ISTANBUL TECHNICAL UNIVERSITY ★ EURASIA INSTITUTE OF EARTH SCIENCES

SPATIAL AND TEMPORAL PATTERNS OF A ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) INVASION

M.Sc. THESIS

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İSTANBUL TEKNİK ÜNİVERSİTESİ ★ AVRASYA YER BİLİMLERİ ENSTİTÜSÜ

BİR ZEBRA MİDYESİ (*DREISSENA POLYMORPHA*) İSTİLASININ MEKANSAL VE ZAMANSAL ÖRÜNTÜLERİ

YÜKSEK LİSANS TEZİ

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OCAK 2015

Oğuzhan KANMAZ, a M.Sc. student of ITU Eurasia Institute of Earth Sciences 60111005 successfully defended the thesis entitled **"SPATIAL AND TEMPORAL PATTERNS OF A ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) INVASION "**, which he/she prepared after fulfilling the requirements specified in the associated legislations, before the jury whose signatures are below.

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Date of Submission : **13 December 2014**
Date of Defense : **19 January 2015**

to Walter Bishop and Mr.Spock,

FOREWORD

I am a biologist. Consciously. Without any regret. Superior to any other possible title that I can achieve in the future. Too indoor to work in field, too clumsy for ’lab’, to obsessively skeptic to measure anything. In silico approaches have always been a more preferable (than in vivo, in vitro or in situ) way for me to go. At the beginning of my studies, agent based modeling started as a journey to terra incognito which turned to a life-long ambition to explain many problems in biosciences. It can sound a little bizarre but at some point, I began to think we homo sapiens as turtles while I walk on the third planet from the sun as a canvas. I can honestly say that, I enjoyed every single line of the code and every single moment of this study.

For this humble study, I must thank... My Family, for their efforts to raise a scientist (not a John Doe for posterity, with an earthly job) in a developing country, Prof.Dr. Hasan Nüzhet Dalfes my mentor, professor and adviser, Yeliz Yılmaz my unofficial adviser for any bureaucratic obstacle on the way with extreme altruism, Ahmet Tuncer Durak my dear friend and colleague, although we are paradoxically both often and rarely on the same page, Damla Şahin Altun for her valuable advices, the last but the most, Tuğçe Şenel my best friend, love of my life, my colleague... No one else would be this much patient for my fringe or maybe even obscure and rarely fruitful, searches in art and science.

And after all, I guess I can say; Supero omnia. Deal with it...

JANUARY 2015

Oğuzhan KANMAZ
Biologist

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ABBREVIATIONS

km^2 **:** Square kilometre
km^3 **:** Cubic kilometre

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SPATIAL AND TEMPORAL PATTERNS OF A ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) INVASION

SUMMARY

Zebra Mussels *(Dreissena polymorpha)* are freshwater bivalves which are native to the lakes of southern Russia. They are probably one of the most notorious invasive species on the planet. In two centuries, they invaded all Europe and in mid-eighties they reached Laurentian Great Lakes in North America. Their physiological and anatomic advantages over the native species played an important role on the scale of the invasions. They cause tremendous environmental and economic damages. They are active filter feeders. As biofouling pests, they can attach to any solid substrate. Especially raw-water-dependent infrastructures and ships are vulnerable to their monotypic colonization behavior.

Individual based modeling is an emerging computational modeling method. Individual based models contain autonomous agents which can interact with the other agents and the environment on discrete time steps called ticks. In the last decade it was used in many ecological studies. Despite its simplistic nature, it is quite successful to explain complex phenomena which are not suitable to be modeled with conventional mathematical methods.

The model, which was developed for this present study, contains two different types of individuals. The mussels represent the mature zebra mussels which are sessile and the veligers represent the larval forms. The central algorithm of the model is mostly about the interplay between mussels and veligers. They use planktons as the resource. The yearly plankton population density and temperature cycles are highly simplified.

In this study six numerical experiments were conducted to understand the dynamics of a zebra mussel invasion in Laurentian Great Lakes. The reference case roughly encompasses the years between 1986 and 2006. P75 and P125 experiments are about the changing densities of phytoplankton population. T0.1 and T10 experiments are based on the different transportation probability levels. Also SupD is an fictive climate change scenario applied to Lake Superior to observe the population densities.

The results showed that the relation between zebra mussel populations and phytoplankton densities is not linear. Also, it was observed that transportation probability has impacts on both the population density and the speed of the invasion. The results of SupD experiments implied that even a slight climatic change can create drastic differences.

BİR ZEBRA MİDYESİ (*DREISSENA POLYMORPHA*) İSTİLASININ MEKANSAL VE ZAMANSAL ÖRÜNTÜLERİ

ÖZET

Zebra midyeleri *(Dreissena polymorpha)* muhtemelen dünyadaki en tanınmış ve kötü şöhretli biyolojik istilacılardan biridir. Özellikle son 20 yılda sebep oldukları çevresel ve ekonomik zararlardan ötürü pek çok çalışmanın konusunu teşkil etmişlerdir. Bu çalışmada, son yıllarda pek çok problem üzerinde yaygın olarak kullanılan birey temelli modelleme yöntemi ile Kuzey Amerika'daki Büyük Göller'de gerçekleşen zebra midyesi istilasının incelenmesi amaçlanmıştır.

Zebra midyelerinin kaynağı Rusya'nın güneyindeki göllerdir. Ural Nehri'nden toplanmış olan örnekler 1771 yılında Alman zoolog Peter Simon Pallas tarafından tanımlanmışlardır. Sonraları özellikle gemilerin balast tankları yoluyla dünyanın pek çok farklı yerine yayılmışlardır. Sahip oldukları fizyolojik ve anatomik avantajlarla ulaştıkları yerde kısa sürede yerel türlerle girdikleri rekabeti kazanmışlardır.

İstila biyolojisi 1950'li yıllardan bu yana çalışılmaktadır. Buna karşın biyolojik istila ve istilacı tür kavramlarının tanımı konusunda hala fikir birliği yoktur. Bunun sebebi, konunun pek çok farklı açıdan ve farklı disiplinlerden gelen araştırmacılar tarafından çalışılmasıdır. İstilacı türlerin ortak özellikleri, bölgeye ait olmamaları, ulaştıkları ekosistemde yayılarak ve sahip oldukları avantajları kullanarak baskın tür haline dönüşmeleri, çevresel ve ekonomik zararlara sebep olmalarıdır

Biyolojik istilalar belirli evrelerden oluşur. Bu evreler en genel haliyle taşınma, giriş, yerleşme ve yayılma olup birinden diğerine geçiş çeşitli fiziksel ve ekolojik engellerin aşılması ile gerçekleşir. Doğal ve insan kaynaklı olmak üzere iki tip biyolojik istiladan söz edilebilir. Doğal istilalar genellikle ilgili türü coğrafi olarak sınırlayan bir engelin ortadan kalkması ile gerçekleşir. İnsan kaynaklı istilalarda, tür insanlar tarafından taşınır. Bu taşınma, kasıtlı yada kazara olabilir. Bir türün evcil hayvan yada tarımsal bitki olarak taşınması kasıtlı taşınmaya, mikroorganizmaların, kemirgenlerin yada tarım için zararlı böceklerin taşınması ise kazara taşınmaya örnek verilebilir.

Zebra midyesi istilaları yaklaşık 200 yıldır süregelmektedir. Doğal yaşam alanlarının dışında ilk kez 1792 yılında Macaristan'da tespit edilmişlerdir. İlerleyen yıllarda tüm Avrupa bu durumdan etkilenmiştir. Günümüzde bu ilerleyişin altında yatan sebebin o yıllarda Avrupanın ırmaklarını birlerştiren insan yapımı kanalların yaygınlaşması olduğu düşünülmektedir. Zebra midyelerinin Kuzey Amerika istilasının başlangıç tarihi yaklaşık olarak 1986 yılıdır. Pek çok araştırmacıya göre St. Lawrence kanalını kullanan gemilerce taşınmışlardır. Bir kaç yıl içinde tüm Büyük Göller'e yayılmışlardır. 1992 yılı itibariyle Mississippi Nehri'yle kıtanın diğer göl ve ırmaklarına ulaşmaya başlamışlardır.

Zebra midyeleri oldukça dayanıklı canlılardır. Diğer pek çok midye türünden daha uzun yaşarlar. Aktif su süzebilme yetenekleri ile pasif olarak su süzen midyelere kıyasla beslenme açısından üstündürler. Büyük Göller faunasının önemli bir kısmını tatlı su midyeleri oluşturur. Zebra midyeleri burada girdikleri rekabette bu üstünlükleri sayesinde yerel türlerin %12'isinin soyunun tükenmesine yol açmışlarıdr.

Byssus adı verilen iplikli yapıları ile her tür doğal, yapay ve canlı yüzeye tutunabilirler. Bu yüzeylere birbirlerinin kabukları da dahildir. Monotipik kolonileşme gösterirler. Planktonik larvaları suyun ulaştığı hemen heryere girebildikleri için borularda kolonileşerek tıkanmalara yol açarlar. Bu durum güç santralleri ve fabrikalar açısından oldukça maliyetli sonuçlar doğurur. Ayrıca gemilerin yüzeylerine yapışarak yakıt kullanımını arttırdıkları gibi, motor ve soğutma borularını da tıkayarak ciddi hasarlara yol açabilirler.

Bu çalışmada kullanılan yöntem olan birey temelli modellemenin kökleri ünlü matematikçi John von Neumann'ın kendi kendini kopyalayabilen kuramsal bir makina üzerine geliştirdiği düşüncelere dayanır. Bu fikir zamanla pek çok araştırmacının da katkılarıyla bugünkü birey temelli modellemenin ortaya çıkmasını sağlamıştır.

Birey temelli modelleme geleneksel yöntemlere göre oldukça sade bir mantığa dayanır. İçerdiği bağımsız bireyler, belirlenmiş basit kurallara uyarak, kesikli zaman adımları içerisinde, birbirleri ve çevreleri ile etkileşir ve sonuçlar üretirler. Matematiksel yalınlığına rağmen karmaşık sistemlerin modellenmesindeki gücünü son 20 yılda yapılan pek çok araştırmada göstermiştir. Bu araştırmaların sosyal bilimlerden biyolojiye kadar pek çok alanda örnekleri mevcuttur.

Bu çalışmada NetLogo isimli bireysel temelli modelleme ortamı kullanılmıştır. NetLogo 1999 yılında Uri Wilensky tarfından geliştirilmiş olup en yaygın birey temelli modelleme ortamlarından biridir. Olaya dayalı programlama dillerinden olan Logo'dan geliştirilmiştir. Öğrenimi oldukça kolay bir dil olmasına rağmen geleneksel programlama dillerinde mevcut olan bazı döngülerin yokluğu kendine özgü bir kullanımı da beraberinde getirir.

Zebra midyelerinin yaşam döngüsü gerçekte oldukça karmaşık olmasına rağmen modelde iki aşamaya indirgenmiştir. Olgun midyeleri temsilen midye, planktonik aşamayı temsilen ise veliger adı verilmiş olan bireyler oluşturulmuştur. Modelin merkezi algoritması daha çok bu iki tip bireyin dahil olduğu başkalaşım döngüsü üzerine kuruludur. Yine basitleştirilmiş bir döngü içinde miktarları değişen fitoplanktonlar birey olmayıp çevresel bir değer olarak yer alırlar. Midye ve veligerler kaynak olarak fitoplanktonları kullanırlar. Midyeler hareketsiz olup ortamdaki fitoplanktonu fizyolojik faaliyetlerini sürdürmek ve üremek için tüketirler. Veligerlerin farkı hareketli olmalarıdır. Tükettikleri fitoplanktonları belli bir gelişimsel eşiği aştıktan sonra yüzeylere tutunarak midyeye dönüşmek için kullanırlar.

Modelde 2 saatlik süre 1 zaman adımı olarak belirlenmiş olup, bir yıl 4380 zaman adımından ibarettir. Fitoplankton ve sıcaklık döngüleri bu temsili yıllar içinde dalgalanmalar gösterir. Modeldeki beş gölde gerçeklerine benzer olarak belirlenmiş olan farklı koşullar hüküm sürer ve birbirlerinden bağımsızdırlar. Modeldeki bir diğer önemli konu ise taşınmadır. Veligerler göllerin içerisinde serbestçe hareket edebilirler fakat gölden göle geçiş belli kurallara bağlıdır. Doğu yönünde, belirlenmiş bir olasılık ile bir gölden diğerine aktarılabilirler. Aksi yönde ise göllerin birbirlerine bağlandıkları yerlere yaklaştıklarında doğrudan diğer göle sürüklenirler.

