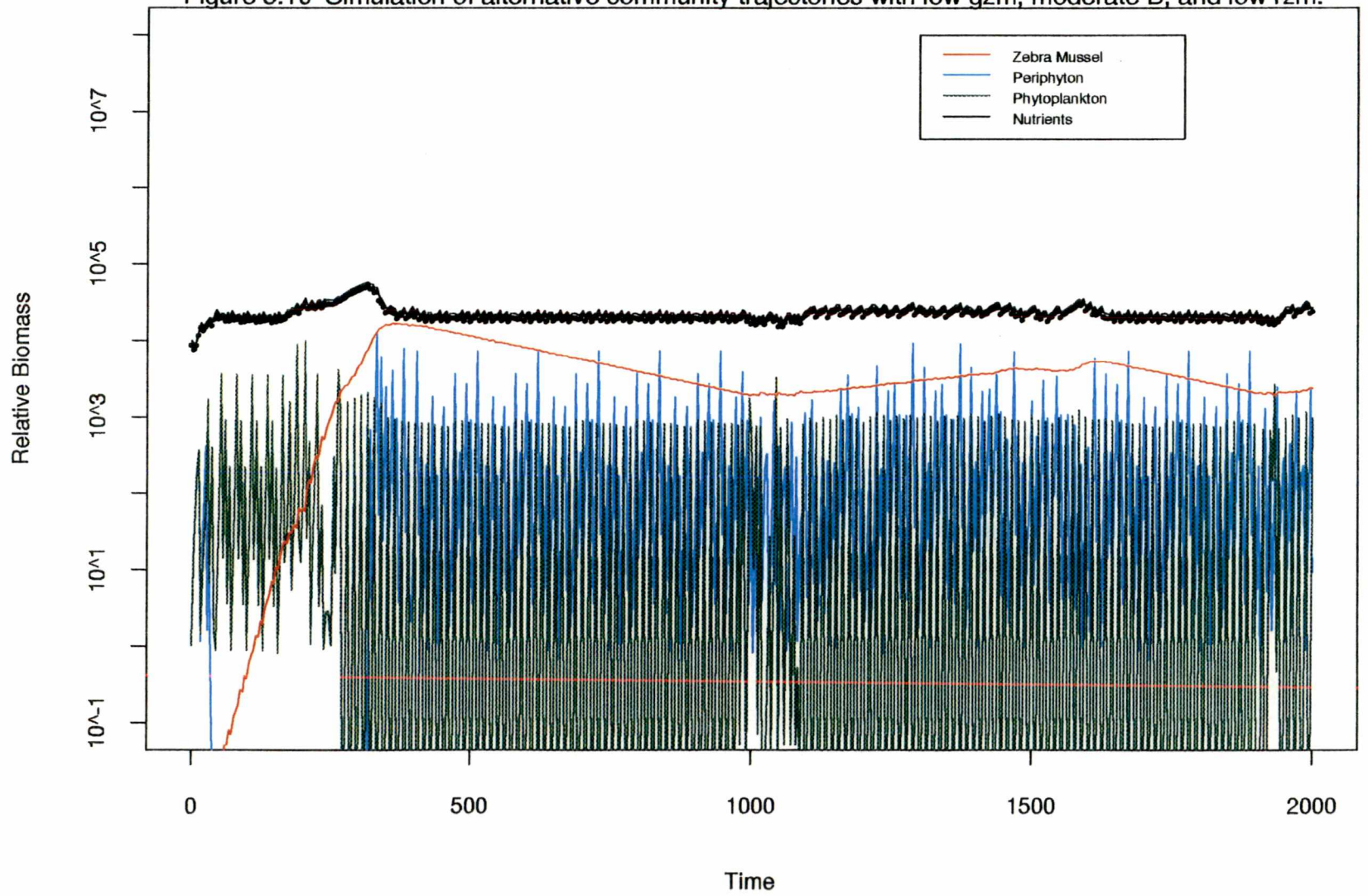


Figure 3.11 Simulation of alternative community trajectories with moderate gzm, moderate B, and low rzm.

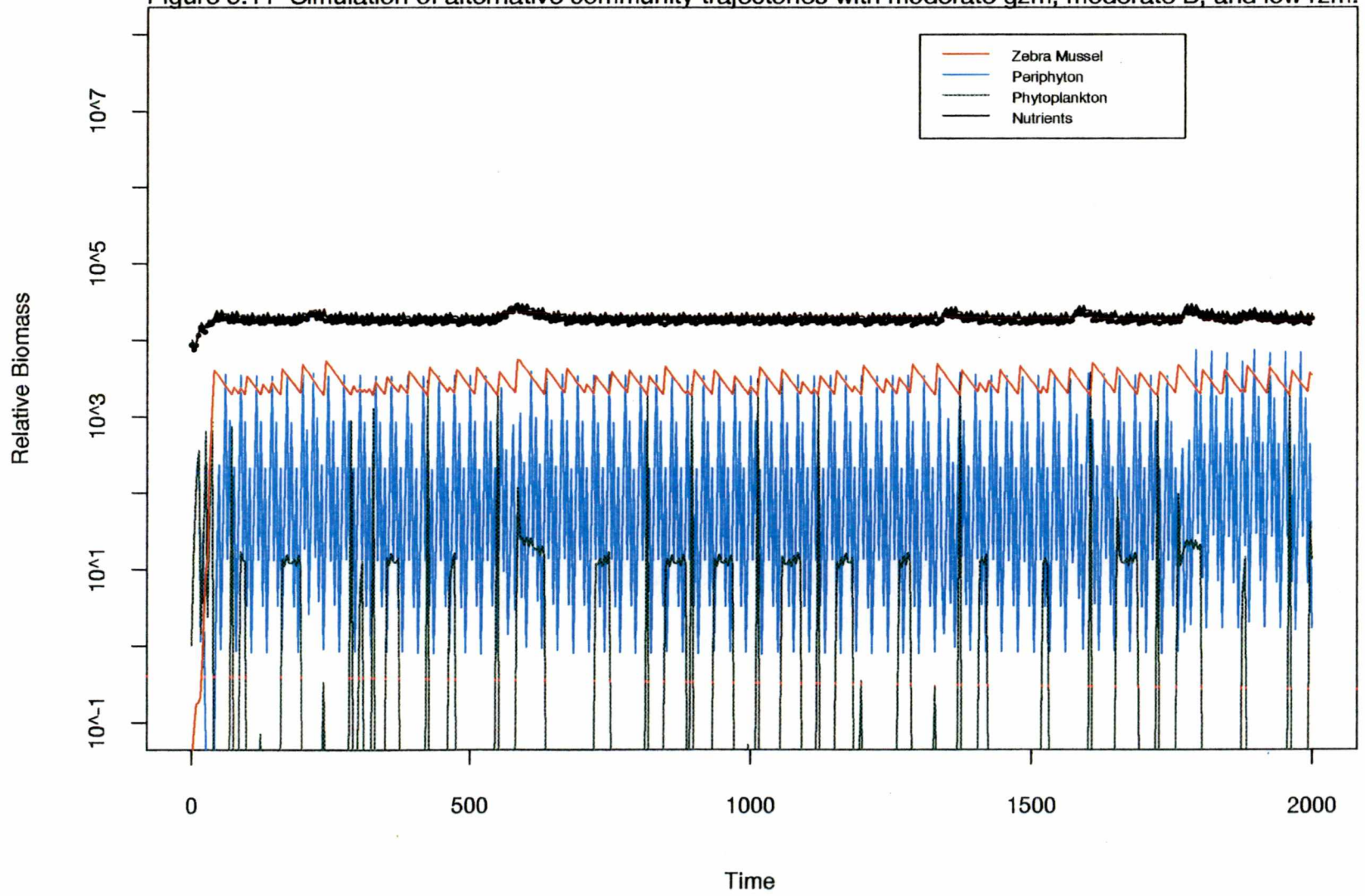


Figure 3.12 Simulation of alternative community trajectories with high gzm, moderate B, and low rzm.

