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Abstract: The family Unionidae (freshwater mussels) is geographically diverse with species found worldwide; their greatest diversity is found in North America. Zebra mussels (*Dreissena polymorpha*) are an exotic species introduced into North America in the 1980's that has since become a threat to economic interests and native mussel species in the region. IIHR-Hydroscience and Engineering and WL|Delft Hydraulics are developing a numerical model of mussel population dynamics for the purpose of analyzing alternative management strategies of zebra mussels and Unionidae in the Upper Mississippi River (UMR). The Mussel Dynamics Model (MDM) simulates interaction of mussels and the hydraulic environment. This paper describes the approach taken in the MDM. Environmental conditions are defined by water quality parameters and using a 3D hydrodynamics model to solve for flow conditions. Incorporated is a habitat suitability index model (HSI) that uses basic rules of species tolerance to various environmental conditions, including host fish distributions. This information along with the biological and ecological characteristics of mussels is used in an individual based population dynamics model that simulates change of stage, competition, feeding and growth, reproduction, dispersal and settlement, motion, and mortality. The MDM has been run on a reach of pool 16 in the Mississippi River with positive results. Food competition between native and invasive species was simulated and the results are in agreement with observed survival rates of unionids reported in the literature. Currently efforts are underway to redesign the model to facilitate portability, to decrease computational time, allow for larger grid sizes, and to develop a user friendly interface. The HSI has been translated into C with an increase in processing speed and the ability to handle millions of grid points, a significant improvement over the original code.

Keywords: freshwater mussels; zebra mussels; individual based; population dynamics, competition;

1. INTRODUCTION

Freshwater mussels of the family Unionidae have a worldwide distribution with their greatest abundance and diversity in North America. There are approximately 300 known species of unionid mussels in the US and Canada, and at least two thirds of these species are listed by the Natural Heritage Network as extinct or possibly extinct, imperilled, or vulnerable [Lydeard et al, 2004]. The combination of over-harvesting, habitat destruction and alteration, and pollution has contributed greatly to the imperilled status of freshwater mussels in North American waterways [Lydeard et al, 2004; Vaughn and Taylor, 1999; Watters, 1996]. Additionally, the introduction of the exotic species of zebra mussel *Dreissena polymorpha* in the 1980's to the Great Lakes region has further contributed to the decline of native mussels—since the 1990's they have spread rapidly into the Upper Mississippi River. Zebra mussels settle on and smother native mussels [Lydeard et al, 2004] and compete with native mussels for food [Baker and Levinton, 2003; Hart et al, 2001] thus contributing further to native mussel decline.

In order to properly manage both native mussel species and zebra mussels in river systems, the interaction between physical habitat conditions and population dynamics of mussel species must be properly understood. Morales-Chaves [2004], working in conjunction with IIHR—Hydroscience and Engineering and WL|Delft Hydraulics, developed a mussel dynamics model in order to assess the effects of habitat modifications and zebra mussels on native mussel species in the Upper Mississippi River.

The mussel dynamics model (MDM) continues to be developed for several purposes. (1) In order to improve understanding of the population dynamics of mussels for predictive estimates of future populations; (2) to determine important parameters in the assessment of habitat suitability of native mussels with an emphasis on hydrodynamic conditions; (3) to create a tool for the assessment of potential effects of environmental stressors on native mussel populations; and (4) to evaluate the impact of zebra mussels on native mussel populations.

The general structure of the model is described herein along with a brief description of the model components. This paper focuses on the results of simulated food competition between zebra mussels and the threeridge mussel (*Amblema plicata*), the most abundant native mussel species in the Upper Mississippi River [Hornbach et al, 1992]. Results are in agreement with observed survival rates of unionids reported in the literature. Additionally, further development of the model is discussed.

2. MODEL COMPONENTS

The conceptual framework of the model is shown in Figure 1. Environmental conditions are used as input to a habitat suitability index model. The population dynamics processes simulated for native mussels and zebra mussels are indicated in the diagram with dotted arrows. Competition between zebra mussels and native mussels occurs during the growth process and is indicated with a bi-directional arrow.