Çalışma 6 deney grubu içermektedir. Her deney grubu için model otuzar sefer çalıştırılmıştır. Deneylerdeki modeller 20 yıllık bir süreci kapsamaktadır. Deneyler sırasıyla, Referans Deney, P75, P125, T0.1, T0 ve SupD'dir. Referans deneyde, istilanın yaklaşık olarak 1986 ve 2006 yılları arasındaki süreci incelenmiştir. P75 ve P125, ortamdaki fitoplankton miktarının %25 azaltılması ve artırılması durumunda gerçekleşenler üzerinedir. T0.1 ve T10'da ise taşınma olasılığının 10 kat arttırılması ve 10 kat azaltıması durumunda olacaklar incelenmiştir.

Referans deneyin sonucunda midye sayılarında, fitoplankton döngülerinin yarattığı dalgalanmlardan bağımsız olan üç ila dört yıllık dalgalanmalar gözlenmiştir. Bu dalgalanmaların özellikle istilanın daha kararlı bir dengeye ulaştığı durumlarda oluşması ayrıca ilginçtir. P75 ve P125'ten çıkan ortak sonuç, fitoplankton miktarının veliger ve midye sayıları üzerindeki etkisinin lineer olmayışıdır. Fitoplankton miktarının %25'lik değişimine karşın midye ve veliger sayıları çok daha büyük oranlarda değişime uğramıştır. Referans deneyde gözlenen dalgalanmalar P 75'te daha sönük, P125'te daha şiddetli şekillerde ortaya çıkmıştır. T0.1 ve T10'nun sonuçları, taşınma ihtimalindeki değişimlerin istilayı daha çok zamansal anlamda etkilediği yönündedir. Taşınma ihtimalinin 10 kat azalması istilayı yalnızca birkaç yıl geciktirmesine karşın aynı oranda artış beş göldeki istilayı neredeyse eşzamanlı hale getirmiştir. SupD, Diğer deneylerin hiç birinde kararlı dengeye ulaşamamış Superior gölünün koşullarının varsayımsal bir iklim değişikliği senaryosu dahilinde değiştirilmesine dayanmaktadır. Fitoplankton ve sıcaklığın komşu göllerdeki seviyelere ulaşması halinde Superior gölünde midye ve veliger sayısının yaklaşık 20 kat arttığı tespit edilmiştir.

1. INTRODUCTION

1.1 Purpose of Thesis

In nature, there are boundaries. Mountains, oceans, rivers, valleys, deserts etc. constitute natural boundaries between ecosystems and keep populations separated. This situation has an important role in evolution, because it is a driving force for speciation [1]. Yet, the boundaries are not absolute and can be passed with the help of natural or artificial factors. Once a new ecosystem is reached and the survival takes place, changes are not uncommon. The new comers (non-natives) are the invaders now. They join the competition and open their place in niche space, at the expense of eliminating the natives. In an informal sense, biological invasion can be summarized like this.

Zebra mussels *(Dreissena polymorpha)* are probably one of the most notorious and well known invasive species on the planet. Zebra mussel-related economic and environmental issues became more recognizable in scientific and public area after they have reached Great Lakes. Their tremendous economic cost and drastic environmental changes they caused, made them a very serious problem.

In this study, zebra mussel invasion in Great Lakes of North America is modelled by using individual based modelling methods. Despite the simplistic nature of the model, it can also be considered as an example to demonstrate the usefulness of individual based modelling which is an emerging method in the field of computational ecology.

1.2 Biological Invasions and Invasive Species

Definition of biological invasion has become a problematic situation since the beginning of invasion biology. Even today it is hard to find a formal definition in various sources. According to Valery et al [2] "This confusion appeared at the birth of invasion ecology: indeed, in its founding book, The Ecology of Invasions by Animals and Plants, Charles Elton (1958)" and as an intense review of the concept they propose following definition: "A biological invasion consists of a species acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population."

An invasive non-native species is any non-native animal or plant that has the ability to spread, causing damage to the environment, the economy, our health and the way we live [3]. However there is no consensus about the invasive species definition. Even to name those invasive species, there are more than twenty different namings are used and those namings are based on forms at different stages of invasions [4]. Also the discipline of the researcher plays an important role on the choice of naming.

Invasions have stages and there are physical or biological barriers to pass from one stage to the next. A biological invasion, generally have four stages: transportation, introduction, establishment and spread [5]. Those stages are separated by biological (based on physiological or ecological properties of the invader) or physical boundaries.

Another important concept about biological invasions is based on the way they reach a certain place. A biological invasion can be natural or artificial. Natural invasions are mostly caused by changing geological conditions of the earth. The barriers like oceans, mountains, rivers which avoid large scale species movement, can be altered by time with natural processes. But artificial effects are more unpredictable. Introductions can be deliberate or accidental. Pests can be carried from one continent to another, agricultural plants or pets can survive out of the places where they intended to be or even some cases biological pest control agents can be out of control like in the cane toad *(Rhinella marina)* invasion in Australia [6].

1.3 Zebra Mussels

Zebra mussels (*Dreissena polymorpha*) are bivalve freshwater molluscs, native to the lakes of Southern Russia. They are typical members of Dreissenidae family which has been present on earth for 230 million years, since right before The Triassic. They were described by the German zoologist Peter Simon Pallas in 1771 however the specimens were collected in 1769 from the lower course of Ural River [7]. Southern Russia is their native habitat. ’Zebra mussel’ name comes from their striped shell patterns which is common but not universal for all the members of the species. They are relatively small organisms with a 2 cm shell length and the shape of the shell roughly looks like a capital letter ’D’.

Zebra mussels are filter feeders. They consume algae by filtering water with their siphon. Because of their sessile nature, they need water flow for this process. It is the underlying reason why they prefer pipes, where a constant water flow is present, to foul. They are monotypic colonists and extremely successful to attach to almost every possible surface available by using their byssus which is an uncommon property for a freshwater bivalve. These surfaces can be natural or artificial. Another organism and even each other’s shells are possible options for them.

Zebra mussels follow external fertilization and embryology. A female individual can produce 30000 – 40000 eggs in a reproductive cycle [8]. Like many similar invertebrate species, zebra mussels have a complex life cycle which contains multiple stages during metamorphosis (Figure 1.1). The first one is trochophore stage which the velum develops and planktonic shell is secreted. The second stage is the veliconcha. The last obligate free-swimming occurs in this stage. The pediveliger is the last stage which veligers are ready to attach a suitable surface [9]

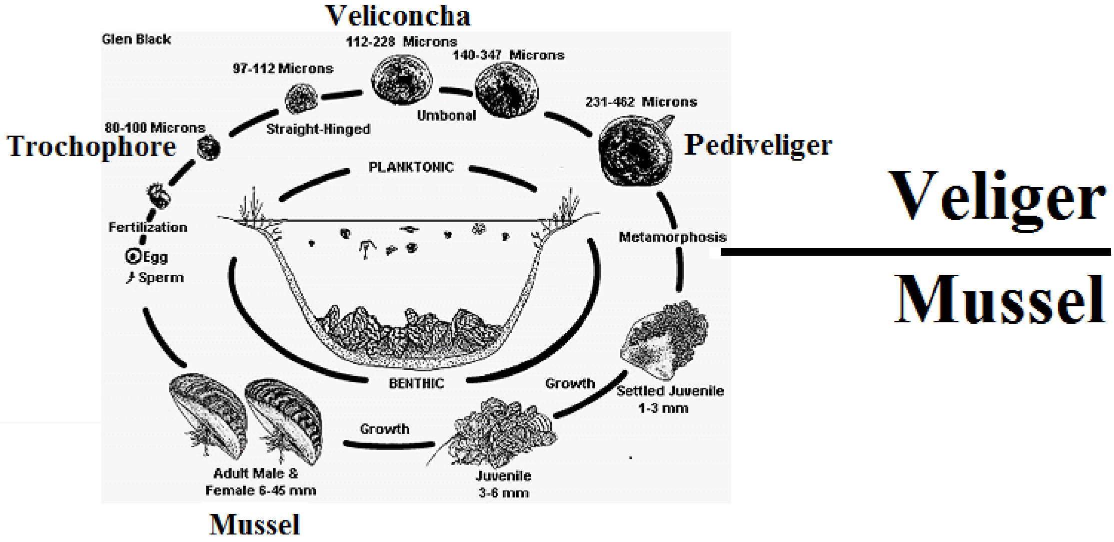

Figure 1.1: Life cycle of zebra mussel.

1.4 Brief History of Zebra Mussel Invasions

The history of zebra mussel invasions goes back to eighteenth century. The underlying reason of their rapid invasion is building of the artificial waterways which connect the rivers of Europe. Ships carried them in the ballast tanks and on the hulls. In 1794, zebra mussels were observed by German Zoologist Grossinger in Hungary. Their presence in England and Ireland were documented in 1820's. They were seen in Netherlands in 1827. They reached Sweden in 1920's [10].

In 1988 they were first discovered in Lake St. Claire, yet further examination showed that the estimated date of initial introduction was 1986. It was the beginning of zebra mussel invasion in North America. It is thought that they were transported by the ships which use St. Lawrence Seaway to reach the lakes. In 1988 they were detected in east basin of Lake Erie and just one year later they invaded the entire lake [11]. In the following years the Great Lakes were totally invaded.

Zebra mussels used Chicago Sanitary Shipping Canal to reach the Mississippi River from Lake Michigan in 1992 and before the end of the year, they were detected in many water bodies from Minneapolis to St. Louis. Today, the zebra mussel invasion is still ongoing despite all the precautions.

1.5 Environmental Impact

Zebra mussels are physiologically strong organisms. They live longer than many other bivalves. They can actively pump water and this ability makes them superior to passive filter feeders [12]. An environment like Great Lakes which has the greatest diversity of fresh water bivalves with 297 species [13] and constitutes an extremely suitable habitat for zebra mussels.

Monotypic colonization is the typical characteristic of zebra mussels. With their byssus, a strong filamentous structure secreted by bivalves, they can attach to any substrate that is natural, artificial or biological, which even includes other zebra mussels. Combined effect of active filtering and this kind of colonization, makes them a virtually impossible rival in competition with other bivalves. Fresh water mussels constitute the 1/3 of the fauna of Great Lakes, yet 12% of them are extinct and 60% are threatened, [13] zebra mussels are an important part of this biodiversity loss.

While zebra mussels are filtering water, beside organic materials they also remove inorganic particles. As a result, they cause changes in turbidity of water. Lower turbidity provides more sunlight for photosynthetic organisms like algae. There are many examples of zebra mussel-related algal blooms [14]. Furthermore, avian botulism is another consequence of zebra mussel invasion. Because of the toxic materials they accumulated by filtering, they caused thousands of bird deaths which fed on them [15]. It is a significant example of biomagnification of toxics in the food web [16].

Zebra mussels are effective ecosystem engineers alongside of being aggressive invaders [17]. Their ability to control the availability of resources which are used by other organisms makes them perfectly fit the definition of ecosystem engineer [18]. Beyond their known and studied impacts, there may be unpredictable consequences of zebra mussels which can occur in the future.

1.6 Economic Impact

Results of zebra mussel invasions are obvious thus they are hard to be ignored by governments and societies. Especially after mid-eighties, which is the beginning of the North American invasion, public awareness have raised exponentially. Probably, it was caused by the tremendous costs of the invasion which is easier to comprehend than the environment issues.

As mentioned in the previous section, zebra mussels can attach any solid substrate and artificial ones are not exceptional. In the larval stage they can reach anywhere contains water. For instance, pipes constitute quite suitable substrates for them. They continue to colonize until a pipe partially or totally blocked. Hence, one of the most typical damage they cause is to block pipes which deliver drinking and process water to cities and industrial facilities and cooling water to power generating stations [19]. It is a serious problem for any raw-water-dependent infrastructures.

Zebra mussels also have impacts on ships and docks. By attaching to hulls of ships, they increase drag. It increases fuel consumption [20]. Engines and cooling pipes are vulnerable to be blocked by them. In United States, yearly cost of zebra mussels to water consuming industrial facilitates is $500 million [21].