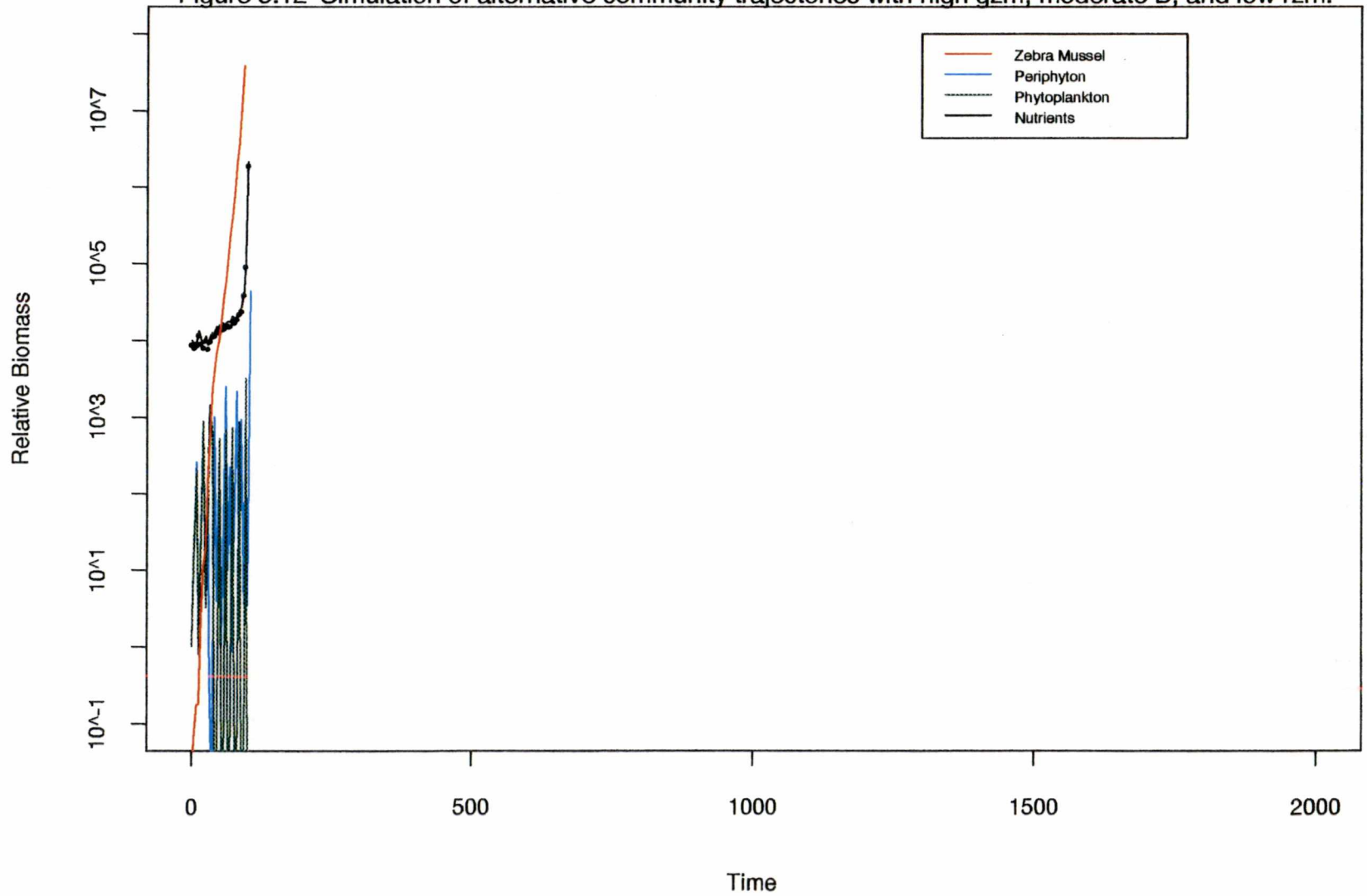


Figure 3.13 Simulation of alternative community trajectories with low gzm, moderate B, and moderate rzm.

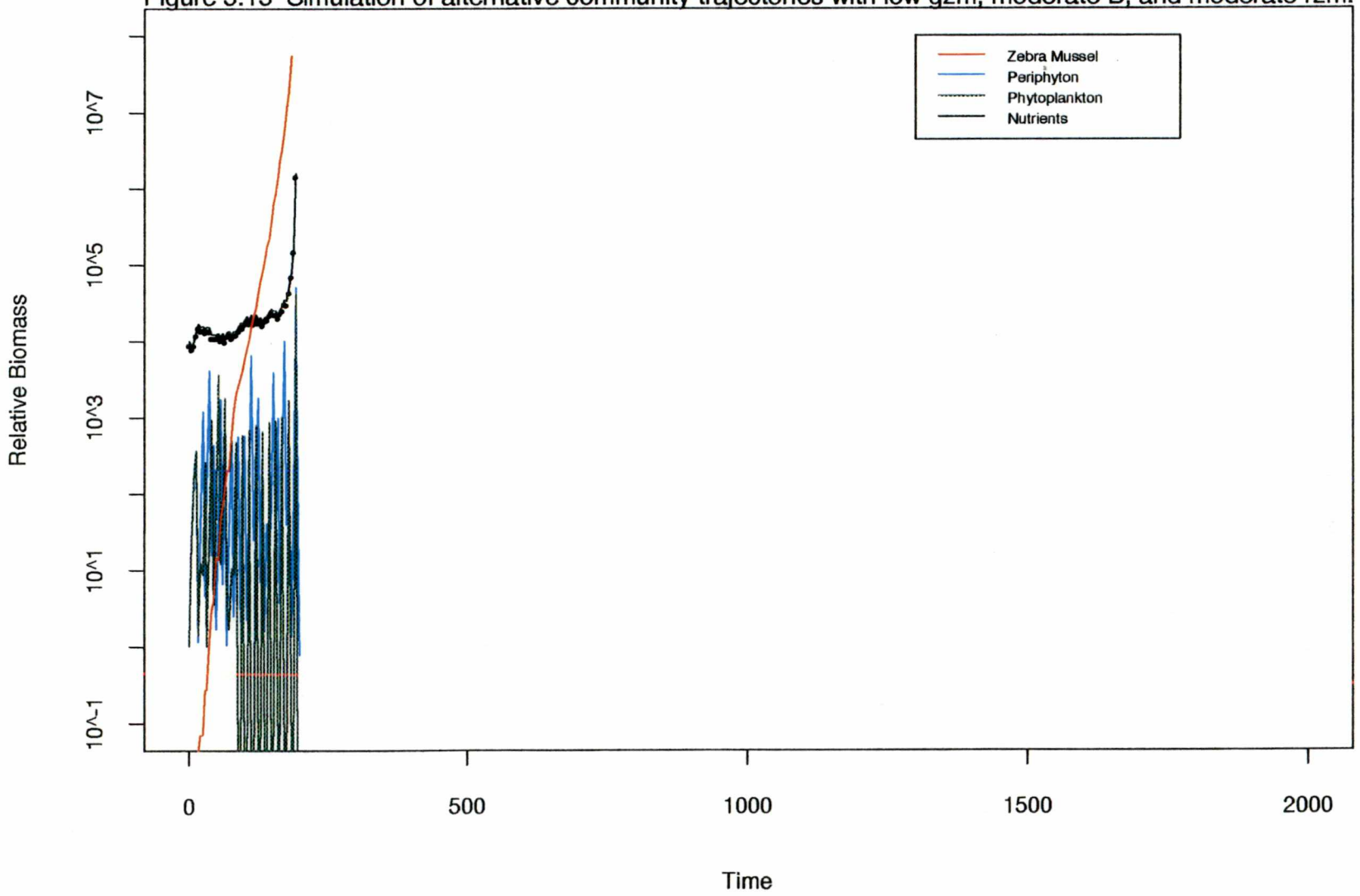


Figure 3.14 Simulation of alternative community trajectories with moderate gzm, moderate B, and moderate rzm.