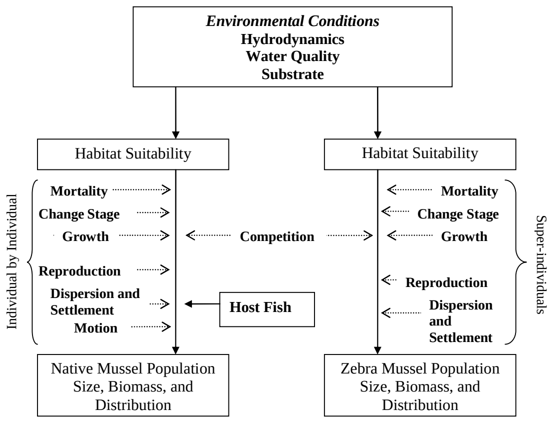

Figure 1 Conceptual framework of the model

2.1 Environmental Conditions

The environmental conditions are defined independently of the population dynamics component of the model. A water quality module defines the temperature, food concentrations, and other relevant substances in the flow. A host fish module defines the probability of the presence of host fish—on which the parasitic larval stage of native mussels depends—within the domain and is critical to native mussel survival and dispersion. The physical characteristics of the flow are defined in the hydrodynamics module. The domain is modelled in three dimensions, and the 3D hydrodynamics equations are solved within the domain (see section 3.2). Taken together, along with the relevant information on mussel biology, these three modules are used to create a habitat suitability score with the use of a Habitat Suitability Index model (HSI).

2.2 Habitat Suitability

The determination of suitable habitat areas is a question of importance in ecology independent of population dynamics modelling. The successful prediction of areas that are potential sites for mussel bed formation is of vital interest in managing river systems for native mussels. Habitat suitability for native mussels depends on the physical conditions of the local environment. The properties of the flow in three dimensions must be accurately modelled in order to determine the physical characteristics important to mussels, such as near bed velocity, bed shear stress, substrate, bed mobility, water depth, and the intensity of turbulent fluctuations. Mussel tolerances are taken from the literature and used in conjunction with the physical flow characteristics to determine areas (or cells within the domain) that are suitable for mussels to survive using a spatially explicit approach.

2.3 Population Dynamics

The core of the MDM is an individual based model for the analysis of population dynamics. Individual based modelling approaches [see DeAngelis and Gross, 1992] have been effectively used in ecological modelling and ecohydraulics [Mynett and Chen, 2004; Chen et al, 2002]. The MDM simulates mussel population dynamics including change of stage, competition, feeding and growth, reproduction, dispersal and settlement, motion, and mortality. Zebra mussels are modelled using a super individual approach [Sheffer et al, 1995]. This approach is used for zebra mussels due to the large population sizes, densities, and short life span (2-3 years) for this species in order to reduce computational time.

3. MODEL APPLICATION

The MDM is applied to a reach of pool 16 in the Upper Mississippi River (Figure 2) at the location of the Lucille A. Carver Mississippi Riverside Environmental Research Station of The University of Iowa. The reach is approximately 10 km in length.

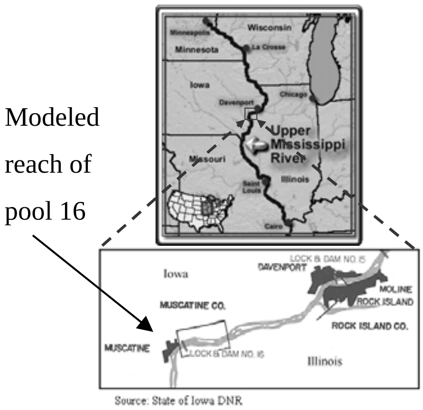

Figure 2 Pool 16 of the Upper Mississippi River borders Iowa and Illinois [Source: State of Iowa DNR; USGS, UMESC].