2. MATERIAL

2.1 The Laurentian Great Lakes

The Laurentian Great Lakes, also known as Great Lakes of North America, is an interconnected lake system in North America which contains Lake Superior, Lake Michigan, Lake Huron, Lake Erie and Lake Ontario (Figure 2.1). They are located in United States-Canada border. St. Lawrance River, which gives the name ’Laurentian’, connects them to Atlantic Ocean [22]. They have the largest surface on earth as a freshwater system with 244000km^2. They contain 23,000 km^3 of water. This amount of water is enough to cover entire United States about 3 meters high [23]. Only the polar caps contain more fresh water [24]. Formation of The Great lakes began to form at the end of the last glacial period around 10,000 years ago.

Figure 2.1: Map of Laurentian Great Lakes.

Lake to lake flow is caused by the surface level differences between the lakes. The water flows to Lake Huron and Lake Michigan from Lake Superior. Lake Huron and Lake Michigan have similar surface levels and they are hydrologically considered as one big lake. Lake Huron empties its waters to Lake Erie. A drastic change of surface level occurs at Niagara Falls which located between Lake Erie and Lake Ontario. Finally the water reaches to Atlantic Ocean by St. Lawrance River [25]. (Figure 2.2) The relation between the flow and veliger transportation, which will be explained later, has an important role in the model.

Figure 2.2: General water currents map of Laurentian Great Lakes.

The Great Lakes map which is used in the model, is highly simplified. This simplification process is performed by NetLogo based on the defined grid count in the code. For a more detailed result, the grid count can be increased, but due to scarce computational power, in this study, a 108 x 68 grid is used (Figure 2.3).

2.2 Individual Based Modelling

2.2.1 Brief History

Agent based models are computational models which have significant success in explaining emergent phenomena and swarm intelligence. For some certain reasons, in ecology they are mostly named as ’individual based models’. Despite conventional mathematical models, they contain relatively simple mathematical relations. The autonomous agents which are controlled by those relations exhibit many non-linear

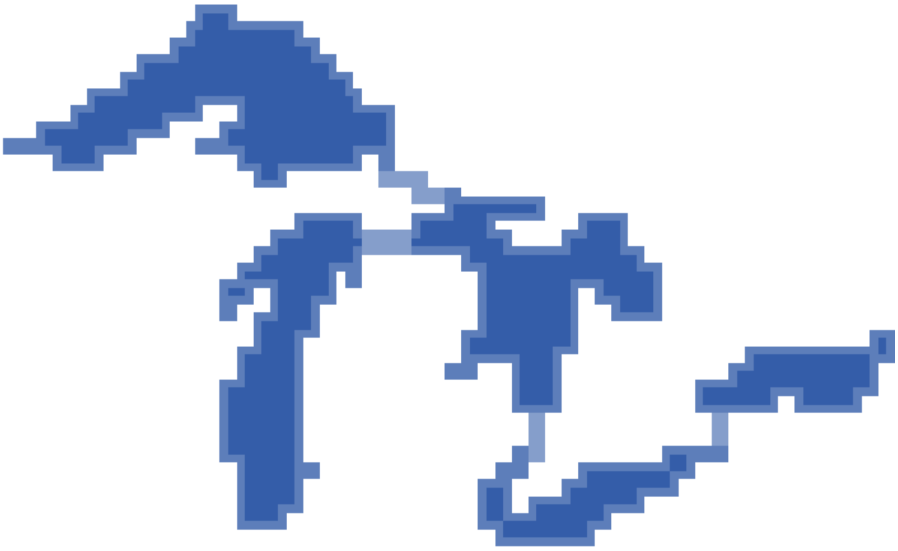

Figure 2.3: The simplified map of Laurentian Great Lakes which used in the model.

behaviours and complex patterns, that are virtually impossible to obtain with any other method.

Earliest example of individual based models is probably the Von Neumann Machine, which is a theoretical device with the ability of reproducing. After its development by one of the most influential mathematician of the twentieth century John Von Neuman, the idea expanded by Stanislaw Ulam. Ulam added cells and named the system as cellular automata. Today, a cellular automata can be considered as a subset of agent based models. Conway's Game of Life is also a widely known example worth to be mentioned. It has four rules about neighboring cells for reproducing, staying alive and death. It can be easily created in agent based modelling environments by using agents or patches.

Development of computer technologies, let agent based modelling be used widely in many different disciplines from both social and natural sciences. For instance, it is used by many researchers for ecological problems like, population dynamics, epidemics, invasion etc. and significant results are obtained. Beyond the other properties of individual based models, modular structure property makes the development stage considerably easier, also the abstraction property is important to model the systems which are partially understood.

In the last two decades many agent based modelling softwares are developed. They have differences about their purposes and popular in different disciplines. There are at least 50 software environments are available by 2014 which supports lots of common programming language interoperability [26]. Yet in many researches custom solutions are also used. The blurred lines between similar paradigms, like multi-agent modelling, discrete modelling, artificial life and even system modelling or more deeper approaches like agent oriented programming, make it hard to classify the environments. Swarm, AnyLogic, Repast, StarLogo, Ascape are some of the leading softwares in use.

2.2.2 NetLogo

NetLogo is an agent based / individual based modelling language and an integrated modelling environment. It is developed by Uri Wilensky from Northwestern University's Center for Connected Learning and Computer-Based Modeling. The first version appeared in 1999. The initial aim was teaching kids programming. NetLogo Language is based on Logo language. It uses an event driven programming paradigm which means the program flow depends on the inputs from elements of model or even user (via HubNet extension). The basic elements of a model are turtles, links, patches and observer. It comes with a wide model library which contains examples of many different disciplines like biology, sociology, computer science and engineering.

In NetLogo, agents or individuals are called 'turtles', because of historical reasons. 'Patches' are the spatial elements of a model. Their behavior is similar to cellular automata. 'Links' are a special kind of turtles which are generally used for abstract, hierarchical and directed relations. Also another basic concept is 'tick'. Ticks are discrete time steps which constitute a temporal dimension for a model.

Procedures in NetLogo are equivalent of the functions in other more conventional programming languages. They control the relations between patches, turtles, ticks and even observer. Commands are built-in functions. Beside very general purpose commands like count, move or hatch, there are also specific commands like downhill or diffuse. Also the commands like stamp (lets the individuals leave a mark where they die) or pen up/down (lets the moving individuals leave a trail on canvas) are authentic and useful.

Behavior space is one of the tools contained by NetLogo. It is a parameter space sweeping tool. It can work on all the cores of a multicore processor. Thus the number of running models depends on the architecture of the processor. Also, serial model running is a possible option without maintaining every single model run.

Learning curve of NetLogo is not steep, however absence of many widely used loop structures like ’for’ or ’while’ makes it tricky to use and hard to master. Beyond its pros and cons, it is one of the most used language which worth to mention its name in many studies [27].

3. METHOD

3.1 Structure of the Model

The central algorithm of the model, if there must be a chosen one, is most probably the interplay between mussels and veligers. The reproduction of veligers from mussels and the metamorphosis of veligers to become mussels by fouling to possible places constitute the essence of the entire operation. Both veligers and mussels use phytoplanktons as resource during entire process in all procedures (Figure 3.1).

A tick, the temporal unit, in the model equals to 2 hours. Therefore, a year is 4380 ticks. The year concept constitutes a basis for the cycles of phytoplankton blooms and water temperature changes. All the experiments encompass a 20-year period which can be considered a rough representation of years between 1986 and 2006.

Despite the phytoplanktons are not represented as agents in the model, their role is vital for the individuals. Their amount is a patch attribute and exhibits variation around 10%. Also diffusion occurs to keep the dynamic nature of the canvas. Initial phytoplankton amount has a central role for regeneration procedure as a target value to reach. This value is the same for all the lakes but the peak value differs to explain different conditions. Yearly phytoplankton oscillations are represented with triangle waves. Similar to the nature, in the model there are two blooms in a year: a mid-spring major one and a mid-summer minor one.

Physiology of both mussels and veligers is strictly connected to the phytoplankton density. The resource exploitation amounts of individuals are calculated based on the phytoplankton amount of the patches. Because of this, the phytoplankton blooms are followed by drastic population growths of the invaders and the mortality rates in the periods between blooms are higher. Veliger mortality depends on resource collection while mussel mortality is related to both resources and a stochastic lifespan which is based on the observations of the field studies.

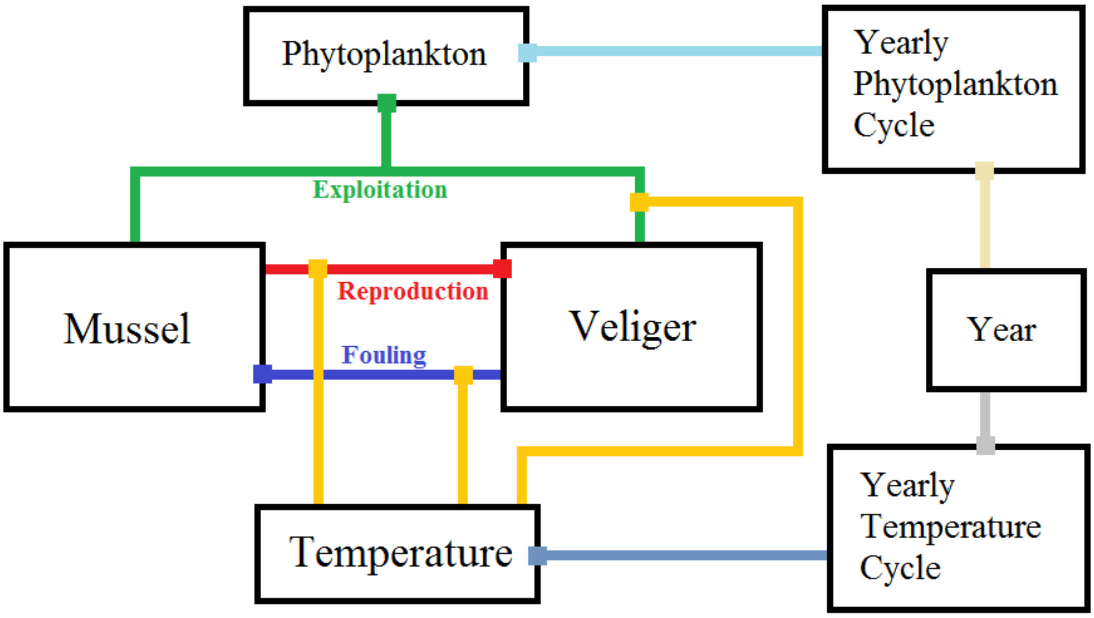

Figure 3.1: Simplified diagram of the model.

Even if it is not obligatory, individual based models require mobility for individuals. For instance, the veligers, in the meaning of mobility, are highly dynamic. They move between patches, a unit per tick. Their movements are random to represent passive movement. Beyond their ordinary intra-lake movement, two transportation procedures control inter-lake movement. The eastward transportation is a purely stochastic procedure. Random individuals are transported to the next lake with a defined transportation probability. However, westward transportation can be considered relatively deterministic. In certain parts of the lakes, veligers drift to the previous lake. The only exception occurs in Lake Ontario where the drift zone causes removal of the veligers as a representation of drift into St. Lawrence waterway. The underlying details are explained in the following sections of the chapter.

Temperature is also an important factor. There are three predefined temperature levels. In the lowest level, resource exploitation is normal for both types of individuals but reproduction does not occur. In the second temperature level, all the related procedures work. The only difference about the third level is the higher resource exploitation rates of veligers. These levels are not standard for all the lakes. For example, Lake

Table 3.1: Effects of temperature levels on mussels.

Temperature Level	Exploitation	Reproduction
1	normal	not occurs
2	normal	occurs
3	normal	occurs

Table 3.2: Effects of temperature levels on veligers.

Temperature Level	Exploitation	Reproduction
1	normal	occurs
2	normal	occurs
3	doubled up	occurs

Superior never reaches the third level which represents the optimal condition for veliger development (Table 3.1 and Table 3.2).

3.2 Spatial and Temporal Procedures

3.2.1 Map.Import

This procedure, despite its name, does not only import the map. As mentioned before, in the model a simplified map is used. By the first part of the procedure, the map is imported and patch number is set as 54 x 34. In the second part, year duration is declared as 4380 which makes a tick two hours and month duration is given based on this value. The third part is about the patch types. NetLogo lets the using of patch colors to assign attributes to the patches. Beyond basic separation of land and water patches, also shore and lake types are defined. Finally, the exit points of lakes, which have a central role in transportation procedures, are described by their patch coordinates. The roles of the variables will be explained in related procedures.