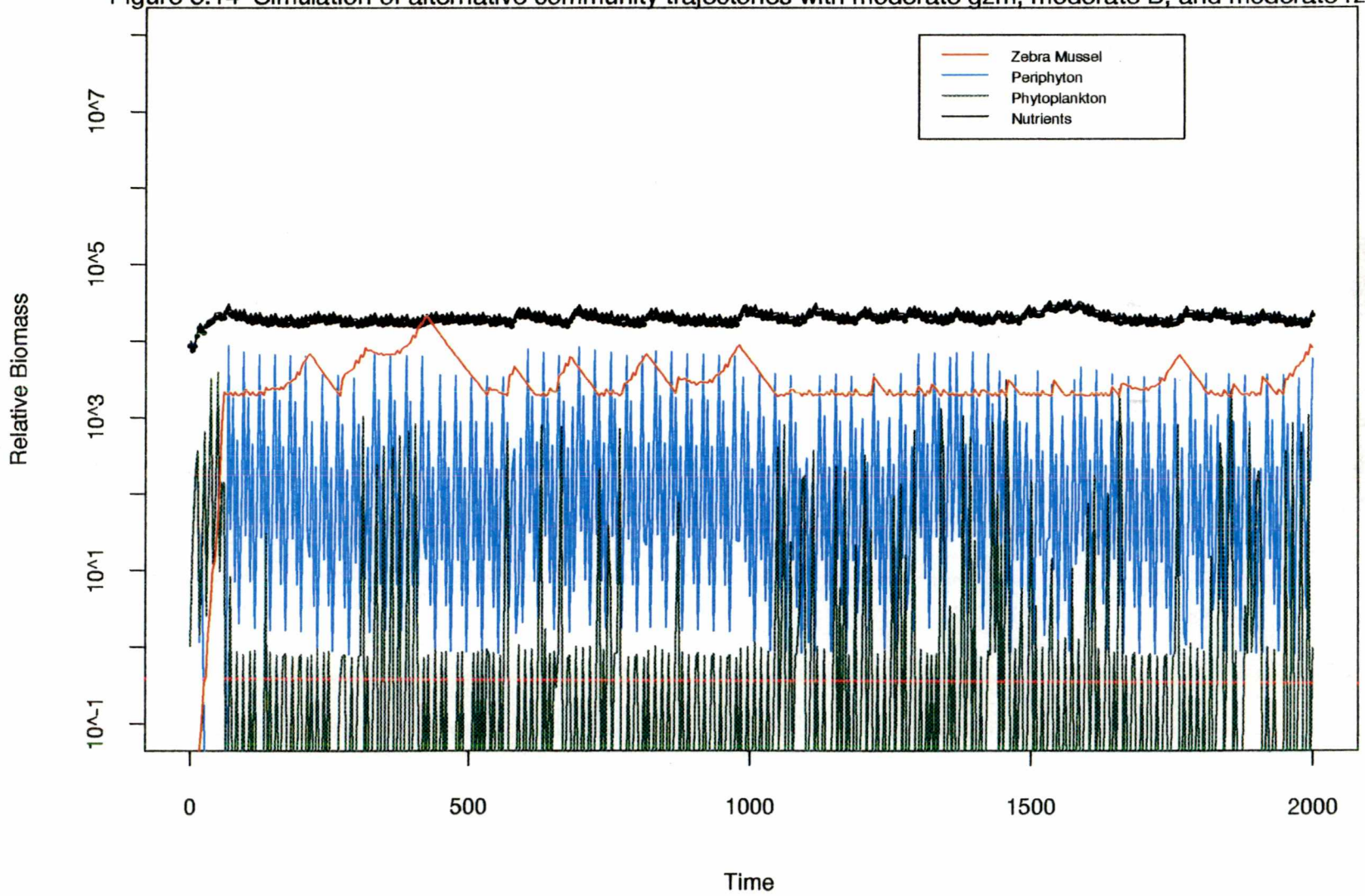


Figure 3.15 Simulation of alternative community trajectories with high gzm, moderate B, and moderate rzm.

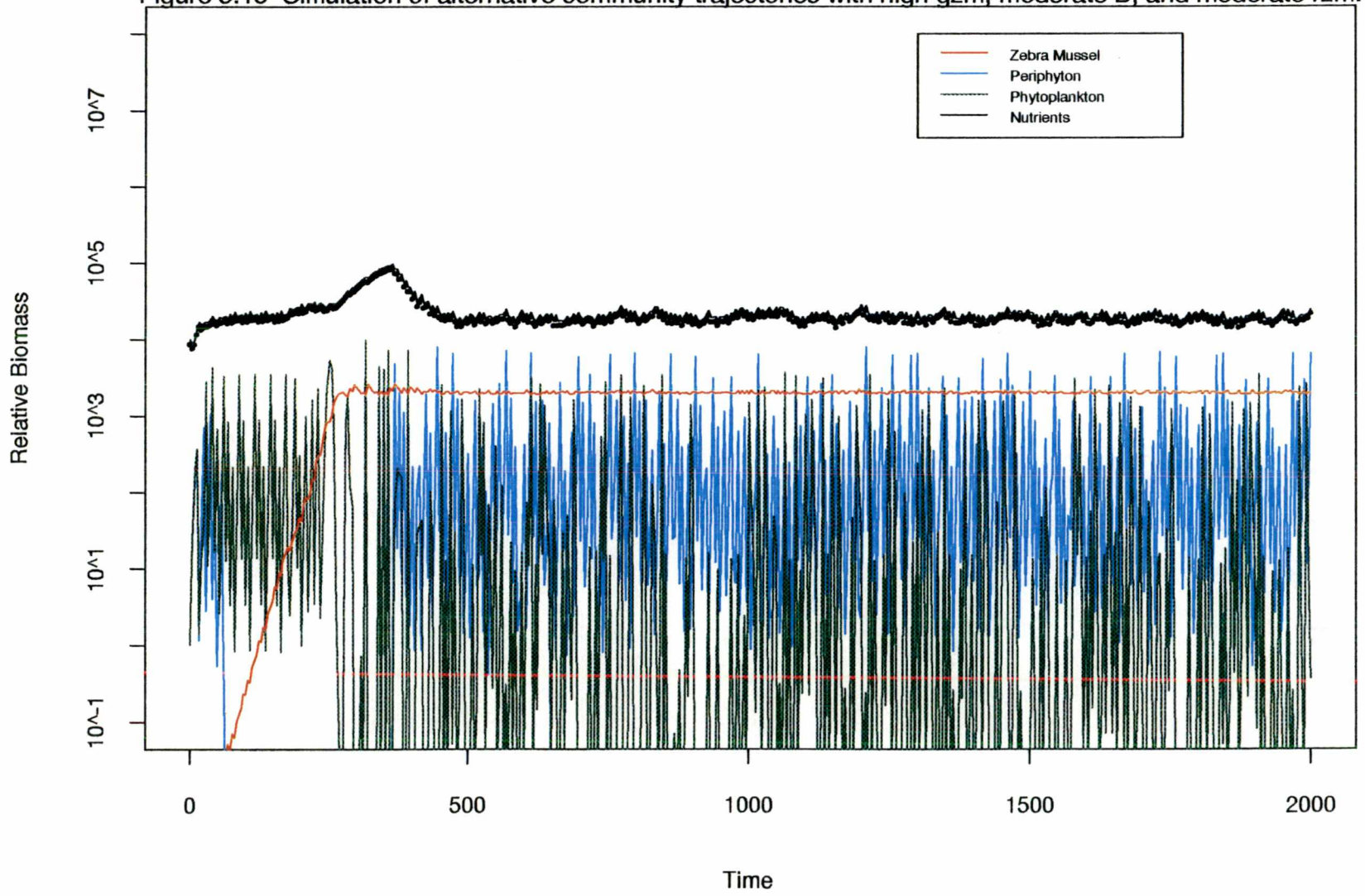


Figure 3.16 Simulation of alternative community trajectories with low gzm, moderate B, and high rzm.

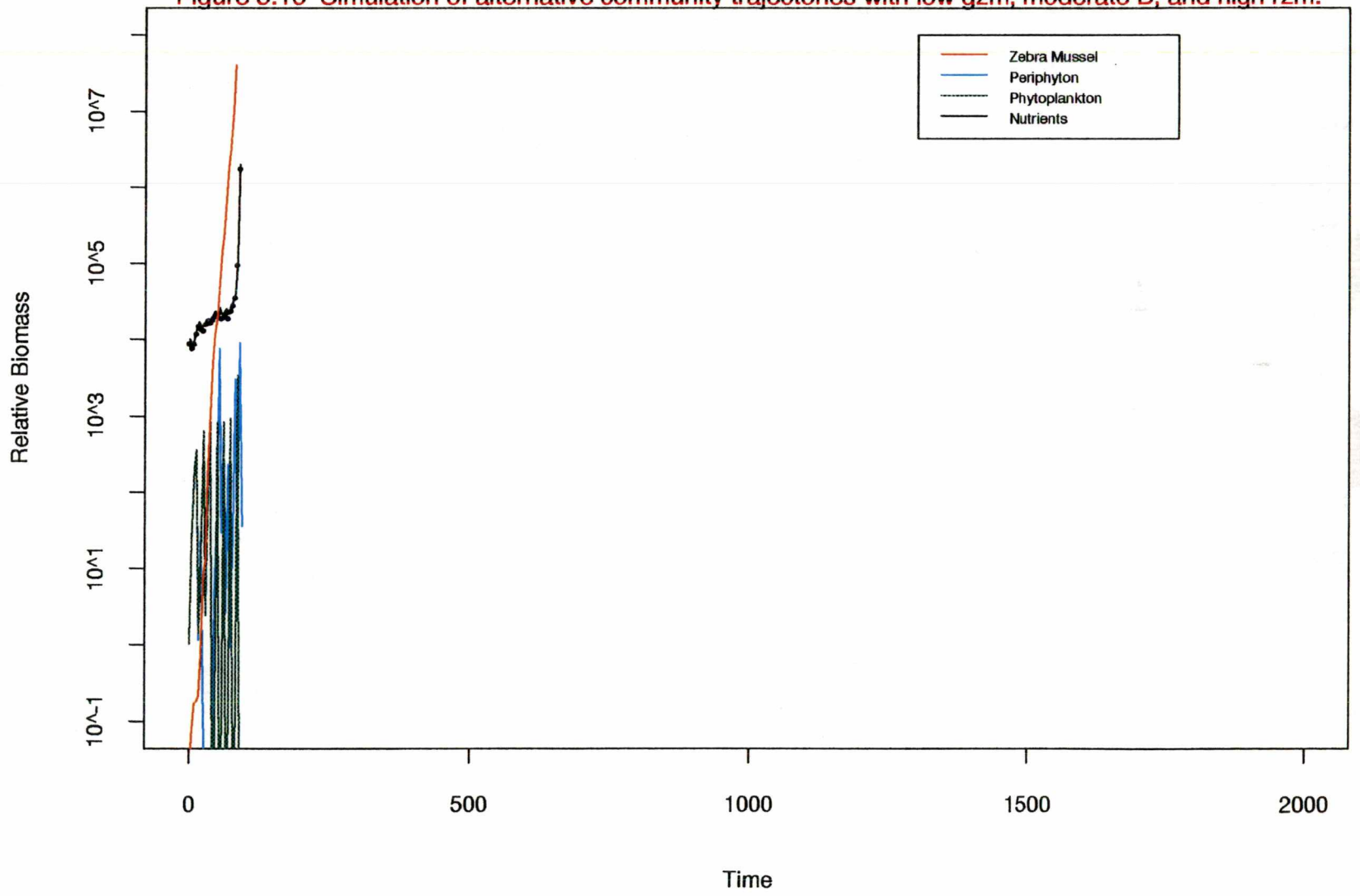


Figure 3.17 Simulation of alternative community trajectories with moderate gzm, moderate B, and high rzm.