A 3D mesh of the river channel consisting of approximately 1.5 million grid points was created using Gridgen®. Bathymetric data were collected by IIHR using a single-beam echosounder synchronized with a differential GPS receiver and deployed from a 5.5-meter Jonboat. The 3D hydrodynamics equations are solved over the domain, independently of the MDM. The Reynolds-averaged Navier-Stokes equations are solved over the domain using U2RANS [see Lai et al, 2003a, Lai et al, 2003b, and Huang et al, 2002]. Upstream boundary conditions are given as a velocity field distributed over the cross-section. Velocity data were collected by IIHR using a RD Instruments, Inc. 1200 kHz Rio Grande acoustic Doppler current profiler (ADCP). The 3D solution of hydraulic parameters are depth averaged and interpolated onto a planiform 2D mesh of the river—consisting of approximately 70,000 grid points—that is used in the MDM [Young et al, 2005].

Six steady state solutions were obtained covering a range of 1.1% to 98.4% of the daily average flow and a maximum return period of 4.2 years in order to represent seasonal flow variation. Data on flow is obtained from the USACE Lock and Dam 16. Modelled flow rates are 566.4, 1132.7, 2038.8, 2831.7, 3964.4, and 5663.4 m^3s^{-1}. The only water quality parameter considered in this application is water temperature obtained from the USGS Long Term Monitoring Program (LTMRP). Food concentrations are obtained from USGS LTMRP data taken at Bellevue, Iowa. The host fish module is limited to an all or nothing approach where the probability of presence is either 0 or 1 depending on whether or not fish were reported in the area (data are obtained from a USACE resource inventory). Improvements to the host fish module are an area for further research.

Morales-Chaves (2004) has run the MDM using the steady state solutions from the hydrodynamics model for the corresponding flow rates to assess changes in suitable mussel habitat areas within the river reach. Additionally, the model was run under various conditions to test the sensitivity of many parameters on native mussel (*Amblema plicata)* and zebra mussel population dynamics [see Morales-Chaves, 2004 and Morales et al, 2006 for details]. In both cases the results show a qualitative agreement with observed data and that the MDM is a useful tool for these purposes. However, given the scope of this paper, only the results from the simulated effects of food competition between zebra mussels and native mussels are presented.

3.1 Feeding and Growth

Mussel feeding and growth is based on filtration rate (F) which is given by

$$F = GR * f(T) * f(F) * ff \qquad (1)$$

where GR is the carbon filtration per unit carbon mass of mussel soft tissue per day, $f(T)$ is the dependency of grazing rate with temperature that is in the form of a Gaussian function, $f(F)$ is an assumed dependency of grazing rate with food availability with values between 0 and 1, and ff is the effective food fraction available to mussels as discussed below. Mussel growth is calculated using the following bioenergetics model.

$$B_2 = \left(1 + AE * IE * F * \Delta t\right) * B_1 \qquad (2)$$

where B_1 and B_2 are mussel biomass at t and t+1, respectively, AE is the assimilation efficiency (0.4), IE is the ingestion efficiency (0.33), and Δt is the time step (5 days).

In times of food shortage some mussels may not filter food but still respire leading to loss of biomass, given by

$$B_2 = \left(1 - R * \Delta t\right) * B_1 \qquad (3)$$

where R is the respiration rate and is dependent on water temperature. Food competition is simulated by providing a feeding order. If a mussel surpasses its starvation mass it dies.

3.2 Food Competition

It is been experimentally confirmed that native mussels compete with zebra mussels in the Hudson