3.2.2 Lake.Names

The lakes in the model have different conditions in the meaning of phytoplankton density and temperature. To handle this situation is possible by naming them with a similar method used in Map.Import procedure. In this procedure patch coordinates are used to name the lakes.

3.2.3 Month.Definitions

Because of the cyclic behavior of phytoplankton and temperature releated procedures, some certain dates are declared with ratios. The alpha and omega values represent the beginning and the end of a year. They are used for year iteration in Year.Reset procedure. The other variables are the dates of beginning, climax and end points of midsummer and mid-spring plankton blooms. Temperature changes which are organized with a stepped nature, also use these values.

3.2.4 Year.Reset

This procedure works as a year counter and date iterator. It adds tick based year duration to defined dates in month.definition procedure and resets the cycle at the end of every year. Also it counts the years during the experiment. Mussel life span which is defined in Mussel.Mortality procedure uses year values as a variable.

3.3 Utility Procedures

3.3.1 Global.Plots

NetLogo Language, to avoid semantic errors about the relations network between patches, turtles and the observer, has strict rules about variables. Local variables in procedures cannot be used to draw plots. These procedures calculate mean value of phytoplankton density of each lake and assign the results to the global variables to draw plots.

3.3.2 Diffusion

Despite, NetLogo has a built-in diffusion command, the nature of the map makes it useless because of avoiding the phytoplanktons diffuse into the land. Diffusion procedure that is used in the model is developed from the scratch. A certain rate controls the diffusion and makes the amounts more dynamic.

3.4 Phytoplankton and Temperature Procedures

3.4.1 Phytoplankton.Resource.Distribution

In the model, phytoplanktons are not in the form of turtles. A numeric patch variable called Phytoplankton.Amount represents their presence on the canvas. An adjustable initial value is used to assign phytoplankton density. There is a slight variation around 10% that is created by randomization, between patches. Also three different phytoplankton levels, a ratio of initial value, are used for different lakes.

3.4.2 Phytoplankton.Resource.Adjustment

This procedure is closely related to the previous one. As mentioned before, the lakes have one of three different levels of phytoplankton density. Calculated ratios from Phytoplankton.Resource.Distribution procedure are used to obtain and assign the lake specific values.

3.4.3 Phytoplankton.Regeneration

Pyhtoplankton amounts in the patches are dynamic. Regeneration algorithm is not different than many other models. While there is no consumer, mussel or veliger, regeneration occurs until the initial value is reached. This process is only limited by initial phytoplankton amount and not cycle-dependent. The regeneration rate is the same for all the lakes.

3.4.4 Bloom.Change.Rates

This procedure is a minor one to set the increase ratio of blooms. Mid-spring value is eleven-fold of initial value while midsummer value is four-fold. It is closely related to bloom.adjustment procedure.

3.4.5 Bloom.Adjustments

The blooms are driven by the Year.Reset and Month.Definition procedures determine the exact ticks of the beginning, the climax and the end of the triangle wave formed blooms. It is same for all the lakes.

3.4.6 Temperature.Adjustment

This procedure is very similar to Bloom.Adjustment. It uses time related variables defined in Year.Reset procedure. It has three values which represent water temperature levels that have significant impact on zebra mussel physiology. Durations of periods with certain temperature levels are lake-specific and based on observation.

3.5 Veliger Procedures

3.5.1 Veliger.Shaper

The color and size of veligers in the model is determined by this procedure. The model uses default agent shape because of initial undeclared choice.

3.5.2 Veliger.Spawn

As a minor procedure, it produces an important constant in the model. Initial veliger number is set as 10 in all scenarios by this procedure. It can be controlled by a slider in the interface. Also, the shape and the color of the created agents are determined by it.

3.5.3 Veliger.Introduce

It is a Lake Ontario-specific version of veliger.transportation procedure. It is not controlled by transportation algorithm but has a similar manner. It spawns veligers randomly and represents transportation of veligers by ballast water of ships.

3.5.4 Veliger.Move

The only moving agents of the model are the veligers like their equivalents in the physical world. The most important role of this procedure is avoiding the veligers move on the patches which are described as land and keep them in the water.

3.5.5 Veliger.Consume

The resource exploitation in the model is closely related to the temperature. This procedure sets the exploitation rate (an adjustable percentage of the resource of the patch that the zebra mussel is present) and the physiological expenditure rate. All the variables are organized by the temperature basis in this procedure. The income and the outcome are calculated and determined to set the related variables of the veligers.

3.5.6 Veliger.Transportation

Veliger transportation concept has a central role in the model and also in this study is used as a criterion in numeric experiments. As explained in 'Structure of the Model' section, the procedure defines a global threshold in the experiments and produce random numbers for each veliger. The comparison between these values controls the eastward transportation process. A secondary comparison, which is like a "head or tails" game, is used as a basis of transportation from Lake Huron to Lake Michigan or Lake Superior (Figure 3.2).

3.5.7 Veliger.Exit

While Veliger.Transportation procedure describes the rules of the eastward transportation, Veliger.Exit is about westward transportation. In certain locations of the lakes, veligers are considered as drifted and placed to the next lake in the network. In Lake Ontario, this exit point means drifting to St.Lewrance river and vanishing from the map (Figure 3.3).

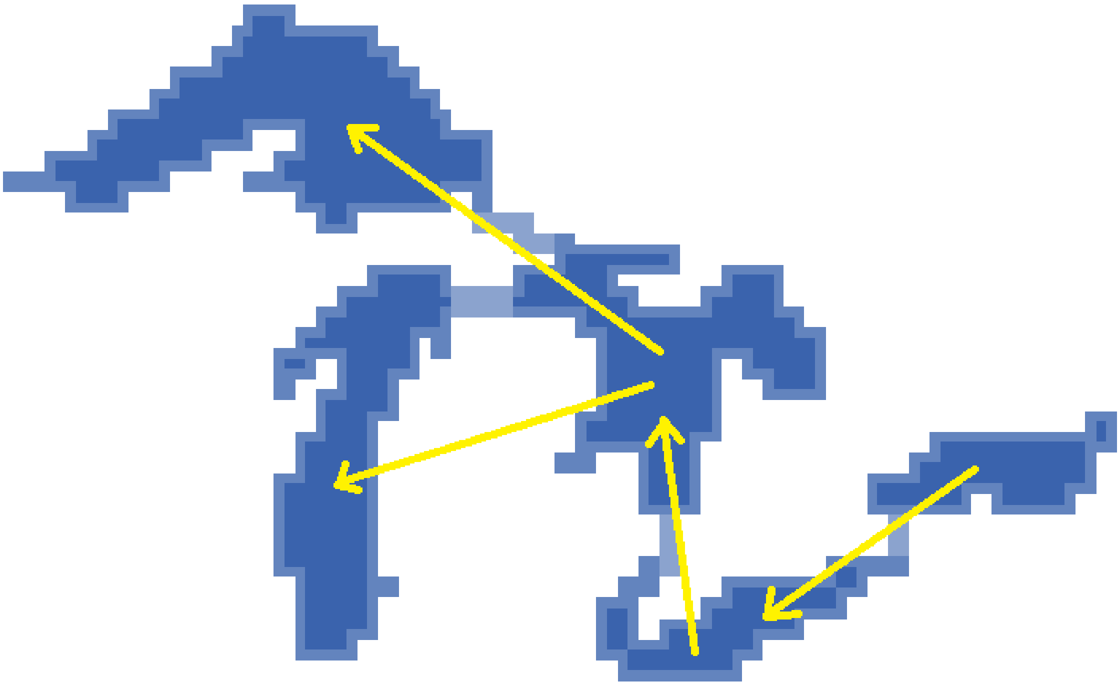

Figure 3.2: Diagram of Veliger.Transportation procedure.

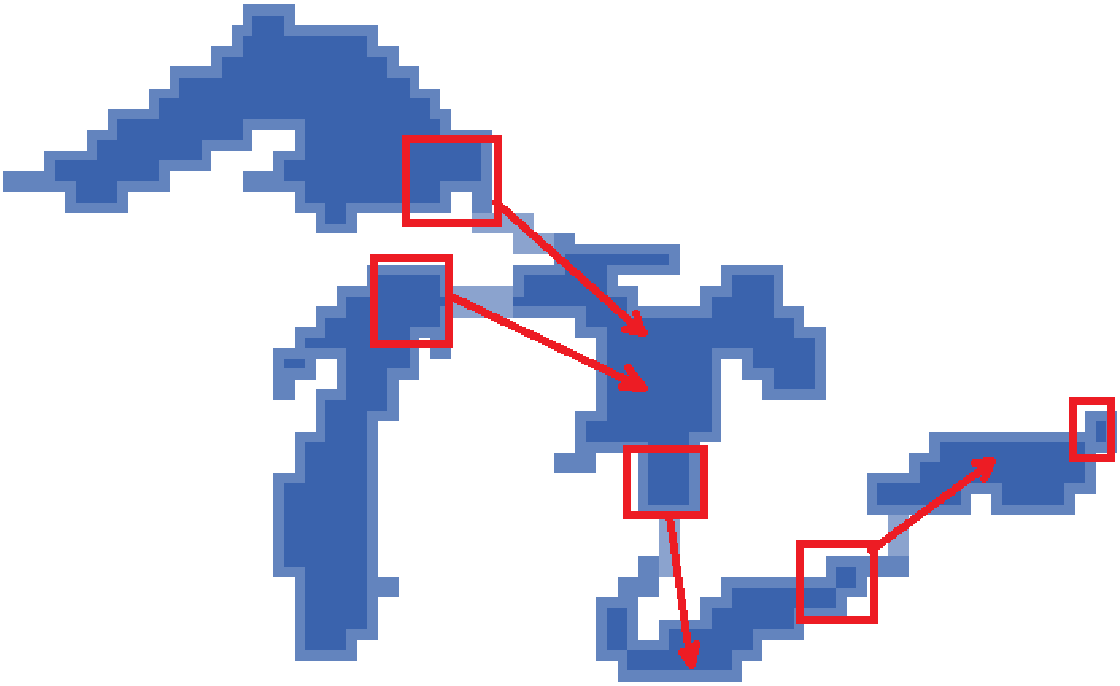

Figure 3.3: Diagram of Veliger.Exit procedure.

3.5.8 Veliger.Mortality

This procedure sets a simple rule about resource related mortality. If the collected resource (cumulative sum that is calculated by the income and the outcome at the end of every tick) equals to zero, veliger dies.

3.5.9 Veliger.Fouling

As explained in 'Structure of the Model' section, metamorphosis and reproduction related procedures are the heart of the model. The veligers which obtained enough resource and reached to an available place become mussels. Metamorphosis thresholds and place restrictions are defined in this procedure.

3.6 Mussel Procedures

3.6.1 Mussel.Shaper

The color, shape and size of mussels in the model are determined by this procedure.

3.6.2 Mussel.Consume

It is very similar to Veliger.Consume procedure. It describes exploitation and consumption rates of mussels. The rates are strictly connected to the phytoplankton density of the patches where the mussels are present.

3.6.3 Mussel.Reproduce

This procedure is the counterpart of the veliger.fouling procedure on the ongoing metamorphosis and reproduction cycle. When a mussel reach a certain resource threshold, produces veligers. The number of veligers is random in a certain interval.

3.6.4 Mussel.Mortality

There are two rules about mussel death in the model. The first one is, like in veliger.mortality procedure, dependent on the lack of resources. The second one is about the randomly predefined life span of a mussel. When a mussel reaches a certain predefined age it dies.

3.7 Meta-Procedures

3.7.1 Setup

Setup is a meta-procedure. It is used at the beginning of every experiment and executed once. It contains static procedures to set the rules and to declare initial variables. The first two commands in this procedure are ’clear-all’, which resets the map and ’reset-ticks’, which resets the tick clock. Both of them are built-in commands of NetLogo. The other procedures in Setup are Map.Import, Phytoplankton.Resource.Distribution, Month.Definitions, Bloom.Change.Rates, Veliger.Spawn and Lake.Names.

3.7.2 Go

Go is a meta-procedure. Once it is executed, it repeats in every single tick and works until a certain stop condition. The only built-in command that used in ’Go’ is ’tick’ which refreshes the tick count after every single tick. The procedures of Go are Phytoplankton.Regeneration, Bloom.Adjustments, Temperature.Adjustment, Year.Reset, Veliger.Move, Global.Plots, Difussion, Transportation, Veliger.Consume, Veliger.Mortality, Veliger.Fouling, Mussel.Consume, Mussel.Reproduce, Mussel.Mortality, Veliger.Exit, Veliger.introduce.