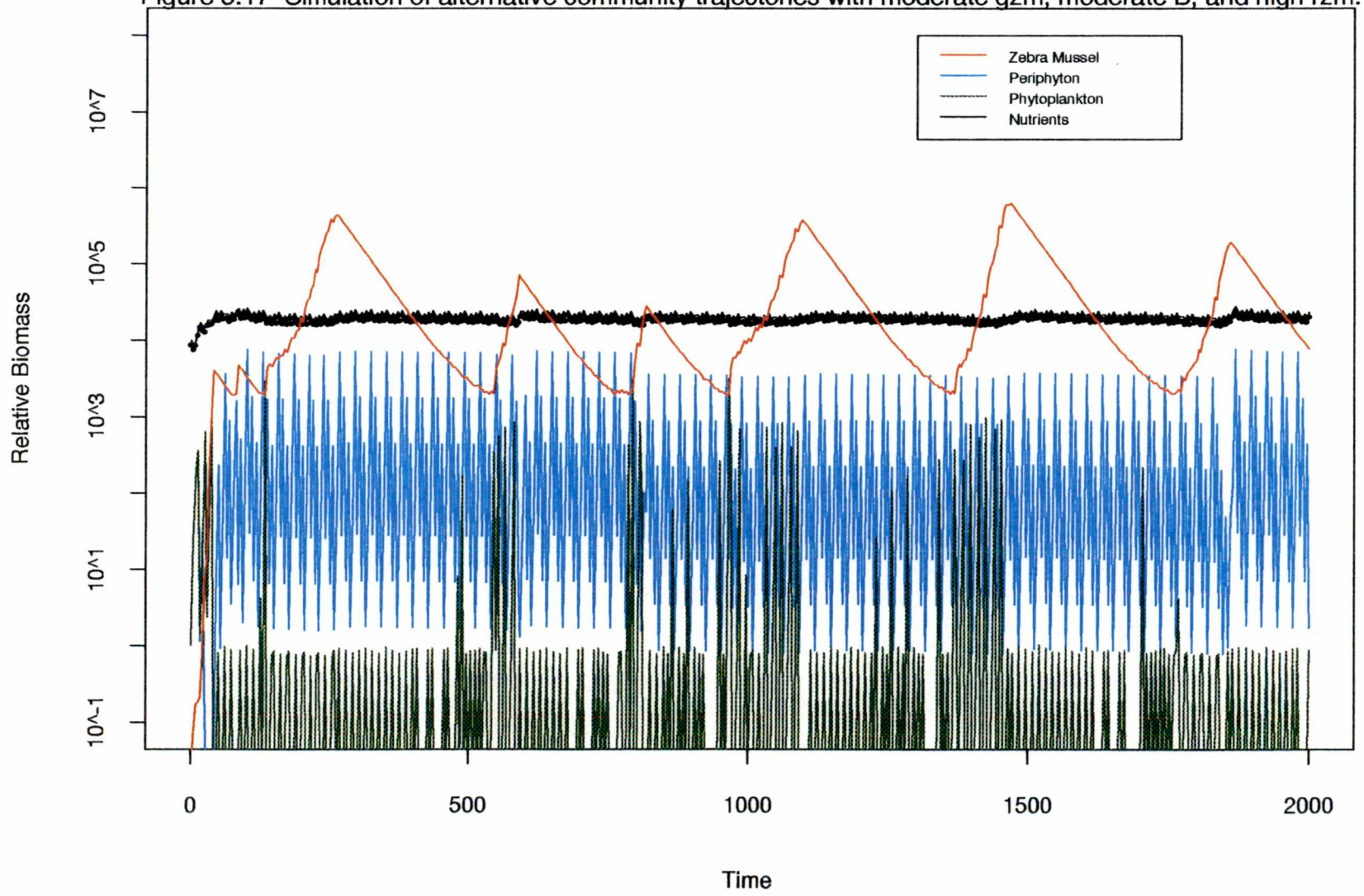


Figure 3.18 Simulation of alternative community trajectories with high gzm, moderate B, and high rzm.

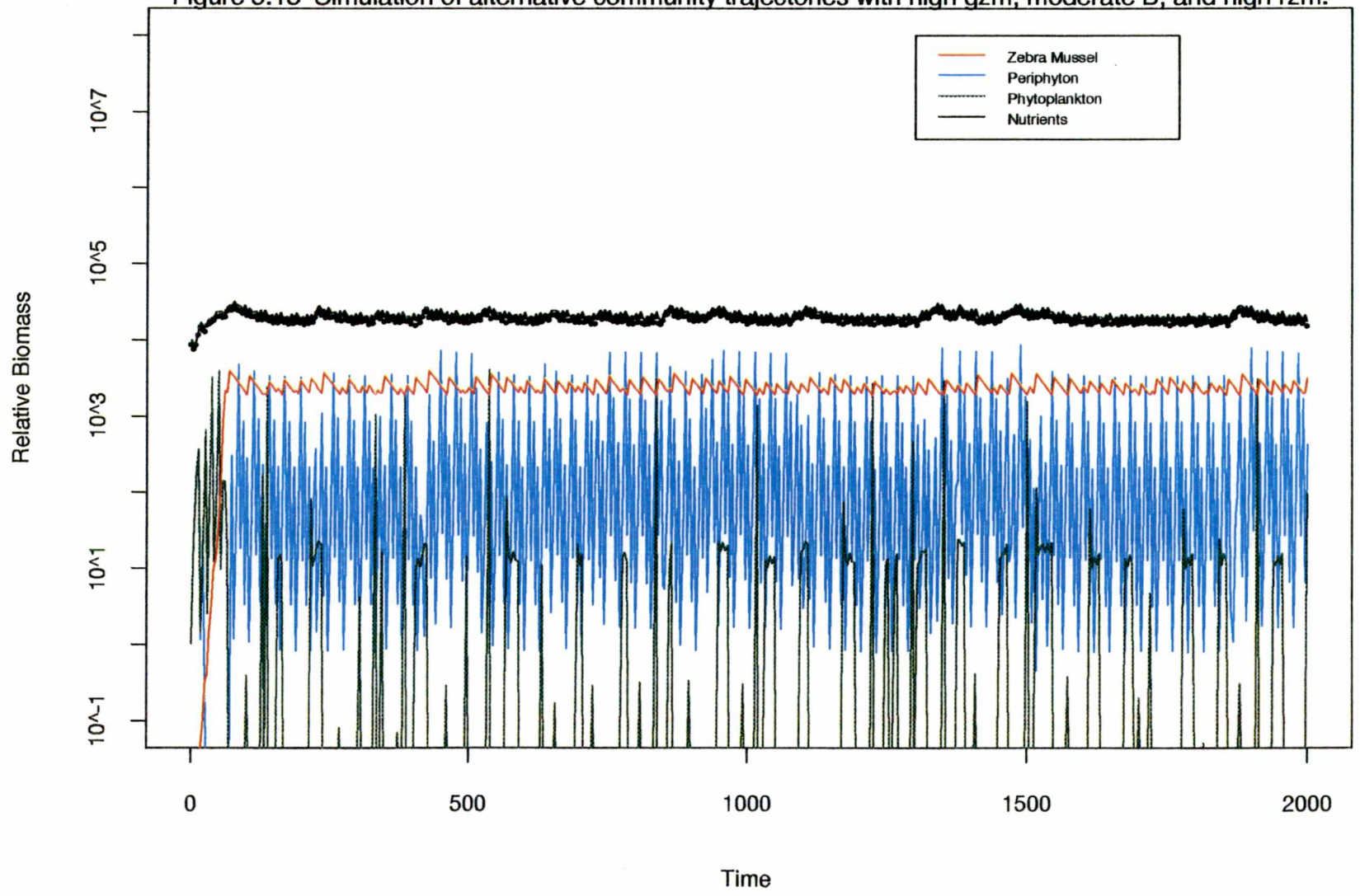


Figure 3.19 Simulation of alternative community trajectories with low gzm, high B, and low rzm.