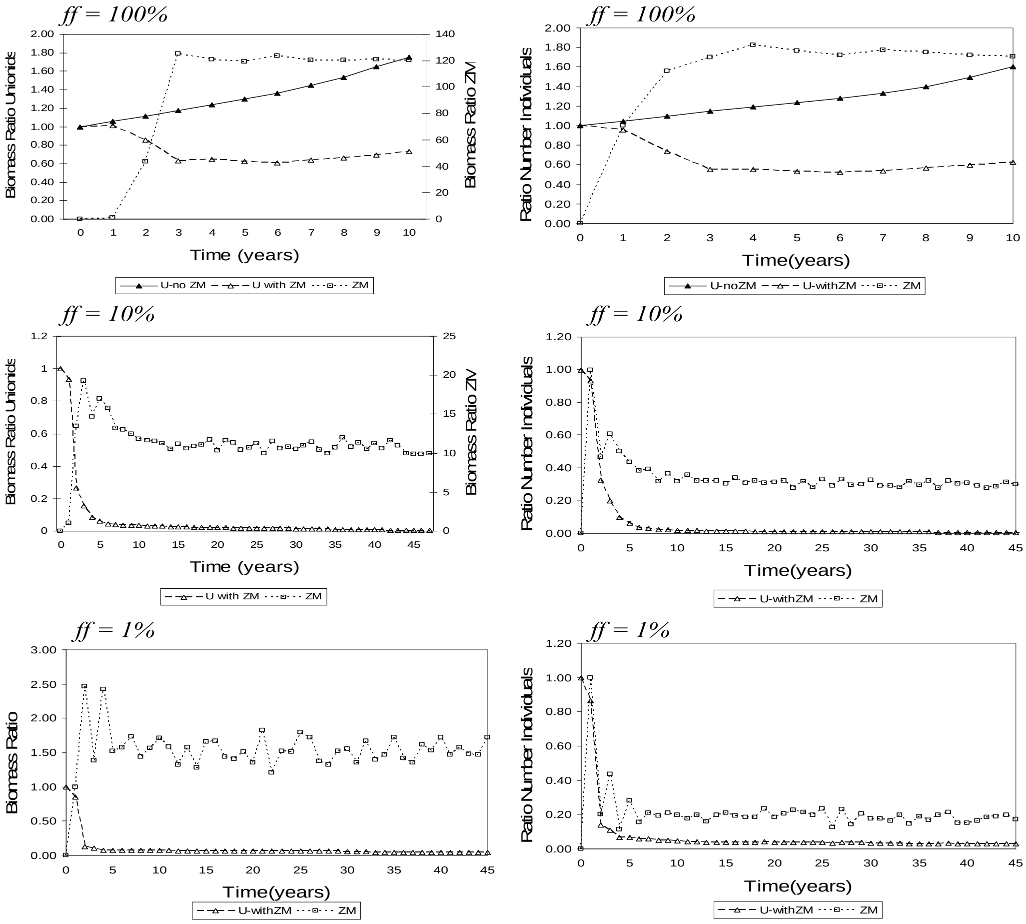

Figure 3 Simulated biomass of unionid mussels (*A. plicata*) and zebra mussels as a result of food competition between the species [from Morales-Chaves, 2004].

River [Baker and Levinton, 2003; Stayer and Smith, 1996], and there is little reason to doubt that this is the case elsewhere. Therefore food competition between these species of mussels represents an important parameter in understanding mussel population dynamics.

The impact of zebra mussel invasion on native mussels (*Amblema plicata*) is examined by testing three cases where the fraction of food available for mussels feeding (*ff*) is different: *ff* = 100%, *ff* = 10%, and *ff* = 1%. In each case, Unionid mussels are initially introduced into the domain as juveniles in suspension and allowed to settle to the river bed. The MDM is run over a simulated time of 60-140 years, without zebra mussels to allow for a population of native mussels to become established within the model domain. Zebra mussels are introduced into the domain as veligers in suspension, so the initial population number is 0. Zebra mussels disperse with the flow and quickly establish in large numbers, which has been seen in nature [Hart et al, 2001].

3.3 Results

Figure 3 shows the results of food competition between zebra mussels and native mussels from the time of zebra mussel introduction, year 0. Zebra mussel results are shown as the ratio of biomass (total number of individuals) in year t to biomass (total number of individuals) in year 1. Unionid results are shown in terms of the ratio of biomass (number of individuals) at year t to initial biomass (number of individuals) at the time of zebra mussel introduction (year 0).

In the case where *ff* = 100%, the introduction of zebra mussels causes a decline in native mussel biomass to 40% of the population in the absence of zebra mussels after a simulated 10 years. The long life span of *A. plicata* allows for continued increase in biomass as the mussels grow without an increase in the total number of individuals. Whereas the short life span of the zebra mussels leads to a relative balance between the number of individuals and total biomass over time.