4. NUMERICAL EXPERIMENTS AND RESULTS

In the study there are six experiment sets. Every experiment set contains 30 numerical experiments. P75 and P125 experiments are conducted to understand the effects of different values of phytoplankton density. In T0.1 and T10 experiments, transportation probability is used as the variable. Conditions of Lake Huron are applied to Lake Superior in SupD experiment for a simple climatic change scenario (Table 4.1).

Table 4.1: Experiment sets and parameters.

Experiment Set	Phytoplankton Density	Transportation Probability
Reference Case	100	1/10000
P75 Experiments	75	1/10000
P125 Experiments	125	1/10000
T0.1 Experiments	100	1/100000
T10 Experiments	100	1/1000
SupD Experiments	100	1/10000

4.1 Reference Case

In the reference case phytoplankton amount is 100 unit, initial veliger number is 10, transportation probability is 1/10000. These experiments represent the zebra mussel invasion in Laurentian Great Lakes roughly between 1986 and 2006. 30 experiments are conducted (Figure 4.1).

In Lake Ontario, veliger count reaches to balance in about two years. During all the experiments, a two to four years periodicity of the maximum peaks can be observed. Also the rising trends of bottoms which are the minima between those peaks are worth to mention. Mussel count shows an initial maximum value around the third year as the representation of the introduction stage, yet this level slightly declines to the equilibrium in average four years. The three year periods of bottoms are quite significant and also a slight uptrend can be seen. The drastic decline of mean phytoplankton amounts reach the equilibrium in a synchronous nature with the

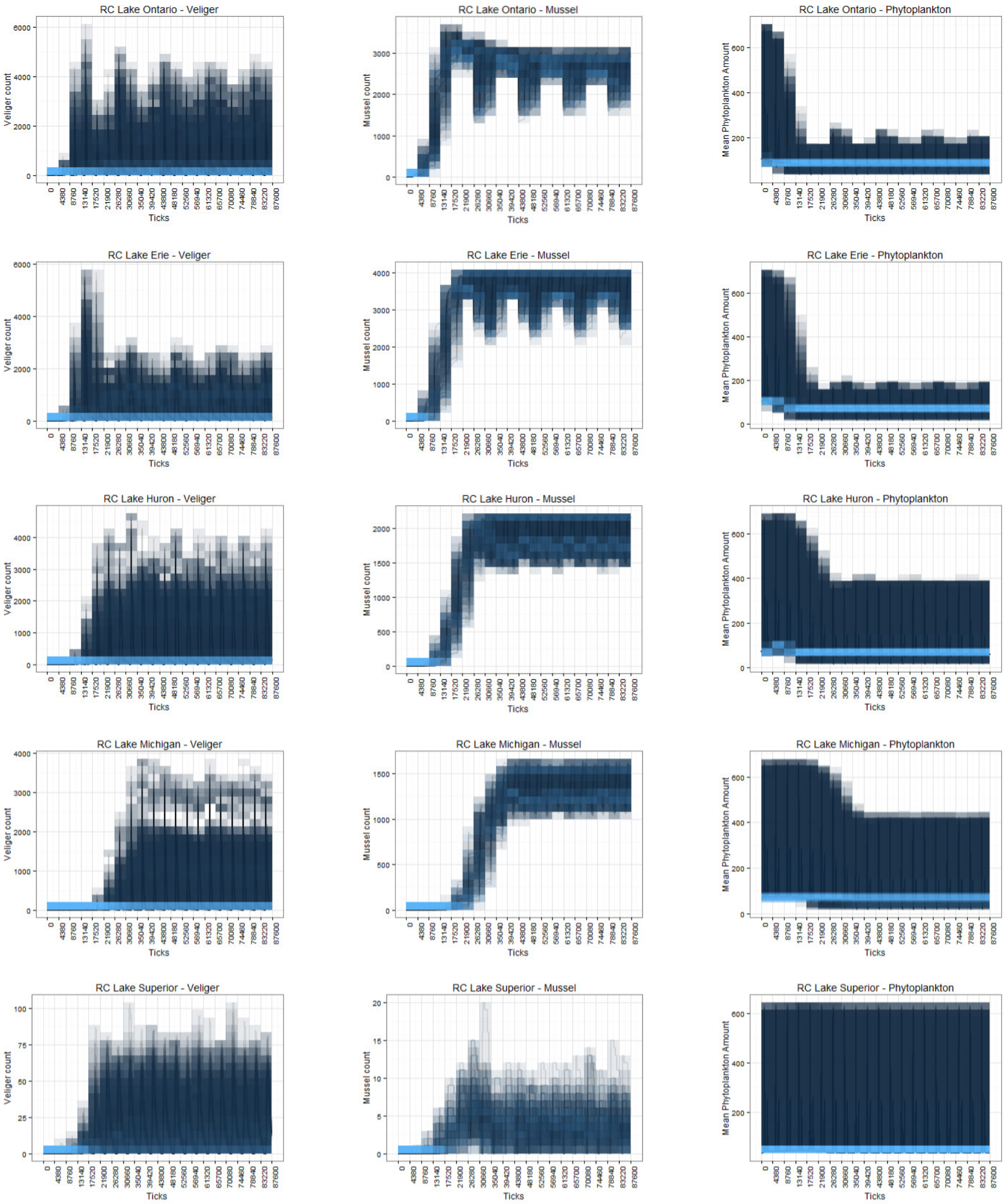

Figure 4.1: Results of Reference Experiments. (For mussels and veligers y axes are not equal.)

invasion. Its significant oscillations are highly dependent on the mussel population density.

The veliger count of Lake Erie reaches its maximum value in about four years. It is followed by a strong decline. The periodicity of the peaks and the bottoms of the mussel population density are also present and it is similar to Lake Ontario. The higher level of mussels effects mean phytoplankton density. One of the most interesting results of the entire experiments can be observed by comparing the Lake Ontario and Lake Erie. Despite, both of them encompass similar conditions, Lake Erie has a more stable and 30% higher mussel population in equilibrium condition. Based on this, it can be said that beside physical conditions, geographical properties alsa have an important role on invasion.

Lake Huron and Lake Michigan show similar results, because of the similar properties they share. The slightly higher values which are observed in Lake Huron are probably a result of early introduction date. In both lakes decline of mean phytoplankton amount is not strong like in the previous ones. The situation in Lake Superior can be considered unimportant. There is a tremendous difference between it and the other lakes in the meaning of the invasion because of the extremely low numbers of the invaders and no visible change in the mean phytoplankton values.

If all the lakes are compared, it can be said that stronger invasion with higher mussel and veliger population densities, causes more significant temporal patterns. At the same time, spatially invasions weaken to east and north.

4.2 P75 Experiments

In P75 Experiments, phytoplankton amount is 75 unit, initial veliger number is 10, transportation probability is 1/10000. These experiments conducted to understand the effects of the lower amount of phytoplanktons on the zebra mussel invasion. 30 experiments were conducted (Figure 4.2).

In these experiments, the most significant characteristic of the mussel population density plots, introduction stages are not as steep as the reference case experiments. It is especially easier to compare in Lake Michigan where the regularity is almost

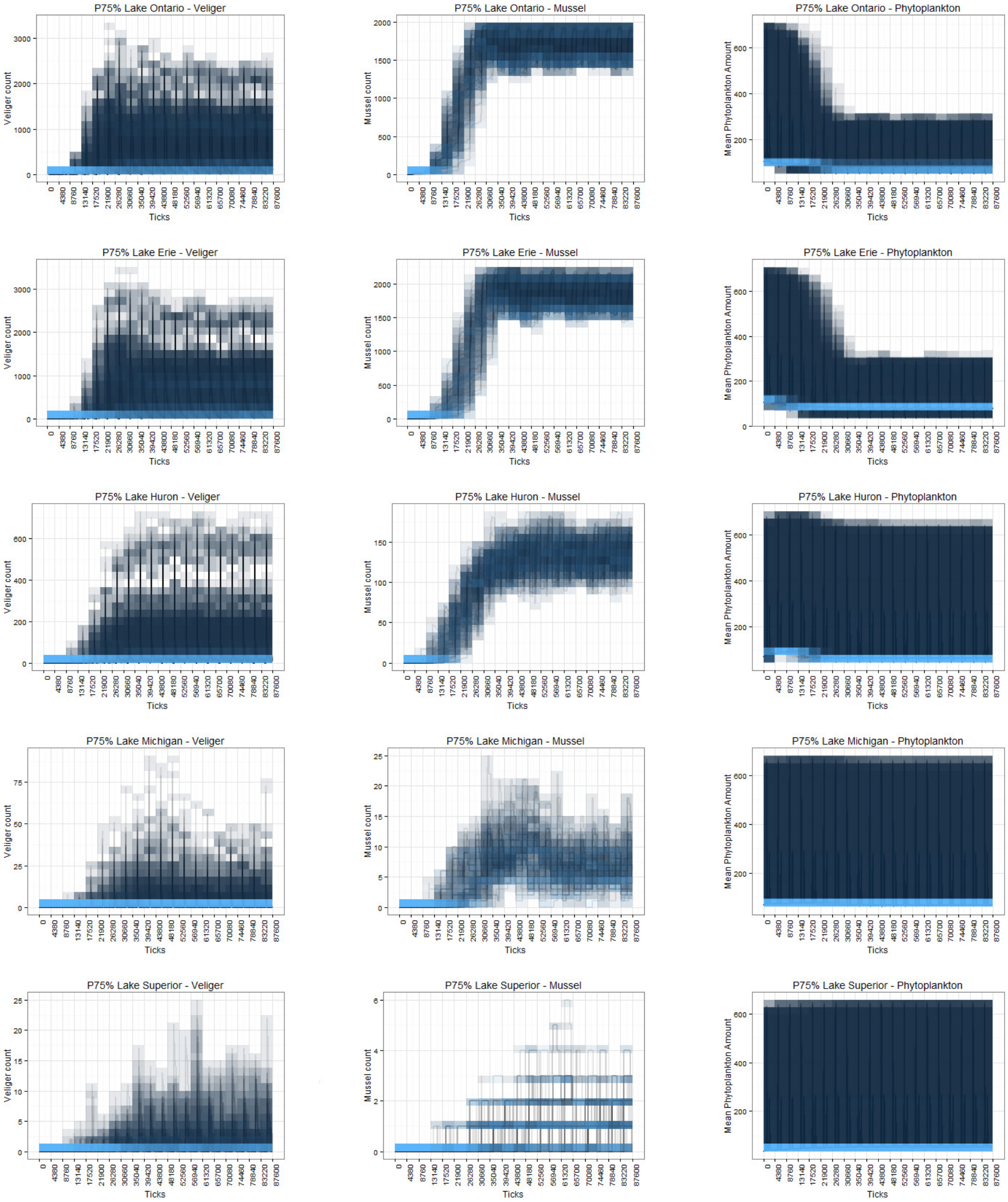

Figure 4.2: Results of P75 Experiments. (For mussels and veligers y axes are not equal.)

completely lost. For Lake Ontario and Lake Erie, periodicity which is present in the reference case experiments is weak but slightly visible. Also the results of the experiments are generally more scattered which imply the higher variation between the outputs. Veliger population density plots are highly irregular and contain no visible periodicity. Mean phytoplankton density plots show that, their initial amounts are not enough for zebra mussel population to reach a certain equilibrium. Probably this insufficient population does not affect phytoplankton population in a drastic way.

With a quantitative perspective, it can be said that 25% less phytoplankton amount does not affect veliger and mussel populations of different lakes in the same way but the only certain thing is that the relations are generally not linear.

4.3 P125 Experiments

In P125 Experiments, phytoplankton amount is 125 unit, initial veliger number is 10, transportation probability is 1/10000. These experiments are conducted to understand the effects of higher amount of the phytoplanktons on the zebra mussel invasion. 30 experiments were conducted (Figure 4.3).

The plots of those experiments are visually similar to the reference case experiments but more significant. Differently, periodical patterns are also present for Lake Huron as a spectacular situation in all experiments. This means there is probably a connection between the periodicity and resource amount.

For all the lakes equilibrium conditions occur at high values, which are non-linearly affected by higher amounts of the mean phytoplankton. As seen in P75 and reference case experiments, the stability of the equilibrium is directly connected to the resource. The supporting example of it is the equilibrium condition of the Superior Lake which is also spectacular like the periodicity in Lake Huron.