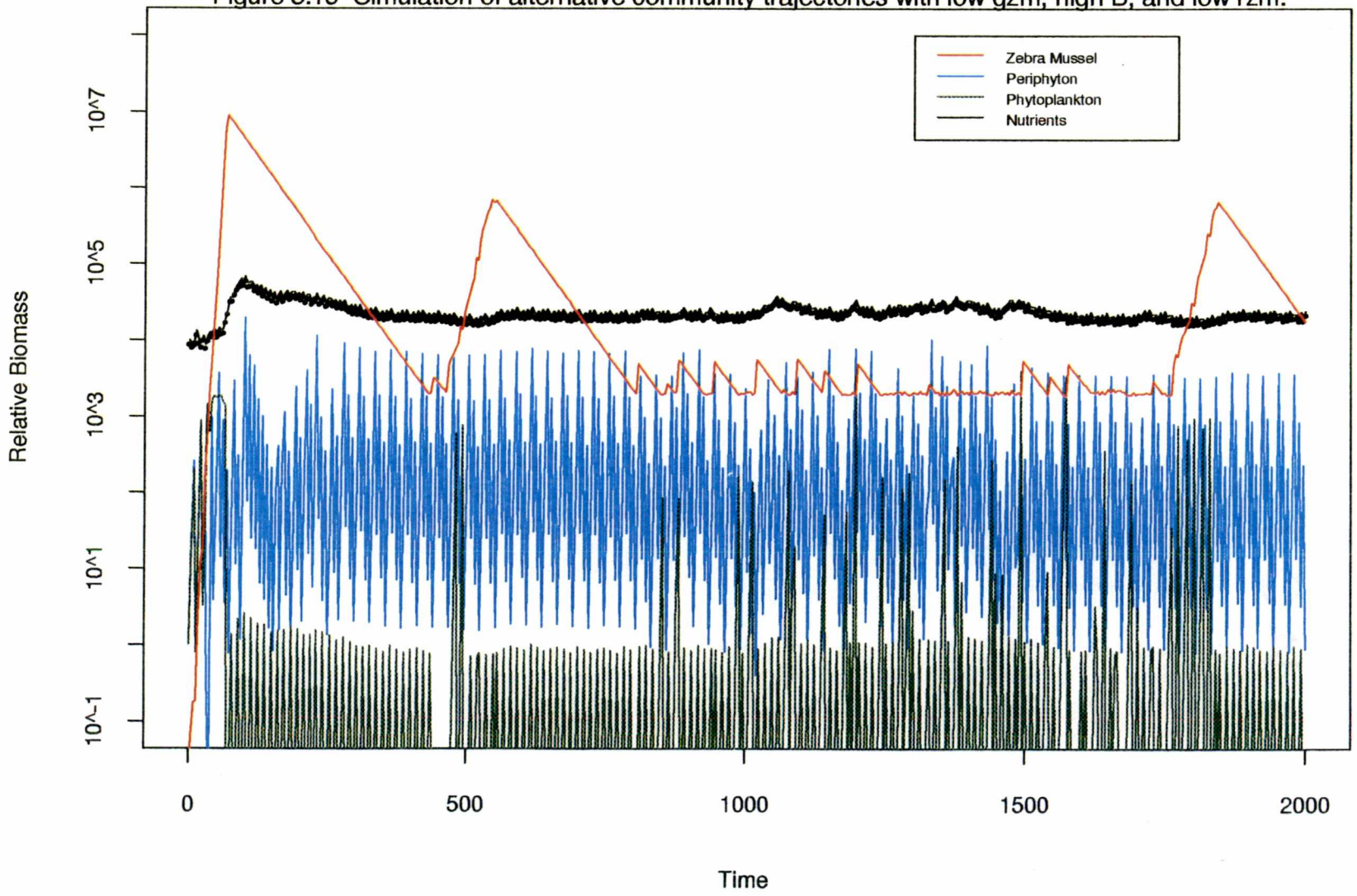


Figure 3.20 Simulation of alternative community trajectories with moderate gzm, high B, and low rzm.

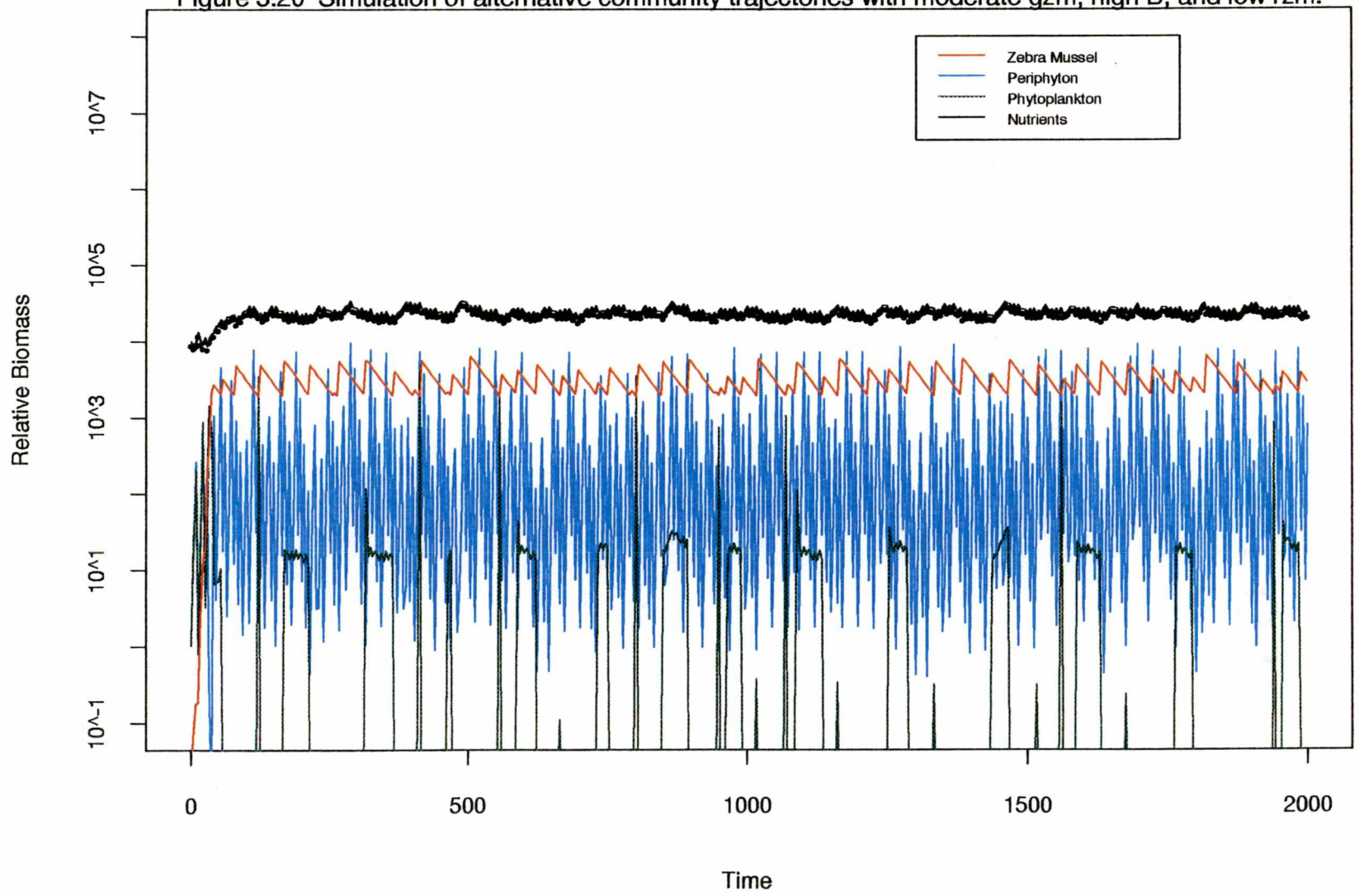


Figure 3.21 Simulation of alternative community trajectories with high gzm, high B, and low rzm.