In the case of *ff* = 10%, zebra mussels are introduced and the model is run for an additional 45 simulated years. Both populations suffer from some food shortage. The initial invasion of zebra mussels causes an immediate sharp decline in native mussel biomass followed by a steady decline for the remainder of the simulation. Zebra mussels appear to establish a stable total biomass while native mussel biomass is still in decline at the end of the simulation period.

In the final case, *ff* = 1%, zebra mussels are introduced and the model is run for an additional 45 years. As in the case where *ff* = 10%, there was an immediate sharp decline in the native population followed by a slow but steady decline in the native mussel population over the simulated period. Again, in contrast, the zebra mussel population seems to reach a stable state.

3.4 Discussion

The results of simulated food competition approximate empirical results obtained by Hart et al [2001] for *A. plicata* Lake Pepin in the Mississippi River, Minnesota, where experiments are done 5-9 years after initial zebra mussel invasion. Simulated survival rates of *A. plicata* with the MDM ranged from around 75% to 90% by the end of the simulation. Hart et al [2001] reports survival rates of *A. plicata* ranging from 65% to 90% in cases of high to moderate levels of zebra mussel infestation.

Additionally the simulated results show that *A. plicata* can survive zebra mussel invasion which is in agreement with observations made in the Hudson River [Strayer et al, 1999]. However, the MDM is limited since the model considers only food competition and does not account for other important interactions or potential effects. For example, zebra mussels may inhibit native mussel movement by attaching to native mussels that could increase energetic costs and native mussel mortality. Furthermore, the effects on native mussel fertilization are unknown, and the simple reduction in space from zebra mussels is not taken into account.

4. WORK IN PROGRESS

The original version of the MDM—not including the hydrodynamics modelling—is written in Matlab®. While Matlab is a powerful tool in many statistical and engineering applications, offering many intrinsic functions that make coding easier (such as matrix inversion), for more involved applications it tends to be slow. Additionally, the current state of the code is not user friendly and, therefore, can be difficult to run. It is more efficient to take the basic concepts and processes in the MDM and begin anew with an approach towards portability, speed, modifiability and usability.

The 3D hydrodynamics model with 1.5 million points requires several days to run, and this time is not affected by any changes in the MDM. However, in order to assess the issue of computational time and grid size handling capabilities the HSI module is translated from Matlab into the C programming language. With the translation into C, the decrease in computational time was significant with a run time of 60-90 minutes using Matlab to a run time of approximately 3 minutes. In addition to the decreased runtime, the size of the computational domain that can be handled by Matlab in a reasonable amount of time is on the order of 10^5 grid points. The C version of the program can be run on grids sizes on the order of magnitude of 10^6 grid points, again a significant improvement.

Given the nature of the physical processes being modelled it seems a better approach to use an object-oriented language to rebuild the model. As of this writing the conceptual model building stage is being revisited in order to develop the software in manner that results in portable, fast, and easily modifiable code. Model architecture is under development and class, object, and process definitions are being outlined.

5. CONCLUSIONS

The original version of the MDM has been developed and tested by Morales-Chaves [2004] and the results were found to be in agreement with observed data on mussel bed location, size, and food competition with zebra mussels with the latter discussed above. Zebra mussels can potentially establish themselves rapidly and have a significant effect on *A. plicata* populations by reducing population size and total biomass.

The updated version of the model will be verified with the existing trial model runs, and it then will be subject to further validation and confirmation. Additionally, since the hydrodynamics, water quality, and host fish modules are independent of the MDM, there is the need and desire to create interfaces with existing hydrodynamics and water quality models, such as Delft3D, FLUENT, or any such model. Such interfaces would facilitate the update of important hydraulic parameters according to time of year and for event based effects. It would also allow for workers using software such as Delft3D to integrate the MDM into their own modelling work.

The potential also exists for MDM to be interfaced with other existing models, such as rainfall-runoff watershed models, in order to provide a further link to terrestrial processes affecting river systems. The development of a user friendly interface will allow for the model to be used more easily by scientists, engineers, and technically proficient managers to assess potential impacts on native mussel population dynamics and the effects of zebra mussel invasions.

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