4.4 T0.1 Experiments

In the T0.1 Experiments, phytoplankton amount is 100 unit, initial veliger number is 10, transportation probability is 1/100000. These experiments are conducted to understand the effects of higher transportation probability of veligers on the zebra

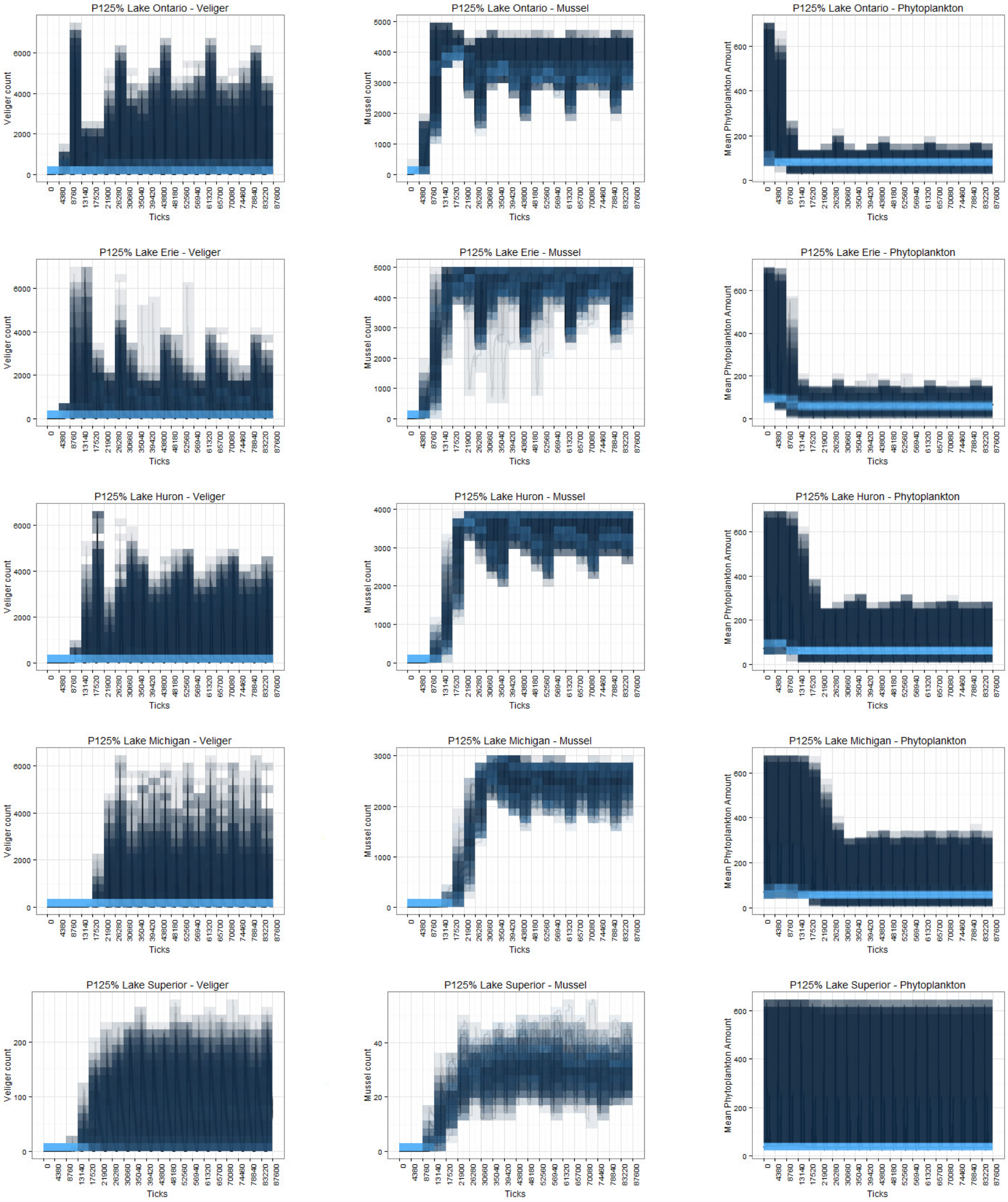

Figure 4.3: Results of P125 Experiments. (For mussels and veligers y axes are not equal.)

mussel invasion. 30 experiments were conducted. The results do not contain Lake Ontario which already contains the initial veliger population (Figure 4.4).

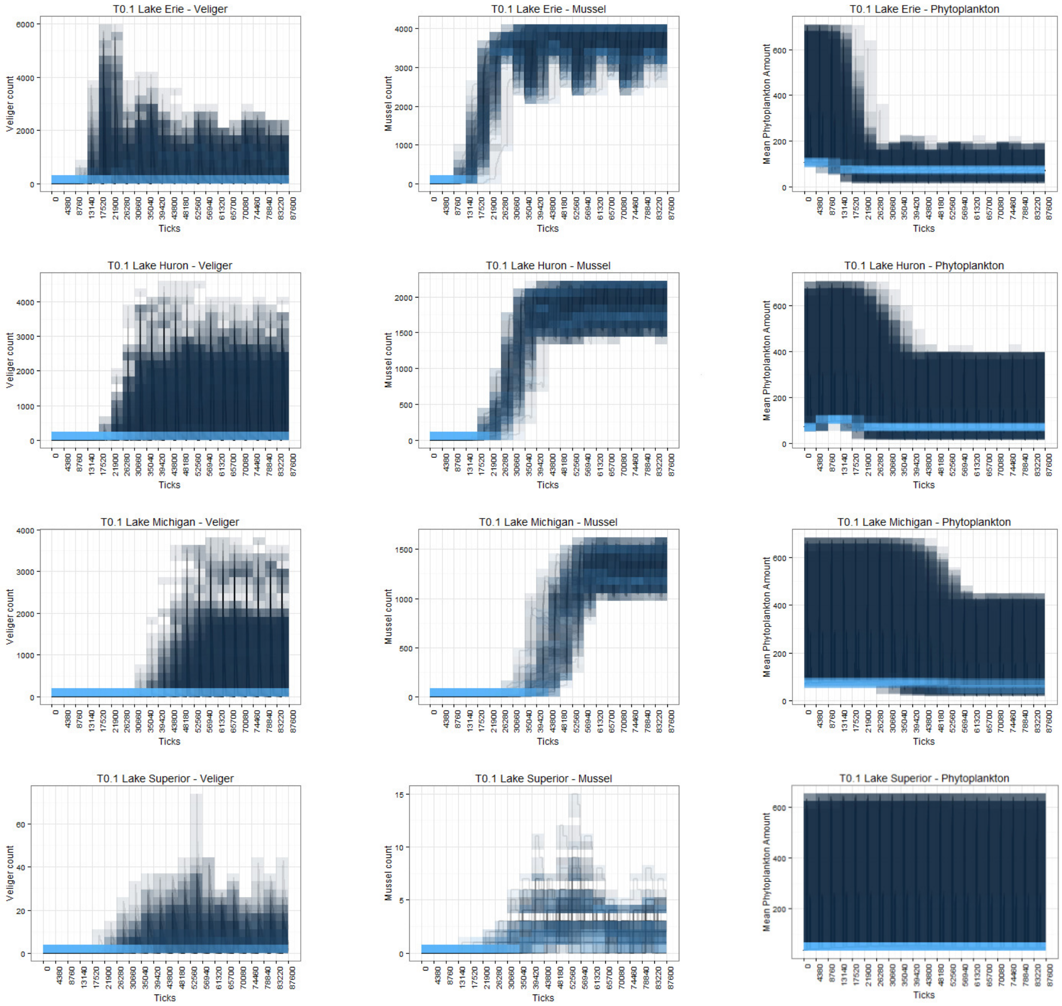

Figure 4.4: Results of T0.1 Experiments. (For mussels and veligers y axes are not equal.)

The population densities are fairly similar to the reference case experiments for both mussels and veligers. Its only exception is the Lake Superior with a 20% to 25% less population density caused by lesser transportation rates. Based on this, it can be said that the difference represents the important role of transported veligers on the population densities of the lakes.

The variation of the arrival times cause more scattered view along the time axis. Thus the equilibrium conditions are delayed. In a general sense, its effects can be compared to the P75 Experiment but in a more proportional manner.

4.5 T10 Experiments

In the T0.1 Experiments, phytoplankton amount is 100 unit, initial veliger number is 10, transportation probability is 1/1000. This experiments are conducted to understand the effects of higher transportation probability of veligers on the zebra mussel invasion. 30 experiments were conducted. Like the T0.1 Experiments, the results do not contain Lake Ontario which already contains the initial veliger population (Figure 4.5).

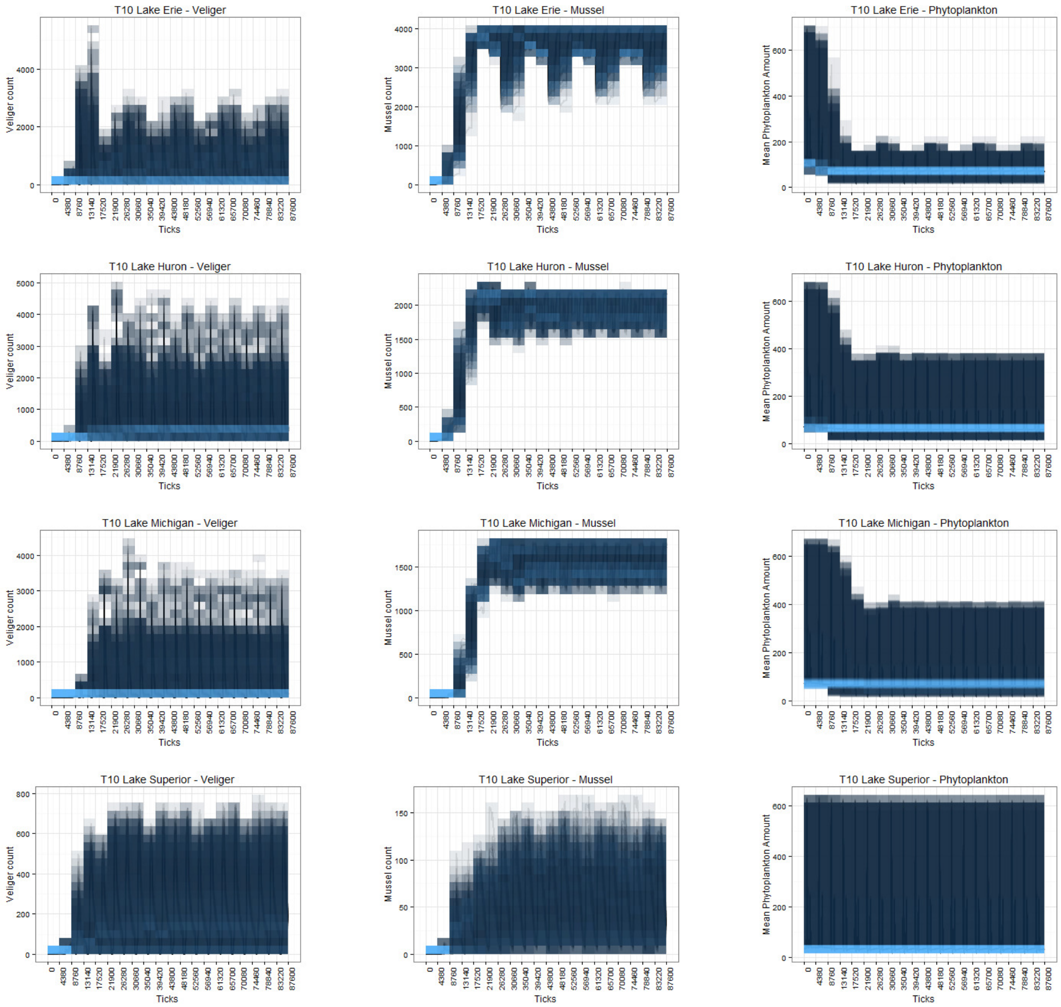

Figure 4.5: Results of T10 Experiments. (For mussels and veligers y axes are not equal.)

Contrary to the T0.1 Experiments, the plots are not scattered. In all the lakes, the invasion occurs almost simultaneously. All the patterns are visually similar to P125 experiments but the levels are more similar to reference case experiments. The periodical declines are quite significant for Lake Erie. Uniquely, a 2-year pattern can be observed in Lake Huron.

4.6 SupD Experiments

The SupD experiments were conducted to understand the results of a fictive climate change scenario. As explained before the lakes have different cycles of temperature and phytoplankton, which are highly simplified. In the model, Lake Superior, based on the measurements from various sources, never reaches the temperature level which is optimum for veliger development. Thus the population density values are quite lower than the other lakes. Conditions of Lake Huron were used for this experiments (Figure 4.6).