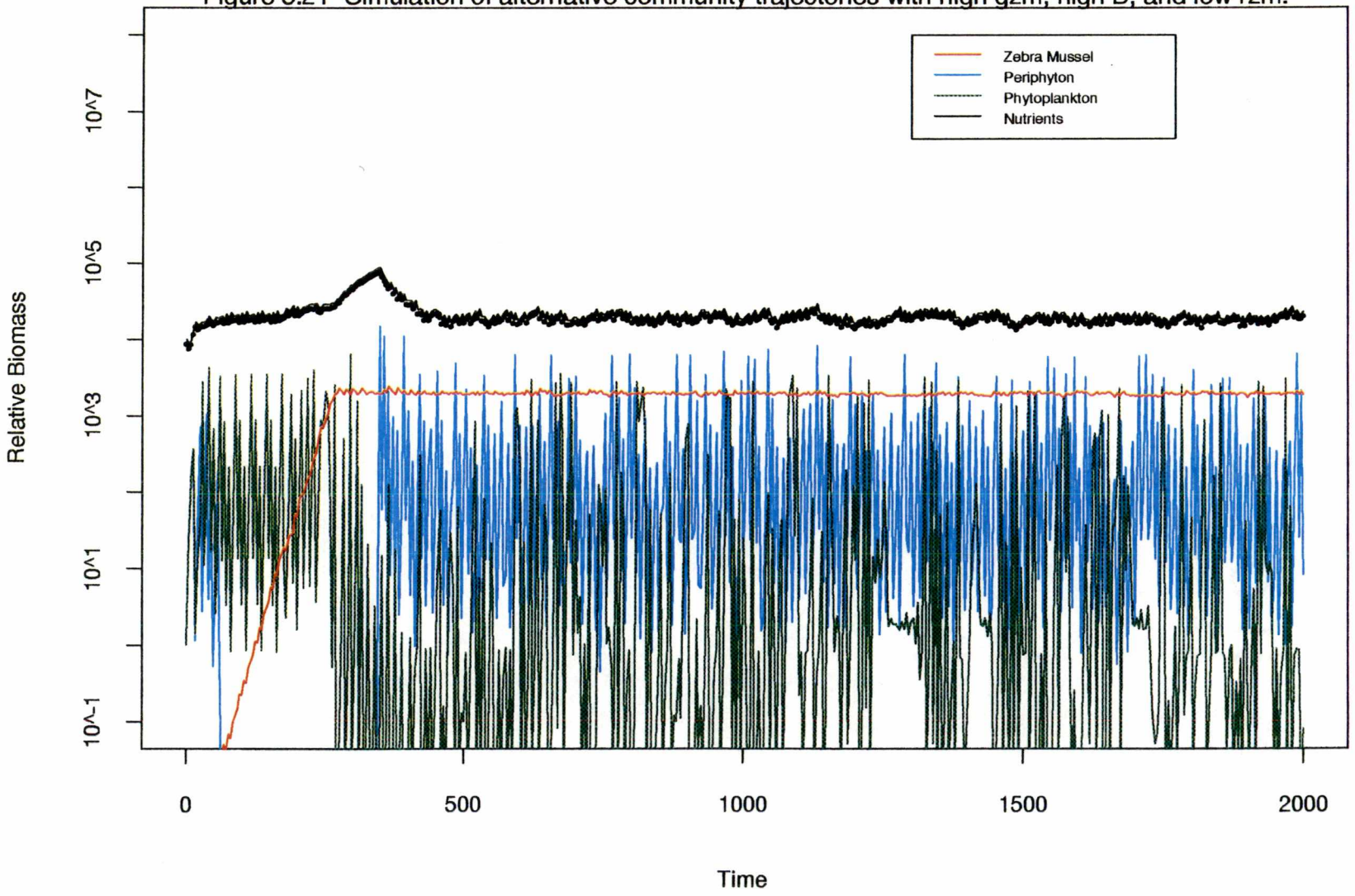


Figure 3.22 Simulation of alternative community trajectories with low gzm, high B, and moderate rzm.

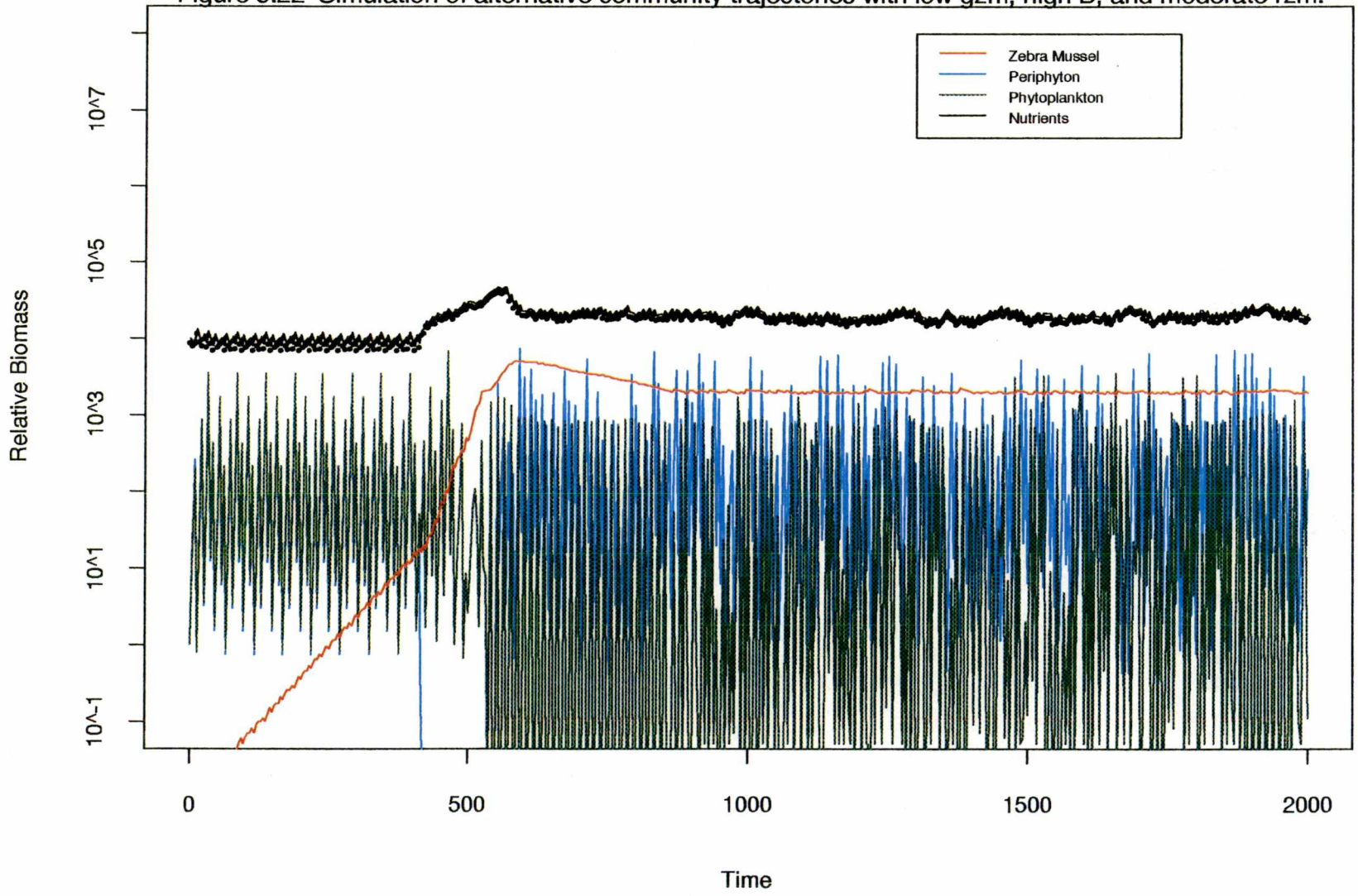


Figure 3.23 Simulation of alternative community trajectories with moderate gzm, high B, and moderate rzm.

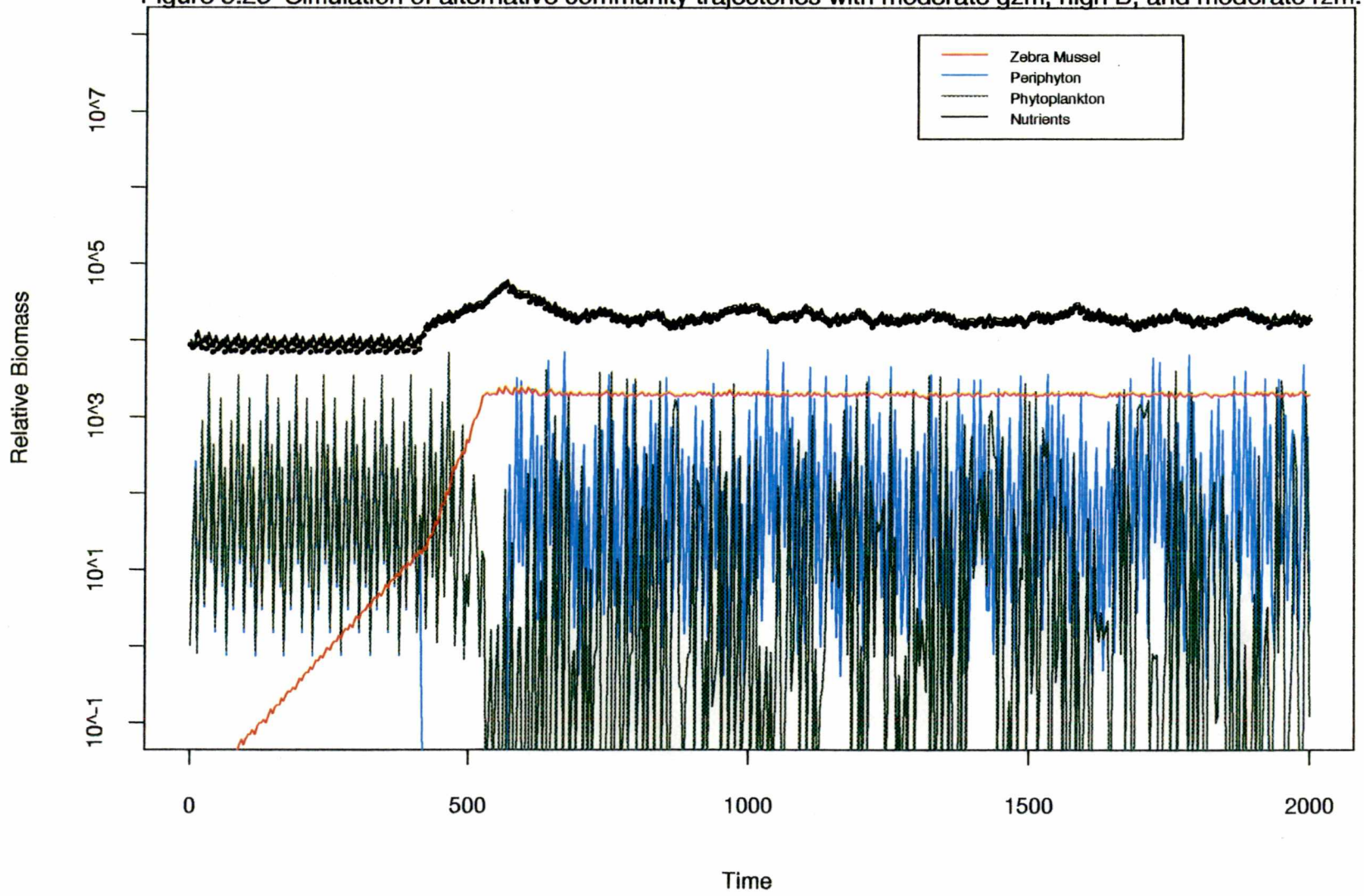


Figure 3.24 Simulation of alternative community trajectories with high gzm, high B, and moderate rzm.

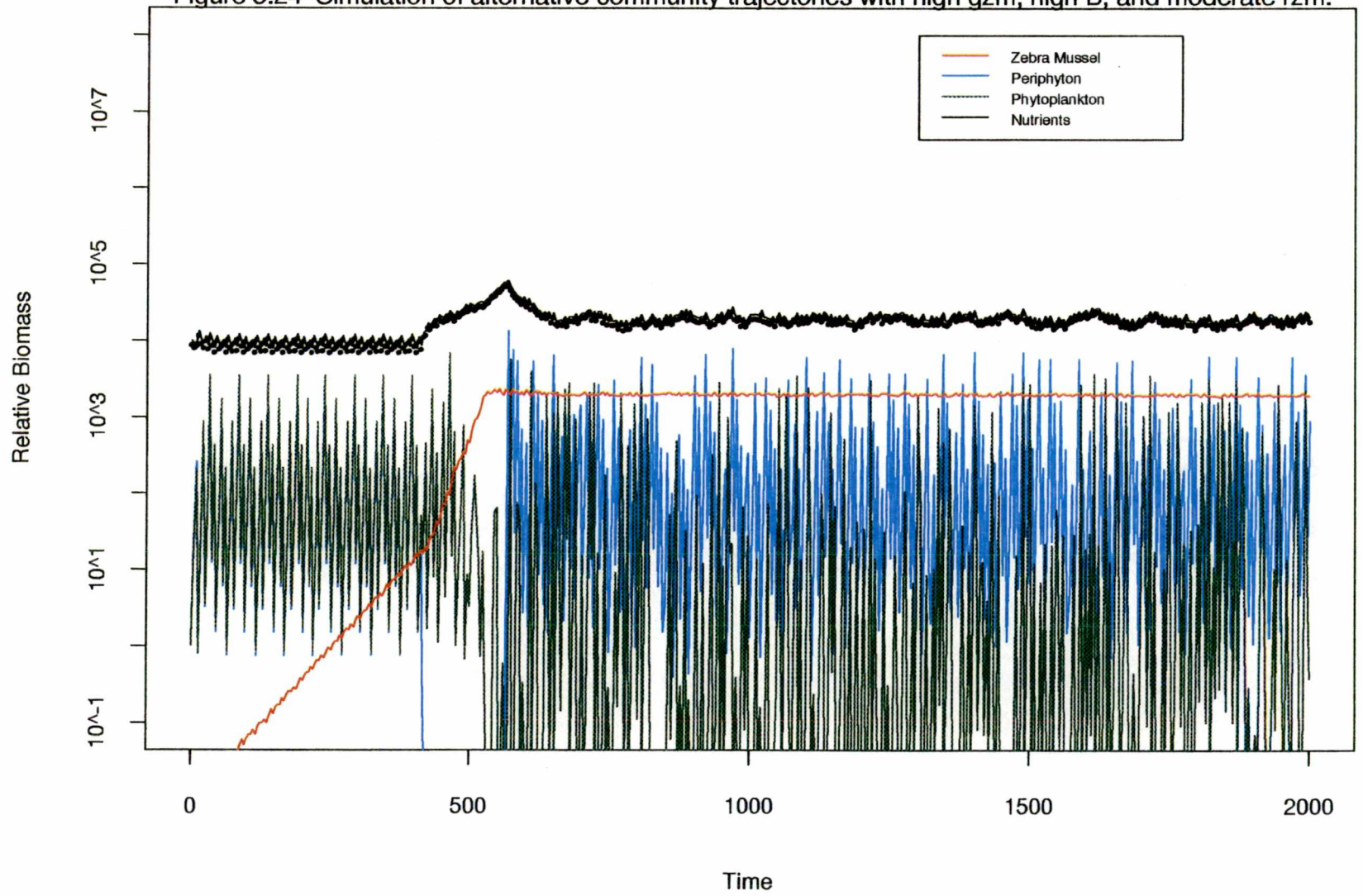


Figure 3.25 Simulation of alternative community trajectories with low gzm, high B, and high rzm.

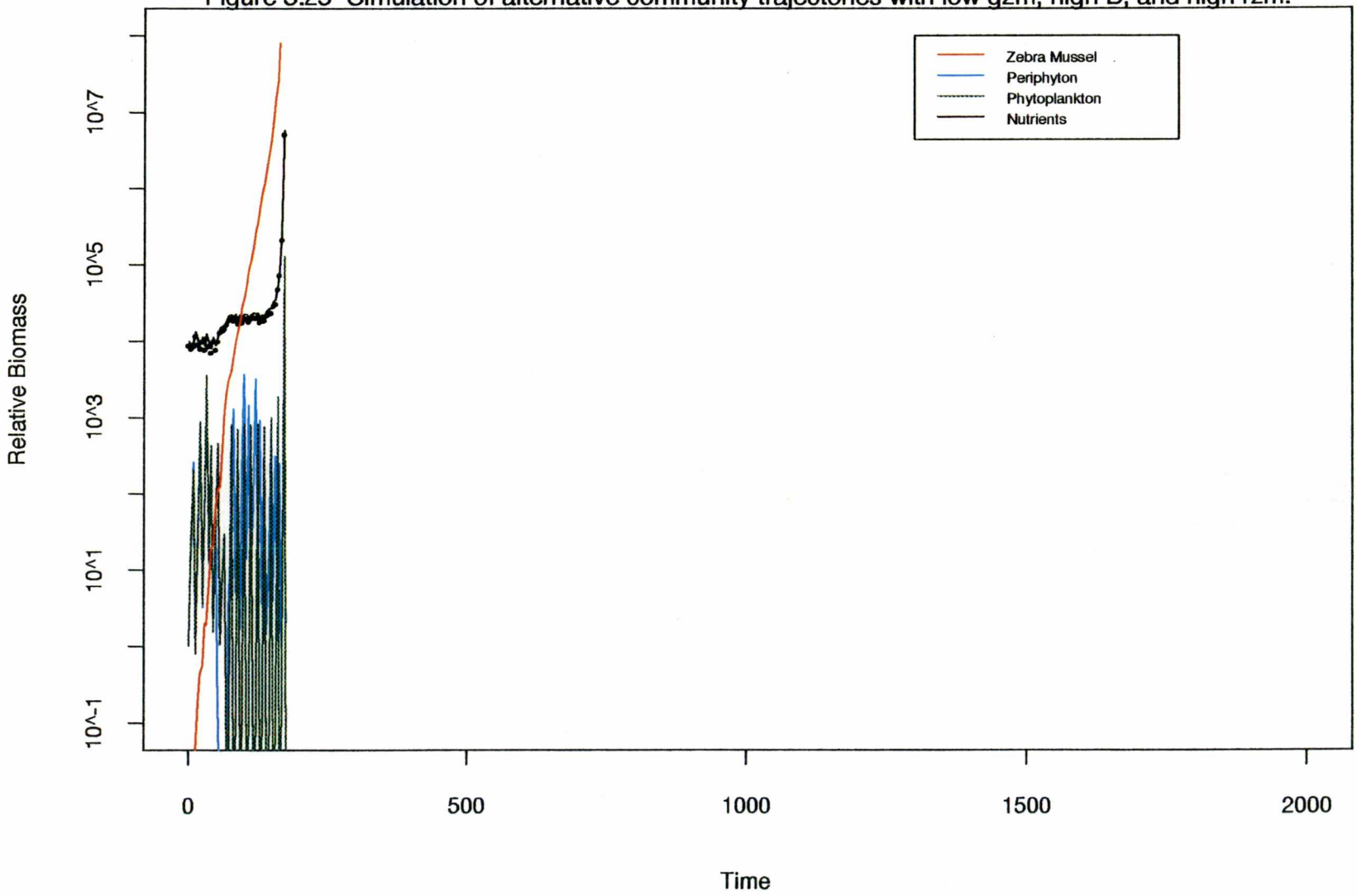


Figure 3.26 Simulation of alternative community trajectories with moderate gzm, high B, and high rzm.