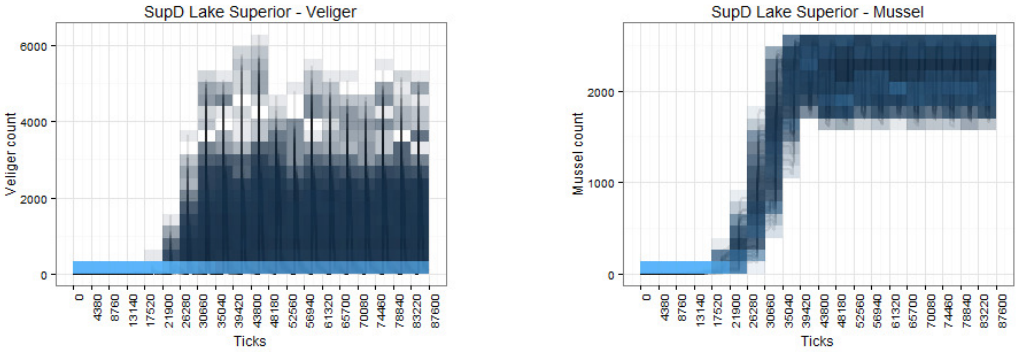

Figure 4.6: Results of SupD Experiments. (For mussels and veligers y axes are not equal.)

The results show that, this kind of change causes drastic differences for the course and the strength of the invasion. If it is compared to the reference case experiments, for instance, equilibrium of mussel population occurs at 150-fold higher levels and even shows a slight periodicity which presents at totally invaded lakes like Ontario or Erie.

5. CONCLUSIONS

There is no doubt that anthropogenic effects are strong enough to change many dynamics of nature. Because of the complex relations between the components of earth system, consequences of these changes are hard to predict. Introduction of zebra mussels to Great Lakes is a purely human mediated incident. In consideration of recent studies on the relation between global change and invader success [28] (even in this present study which is based on a highly simplified model), it is possible to see the results of altered conditions.

As told before in the related chapter, the model which was used in this study, has restricting rules to avoid eastward or upstream inter-lake movement of veligers and this movement is controlled by transportation probability value. Comparison of T0.1, reference case and T10 experiment sets suggests that, increasing value of tranportation rate causes a shorter introduction phase and accelerates the dispersal. This situation is analogue to the long distance jump-dispersal consept which is observed in nature. As it can be seen in the studies on another invasive species, Argentine ants (*Linepithema humile*), invasions are much are much faster than their natural state in the presence of human intervention [29].

Despite the efforts to find a strong relation between boater movement in Great Lakes and zebra mussel invasion, this relation is a poor predictor of invasion probability [30]. In the model, absence of a certain agent which is responsible for transportation can be justified by this situation. According to this, transportation probability values which are obtained by parameter space sweeping methods, are used in a 'black box' procedure. Interestingly, these values are similar to the probability rates which are obtained by the results of gravity models on zebra mussel invasion of Great Lakes [31].

Propagule pressure concept is considered as an elemental part of invasion success in some studies [32]. Also, spatial [33] and temporal [34] effects of propagule pressure on invasions are widely known. Another conclusion of T0.1 and T10 experiment sets is that, increased values of transportation probability causes higher zebra mussel population density. It implies the emergence of propagule pressure.

A special form and a result of propagule pressure occurs in Lake Erie. In all the experiment sets, it is noticed that the invasion weakens in upstream direction. Yet Lake Erie is an exception. Lake Erie always has the highest zebra mussel population density, despite its identical conditions and similar surface area with Lake Ontario. This result is compatible with previous observations [35] and some other models [36]. Downstream spread caused by drifting procedures of the model, ends up with high propagule pressure on Lake Erie. The difference between Lake Ontario and Lake Erie in the meaning of zebra mussel population is similar to observational studies [37]. Alternatively it can be concluded that the location of a lake on a waterbody network is important as physical and biological conditions in case of an invasion.

P75 and P125 experiment sets were conducted to understand the effects of phytoplankton density on zebra mussel population and invasion. Results of these experiments show a non-linear relation between zebra mussel population and altered phytoplankton density. Phytoplankton densities are important for examining the inner dynamics of these experiments. In totally invaded lakes like Ontario or Erie, phytoplankton population density dramatically decreases in a few years. This period overlaps with the introduction phase of invasion. Decreasing rates are matching with observations [38] and results of other models [39].

An important result that come out of the model is the periodical decline patterns. These three to four-year patterns get more evident in full-blown invasion state yet never occur in Lake Superior which does not provide the proper condition for zebra mussel invasion totally. A slight upward trend of the periodic bottoms also worth to mention. It can be tought as a trace of a prolonged lag pattern which is a common situation for human-mediated biological invasions [40]. The underlying reason can be a combined effect of mussel lifespan and phytoplankton blooms. Also, results of some experimental studies on ecological sthoichiometry of zebra mussels suggest negative effects of high and low nutrition conditions [41]. It is another possible explanation for this situation.

SupD experiment set is based on a fictive climatic change scenario. Basically, conditions of Lake Huron were used on Lake Superior to observe the results of a plausible change. According to the observations, Lake Superior is not suitible for a strong zebra mussel invasion because of its climatic conditions and relatively less human activity [42]. There are many studies suggest that long term uptrend of phytoplankton populations [43] and harmful algal blooms [44] is a result of climate change. Increasing summer surface water temperature of Lake Superior makes the SupD scenario worth to consider. As seen in the results of the experiments, altered conditions ends up with 150-fold higher zebra mussel population.

The modular structure of the individual based models is an advantageous attribute to expand the studies for further research. For instance, the predators and/or closely related member of the local fauna and competing invaders like quagga mussels can be used as agents to examine different aspects of a zebra mussel invasion. Moreover detailed maps, more precise cycles, hydrologic properties etc. are possible elements of an expanded version of the model which requires much more time and computational power.

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APPENDICES

APPENDIX A.1 : Source Code

APPENDIX A.1

```
globals [ Mean.Phytoplankton Mean.Veliger Mean.Mussel
          Year.Length Month.Length Diffusion.Rate
          Mean.Phytoplankton.Ontario
          Mean.Phytoplankton.Erie
          Mean.Phytoplankton.Huron
          Mean.Phytoplankton.Michigan
          Mean.Phytoplankton.Superior Year Year.Counter
          Alpha April.1 April.15 April.30 July.1 July.15
          7July.30 Omega May.15 June.1 June.15 October.1
          October.15 November.1 April.Change.Rates
          July.Change.Rates Omegainc Phytoplankton.L1
          Phytoplankton.L2 Phytoplankton.L3 ]
breed [veligers veliger]
breed [mussels mussel]
Veligers-own [ Veliger.Collected.Resource ]
Mussels-own [ Mussel.Collected.Resource Mussel.Age]
patches-own [ Patch.Type Watermass.Type Watermass.Name
              Phytoplankton.Amount Water.Temperature ]
to Map.Import
    resize-world -54 54 -34 34
    import-pcolors "gl.png"
    set Year.Length 4380
    set Month.Length ( Year.Length / 12 )
    ask patches[
        if pcolor = 105
            [ set Patch.Type "water"
            set Watermass.Type "lake"]
        if pcolor = 0
            [ set Patch.Type "land" ]
        if pcolor = 107
            [ set Patch.Type "stream" ]
        if pcolor = 106
            [ set Patch.Type "water"
              set Watermass.Type "shore" ]
        if pxcor > 52 and pxcor = 54
        and pycor < -6 and pycor > -11
            [ set Watermass.Type "exit" ]
        if pxcor > 8 and pxcor < 15
        and pycor <= -15 and pycor >= -16
            [ set Watermass.Type "huron.exit" ]
        if pxcor > 29 and pxcor < 35
```

```
        and pycor <= -21 and pycor >= -22
            [ set Watermass.Type "erie.exit" ]
        if pxcor <= -10 and pxcor >= -11
        and pycor < 8 and pycor > 1
            [ set Watermass.Type "michigan.exit" ]
        if pxcor > -10 and pxcor < -5
        and pycor <= 17 and pycor >= 15
            [ set Watermass.Type "superior.exit" ]
    ]
end
to Lake.Names
    ask patches with [ pxcor > 30 and pxcor < 55
                       and pycor < -5 and pycor > -17 ]
                        [ set Watermass.Name "Lake Ontario"]
    ask patches with [ pxcor > 4 and pxcor < 35
                       and pycor < -20  and pycor > -33 ]
                        [ set Watermass.Name "Lake Erie" ]
    ask patches with [ pxcor > -4 and pxcor < 27
                        and pycor < 10 and pycor > -16 ]
                        [ set Watermass.Name "Lake Huron"]
    ask patches with [ pxcor > -53 and pxcor < -5
                        and pycor < 33 and pycor > 10 ]
                        [ set Watermass.Name "Lake Superior"]
    ask patches with [ pxcor > -27 and pxcor < -9
                        and pycor < 8 and pycor > -31 ]
                        [ set Watermass.Name "Lake Michigan"]
end
to Veliger.Transportation
    ask veligers [
        let Veliger.transport random 1000000
        let Veliger.transport.M.or.S random 2
        if Watermass.Name = "Lake Ontario"
        and Veliger.transport < Transportation.Probability
            [ hatch 1 [ set xcor 19 set ycor -25 ]
            die]
        if Watermass.Name = "Lake Erie"
        and Veliger.transport < Transportation.Probability
            [ hatch 1 [ set xcor 10 set ycor -5 ]
            die]
        if Watermass.Name = "Lake Huron"
        and Veliger.transport < Transportation.Probability
            and Veliger.transport.M.or.S = 1
            [ hatch 1 [ set xcor -15 set ycor 19 ]
            die]
        if Watermass.Name = "Lake Huron"
        and Veliger.transport < Transportation.Probability
        and Veliger.transport.M.or.S = 0
```

```
            [ hatch 1 [ set xcor -17 set ycor 2 ]
            die]
  ]
end
to Veliger.introduce
  let Veliger.introduce.number random 1000000
  if Veliger.introduce.number < Transportation.Probability
  [create-veligers 1 [ set xcor 40  set ycor -11]]
end
to Phytoplankton.Resource.Distribution
   ask patches with [ Patch.Type = "water"]
    [ set Phytoplankton.Amount Phytoplankton.Amount.Global
      let Phytoplankton.Amount.Variation random
        ( Phytoplankton.Amount / 10 )
      set Phytoplankton.Amount
        ( Phytoplankton.Amount
        + Phytoplankton.Amount.Variation ) ]
      set Phytoplankton.L1
      1 * Phytoplankton.Amount.Global
      set Phytoplankton.L2
      0.66 * Phytoplankton.Amount.Global
      set Phytoplankton.L3
      0.33 * Phytoplankton.Amount.Global
end
to Phytoplankton.Resource.Adjustment
  ask patches with [ Watermass.Name = "Lake Ontario"]
    [ set Phytoplankton.Amount
    ( Phytoplankton.Amount )]
  ask patches with [ Watermass.Name = "Lake Erie"]
    [ set Phytoplankton.Amount
    ( Phytoplankton.Amount )]
  ask patches with [ Watermass.Name = "Lake Huron"]
    [ set Phytoplankton.Amount
    ( Phytoplankton.Amount * 0.66 )]
  ask patches with [ Watermass.Name = "Lake Michigan"]
    [ set Phytoplankton.Amount
    ( Phytoplankton.Amount * 0.66 )]
  ask patches with [ Watermass.Name = "Lake Superior"]
    [ set Phytoplankton.Amount
    ( Phytoplankton.Amount * 0.33 )]
end
to Phytoplankton.Regeneration
  ask patches with [ Watermass.Type = "lake"]
  [
  let x pxcor
  let y pycor
  let r  count veligers-at x y
```

```
  if r = 0 and Watermass.Name = "Lake Ontario"
    and Phytoplankton.Amount < Phytoplankton.L1
    [set Phytoplankton.Amount Phytoplankton.Amount
    + (Phytoplankton.Amount * 0.1)]
  if r = 0 and Watermass.Name = "Lake Erie"
    and Phytoplankton.Amount < Phytoplankton.L1
    [set Phytoplankton.Amount Phytoplankton.Amount
    + (Phytoplankton.Amount * 0.1)]
  if r = 0 and Watermass.Name = "Lake Huron"
    and Phytoplankton.Amount < Phytoplankton.L2
    [set Phytoplankton.Amount Phytoplankton.Amount
    + (Phytoplankton.Amount * 0.1)]
  if r = 0 and Watermass.Name = "Lake Michigan"
    and Phytoplankton.Amount < Phytoplankton.L2
    [set Phytoplankton.Amount Phytoplankton.Amount
    + (Phytoplankton.Amount * 0.1)]
  if r = 0 and Watermass.Name = "Lake Superior"
    and Phytoplankton.Amount < Phytoplankton.L3
    [set Phytoplankton.Amount Phytoplankton.Amount
    + (Phytoplankton.Amount * 0.1)]
  ]
end
to Month.Definitions
    set Year.Counter 0
    set Year 1
    set Alpha 0
    set April.1 ( Month.Length * 3 )
    set April.15 ( Month.Length * 3.5 )
    set April.30 ( Month.Length * 4 )
    set May.15 ( Month.Length * 4.5 )
    set June.1 ( Month.Length * 5 )
    set June.15 ( Month.Length * 5.5 )
    set July.1 ( Month.Length * 6 )
    set July.15 ( Month.Length * 6.5 )
    set July.30 ( Month.Length * 7 )
    set October.1 ( Month.Length * 9 )
    set October.15 ( Month.Length * 9.5 )
    set November.1 ( Month.Length * 10 )
    set Omega Year.Length
end
to Bloom.Change.Rates
  ask patches with [Patch.Type = "water"]
  [
  set April.Change.Rates ( ( Phytoplankton.Amount * 11 )
  / ( Month.Length ) )
  set July.Change.Rates ( ( Phytoplankton.Amount * 4 )
  / ( Month.Length ) )
```

```
  ]
end
to Bloom.Adjustments
  ask patches with [Patch.Type = "water"]
  [
    if ticks > April.1 and ticks < April.15
    [ set Phytoplankton.Amount Phytoplankton.Amount
    + April.Change.Rates ]
    if ticks > April.15 and ticks < April.30
    [ set Phytoplankton.Amount Phytoplankton.Amount
    - April.Change.Rates ]
    if ticks > July.1 and ticks < July.15
    [ set Phytoplankton.Amount Phytoplankton.Amount
    + July.Change.Rates ]
    if ticks > July.15 and ticks < July.30
    [ set Phytoplankton.Amount Phytoplankton.Amount
    - July.Change.Rates ]
    if Phytoplankton.Amount <= 0
    [ set Phytoplankton.Amount  0 ]
  ]
end
to Temperature.Adjustment
ask patches with [Patch.Type = "water"
and Watermass.Name = "Lake Ontario"]
  [
    if ticks > alpha and ticks < June.1
    [ set Water.Temperature 50 ]
    if ticks > June.1 and ticks < June.15
    [ set Water.Temperature 54 ]
    if ticks > June.15 and ticks < October.1
    [ set Water.Temperature 62 ]
    if ticks > October.1 and ticks < October.15
    [ set Water.Temperature 54 ]
    if ticks > October.15 and ticks < omega
    [ set Water.Temperature 50 ]
  ]
  ask patches with [Patch.Type = "water"
  and Watermass.Name = "Lake Erie"]
  [
    if ticks > alpha and ticks < May.15
    [ set Water.Temperature 50 ]
    if ticks > May.15 and ticks < June.15
    [ set Water.Temperature 54 ]
    if ticks > June.15 and ticks < October.15
    [ set Water.Temperature 62 ]
    if ticks > October.15 and ticks < November.1
    [ set Water.Temperature 54 ]
```

```
    if ticks > November.1 and ticks < omega
    [ set Water.Temperature 50 ]
  ]
  ask patches with [Patch.Type = "water"
  and Watermass.Name = "Lake Huron"]
  [
    if ticks > alpha and ticks < June.15
    [ set Water.Temperature 50 ]
    if ticks > June.15 and ticks < July.15
    [ set Water.Temperature 54 ]
    if ticks > July.15 and ticks < October.1
    [ set Water.Temperature 62 ]
    if ticks > October.1 and ticks < October.15
    [ set Water.Temperature 54 ]
    if ticks > October.15 and ticks < omega
    [ set Water.Temperature 50 ]
  ]
   ask patches with [Patch.Type = "water"
   and Watermass.Name = "Lake Michigan"]
  [
    if ticks > alpha and ticks < June.15
    [ set Water.Temperature 50 ]
    if ticks > June.15 and ticks < July.1
    [ set Water.Temperature 54 ]
    if ticks > July.1 and ticks < October.1
    [ set Water.Temperature 62 ]
    if ticks > October.1 and ticks < October.15
    [ set Water.Temperature 54 ]
    if ticks > October.15 and ticks < omega
    [ set Water.Temperature 50 ]
  ]
  ask patches with [Patch.Type = "water"
  and Watermass.Name = "Lake Superior"]
  [
    if ticks > alpha and ticks < July.15
    [ set Water.Temperature 50 ]
    if ticks > July.15 and ticks < October.1
    [ set Water.Temperature 54 ]
    if ticks > October.1 and ticks < omega
    [ set Water.Temperature 50 ]

  ]
end
to Year.Reset
    set Year.Counter Year.Counter + 1
    if Year.Counter > Year.Length
    [
```

```
      set Year Year + 1
      set Alpha Alpha + Year.Length
      set April.1 ( April.1 ) + ( Year.Length )
      set April.15 ( April.15 ) + ( Year.Length )
      set April.30 ( April.30 ) + ( Year.Length )
      set May.15 ( May.15 ) + ( Year.Length )
      set June.1 ( June.1 ) + ( Year.Length )
      set June.15 ( June.15 ) + ( Year.Length )
      set July.1 ( July.1 ) + ( Year.Length )
      set July.15 ( July.15 ) + ( Year.Length )
      set July.30 ( July.30 ) + ( Year.Length )
      set October.1 ( October.1 ) + ( Year.Length )
      set October.15 ( October.15 ) + ( Year.Length )
      set November.1 ( November.1 ) + ( Year.Length )
      set Omega  Omega + Year.Length
      set Year.Counter 0
    ]
end
to Diffusion
  set Diffusion.Rate 0.3
  ask patches with [ Patch.Type = "water" ]
  [
    let Neigboring.Patches count neighbors
    with [ Patch.Type = "water" ]
    let Diffuse.Material Diffusion.Rate
    * Phytoplankton.Amount
    let Diffuse.Material.per.Patch Diffuse.Material
    / Neigboring.Patches
    set Phytoplankton.Amount Phytoplankton.Amount
    - Diffuse.Material
    ask neighbors with [ Patch.Type = "water" ]
    [ set Phytoplankton.Amount Phytoplankton.Amount
    + Diffuse.Material.per.Patch ]
  ]
end
to Global.Plots
  set Mean.Phytoplankton.Ontario
  mean [ Phytoplankton.Amount ] of patches
    with [ Patch.Type = "water"
    and Watermass.Name = "Lake Ontario"]
  set Mean.Phytoplankton.Erie
  mean [ Phytoplankton.Amount ] of patches
    with [ Patch.Type = "water"
    and Watermass.Name = "Lake Erie"]
  set Mean.Phytoplankton.Huron
  mean [ Phytoplankton.Amount ] of patches
    with [ Patch.Type = "water"
```

```
    and Watermass.Name = "Lake Huron"]
  set Mean.Phytoplankton.Michigan
  mean [ Phytoplankton.Amount ] of patches
    with [ Patch.Type = "water"
    and Watermass.Name = "Lake Michigan"]
  set Mean.Phytoplankton.Superior
  mean [ Phytoplankton.Amount ] of patches
    with [ Patch.Type = "water"
    and Watermass.Name = "Lake Superior"]
end
to Mussel.Shaper
  ask mussels
  [set color black
    set sıze 0.6
    set shape "circle"
  ]
end
to Veliger.Shaper
  ask veligers
  [set color white
    set sıze 0.5]
end
to Veliger.Spawn
  create-veligers Initial.Veliger.Number
  [
  set xcor 40
  set ycor -11
  set color white
  set sıze 0.5
  ]
end
to Veliger.Move
  ask veligers [
    move-to one-of neighbors
    with [Patch.Type = "water"]
  ]
end
to Veliger.Consume
  ask veligers[
    let Veliger.Percent.Exploit
    ( Phytoplankton.Amount * 0.00019
    + (random 21) / 1000000 )
    if Water.Temperature < 62
        [set Veliger.Percent.Exploit
        Veliger.Percent.Exploit]
    if Water.Temperature >= 62
        [set Veliger.Percent.Exploit
```

```
        ( Phytoplankton.Amount * 0.00038
        + (random 41) / 1000000)]
    set Veliger.Collected.Resource
    (Veliger.Collected.Resource
    + Veliger.Percent.Exploit )
    let Veliger.Expenditure
    Phytoplankton.Amount.Global * 0.0001
    set Veliger.Collected.Resource
    Veliger.Collected.Resource - Veliger.Expenditure
    set Phytoplankton.Amount
    Phytoplankton.Amount - Veliger.Percent.Exploit
 ]
end
to Veliger.Mortality
  ask veligers [
  if Veliger.Collected.Resource <= 0
  [die]
  ]
end
to Veliger.Fouling
   ask veligers [
    let Veliger.Metamorphosis.threshold
    Phytoplankton.Amount.Global * 0.1
    if Veliger.Collected.Resource
    > (Veliger.Metamorphosis.Threshold )
        and Watermass.Type = "shore"
    [hatch-mussels 1
     die]
  ]
  Mussel.Shaper
end
to Veliger.Exit
  ask veligers
  [
    if Watermass.Type = "exit"
    [die]
    if Watermass.Type = "huron.exit"
    [ hatch 1 [ set xcor 7 set ycor -27 ]
       die]
    if Watermass.Type = "erie.exit"
    [ hatch 1 [ set xcor 33 set ycor -14 ]
       die]
    if Watermass.Type = "michigan.exit"
    [ hatch 1 [ set xcor 1 set ycor 5 ]
       die]
     if Watermass.Type = "superior.exit"
    [ hatch 1 [ set xcor 1 set ycor 5 ]
```

```
       die]
    ]
end
to Mussel.Consume
  ask mussels[
    let Mussel.Percent.Exploit
    ( Phytoplankton.Amount * 0.002 )
    set Mussel.Collected.Resource
    (Mussel.Collected.Resource
        + Mussel.Percent.Exploit )
    let Mussel.Expenditure
    Phytoplankton.Amount.Global * 0.0008
    set Mussel.Collected.Resource
    Mussel.Collected.Resource
        - Mussel.Expenditure
    set Phytoplankton.Amount Phytoplankton.Amount -
        Mussel.Percent.Exploit
    ]
end
to Mussel.Reproduce
  ask mussels [
    let Mussel.Reproduction.Threshold
    Phytoplankton.Amount.Global
    if Mussel.Collected.Resource >
    ( Mussel.Reproduction.Threshold )
        and Water.Temperature >= 54
    [ set Mussel.Collected.Resource 0
      let Mussel.Hatch.Count random 10
      hatch-veligers Mussel.Hatch.Count]
    ]
  Veliger.Shaper
end
to Mussel.Mortality
  ask mussels [
    if Year.Counter = 10
    [ set Mussel.Age Mussel.Age + 1 ]
    let Mussel.Lifespan ( 3 + random-float 5 )
    if Mussel.Age > Mussel.Lifespan
    [ die ]
  ]
  ask mussels [
  if Mussel.Collected.Resource < 0
  ;;-2 * Phytoplankton.Amount.Global
  [die]
  ]
end
to setup
```

```
    clear-all
    reset-ticks
    Map.Import
    Phytoplankton.Resource.Distribution
    Month.Definitions
    Bloom.Change.Rates
    Veliger.Spawn
    Lake.Names
end
to go
    Phytoplankton.Regeneration
    Bloom.Adjustments
    Temperature.Adjustment
    Year.Reset
    Veliger.Move
    Global.Plots
    Diffusion
    Veliger.Transportation
    Veliger.Consume
    Veliger.Mortality
    Veliger.Fouling
    Mussel.Consume
    Mussel.Reproduce
    Mussel.Mortality
    Veliger.Exit
    Veliger.Introduce
    tick
end
```

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PUBLICATIONS/PRESENTATIONS ON THE THESIS

- Kanmaz O., 2014: Spatial and Temporal Patterns of a Zebra Mussel Invasion: An Individual Based Modelling Study. *International Symposium - Ecology and Evolutionary Biology*, July 12-13, 2014 Istanbul, Turkey.