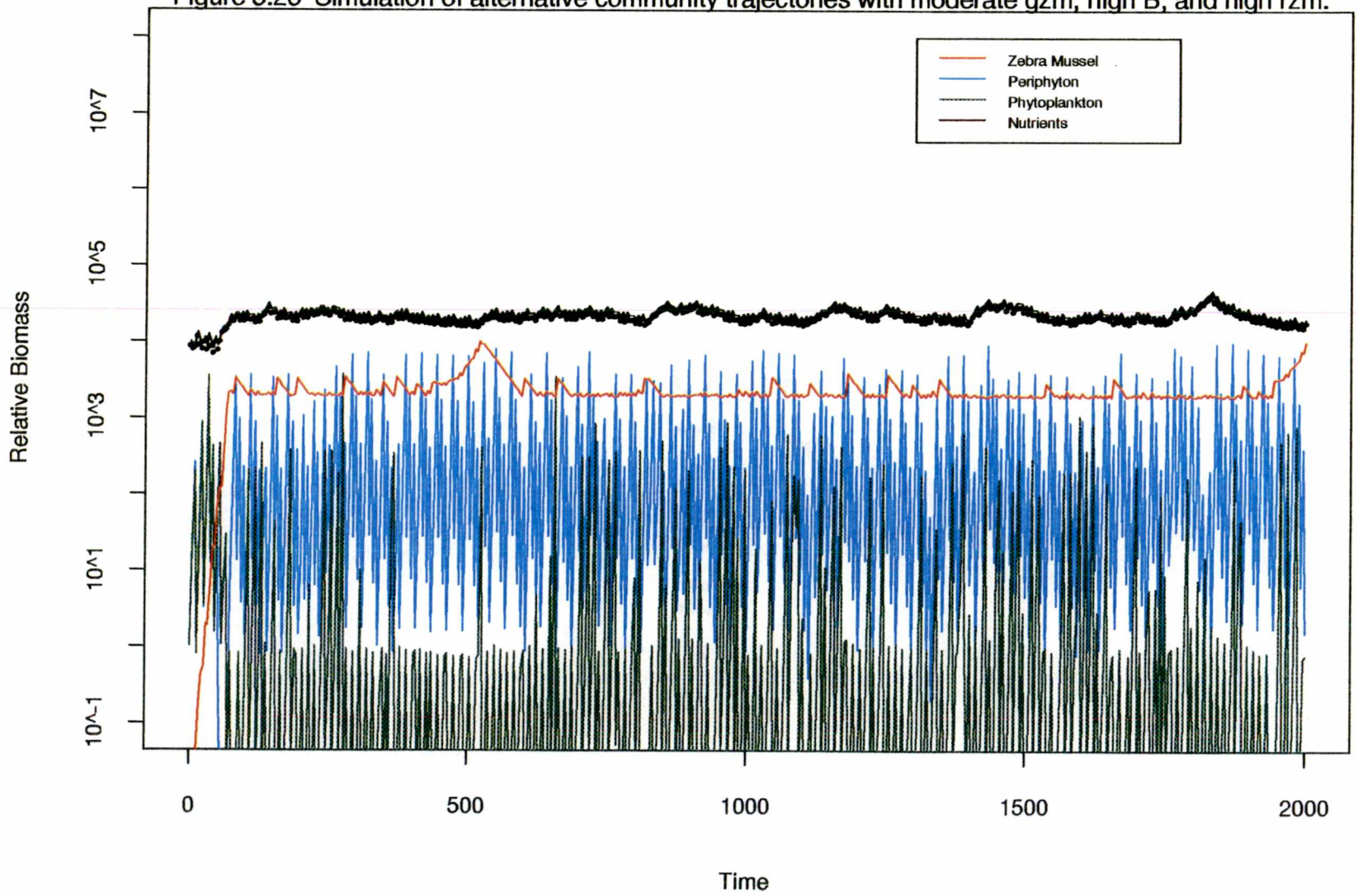
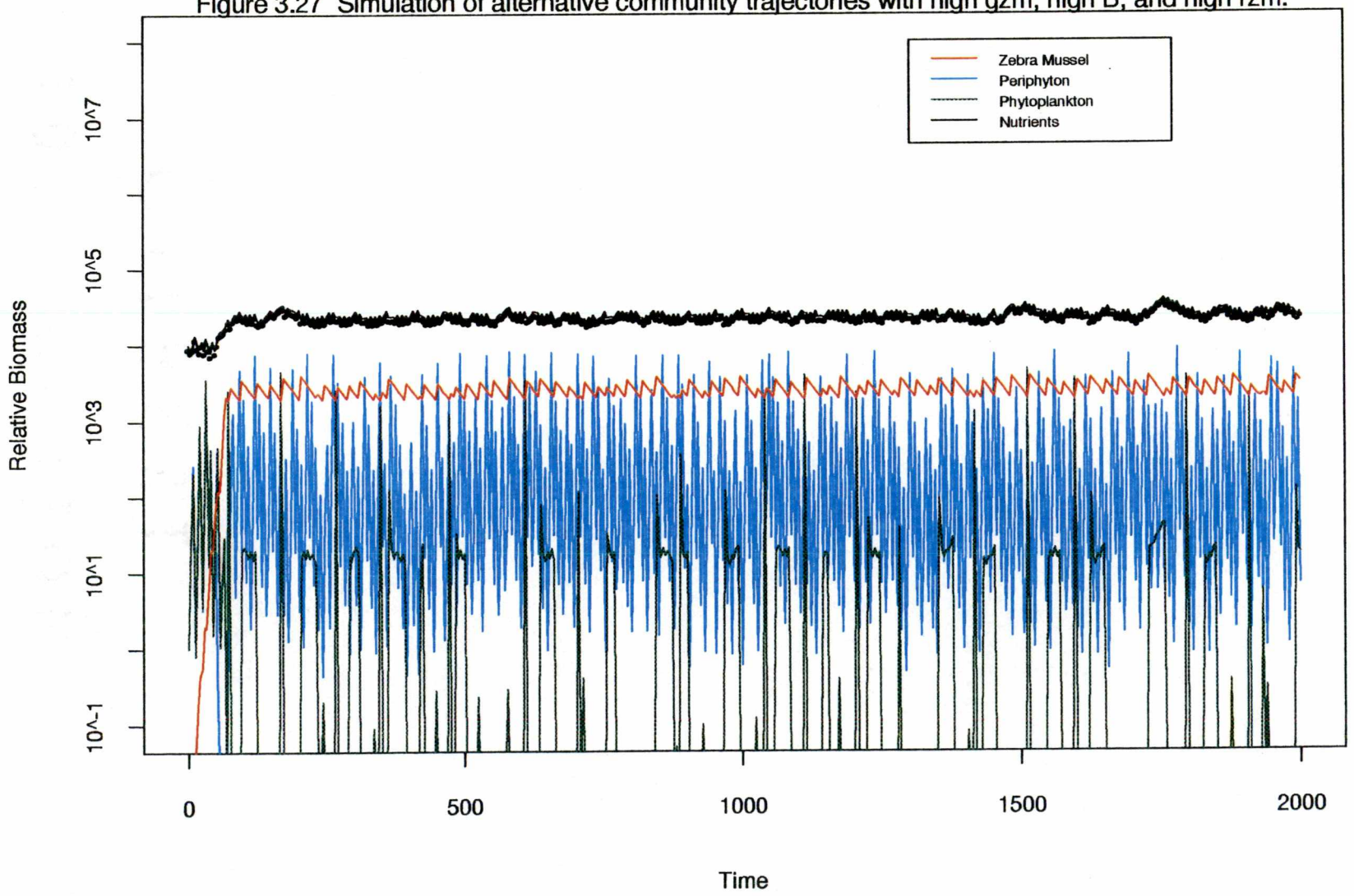


Figure 3.27 Simulation of alternative community trajectories with high gzm, high B, and high rzm.



VITA

Jeffrey Duncan was born the son of Jack and Jane Duncan in Bakersfield, California on May 23, 1964. He attended public schools graduating from El Capitan High School in Lakeside, California in 1982. In 1983, he moved to Sumner County, Tennessee to care for his late grandfather's farm. While there he began attending classes at Volunteer State Community College, ultimately transferring to the University of Tennessee, Knoxville in 1987. He completed his Bachelor of Arts degree in August, 1989. After working for more than a year as a counselor at Tennessee School for the Deaf in Knoxville, he returned to the University of Tennessee to pursue a Master of Science degree in the field of ecology. During this time, he accepted a position in the Health Sciences Research Division of Oak Ridge National Laboratory as an Ecological Risk Analyst.

Mr. Duncan received his Master's degree in August, 1996. He presently remains employed with Oak Ridge National Laboratory and hopes to continue his education toward a Doctorate of Philosophy in ecology.