A model to understand population decline of the Devil's Hole pupfish (Cyprinodon diabolis) and support habitat management decisions

Yuri V Graves
University of Nevada, Las Vegas

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A MODEL TO UNDERSTAND POPULATION DECLINE OF THE DEVIL'S HOLE PUPFISH (CYPRINODON DIABOLIS) AND SUPPORT HABITAT MANAGEMENT DECISIONS

By

Yuri V. Graves

Bachelor of Science
Edinboro University of Pennsylvania
1990

Master of Science
Ohio University
1993

A thesis in partial fulfillment
Of the requirements for the

Master of Science Degree in Environmental Science
Department of Environmental Studies
Greenspun College of Urban Affairs

Graduate College
University of Nevada, Las Vegas
May 2004
The Thesis prepared by

YURI V. GRAVES

Entitled

A MODEL TO UNDERSTAND POPULATION DECLINE OF THE DEVIL'S HOLE PUPFISH
(CYPRINODON DIABOLIS) AND SUPPORT HABITAT MANAGEMENT DECISIONS

is approved in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE IN ENVIRONMENTAL SCIENCE

Examination Committee Chair

Dean of the Graduate College
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ABSTRACT

A Model to Understand Population Decline of the Devil’s Hole Pupfish (Cyprinodon diabolis) and Support Habitat Management Decisions

by

Yuri V. Graves

Dr. Krystyna Stave, Committee Chair
Professor of Environmental Studies
University of Nevada, Las Vegas

After intensive efforts in the 1970s to stabilize the water level in Devil's Hole, the population of the Devil's Hole Pupfish showed slight but steady increase from the 1970s until the mid-1990s when the population began a steady decline. In this study I developed a system dynamics model to help the Devil’s Hole Pupfish Recovery Team understand the recent decline and identify and test potential management strategies and policies to reverse or stop the decline. The model and modeling process was used to identify critical gaps in existing data. Tests simulating pore space manipulation, algae removal and addition of refugia fish resulted in long-term population growth but not quick, short-term changes.
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ACKNOWLEDGMENTS

I thank God for giving me the opportunity to serve in the U.S. Coast Guard and to attend the University of Nevada Las Vegas. I sincerely thank my wife, Maggie, and my two sons, Reino and Austin, for their incredible support, understanding and love during this entire process.

I also thank my thesis advisor, Dr. Krys Stave. Her initial course in System Dynamics hooked me. Her guidance and patience made this entire process enjoyable and educational. I thank Dennis Bechtel, Amanda Brandt, Mike Dwyer, and Josh Hoines for participating in the initial stages of this project.

I would also like to thank Dr. James Deacon and members of the Pupfish Recovery Group and Modeling Group for their expert insight into the complexities related to the Devil’s Hole Pupfish and active participation in the modeling effort. Dr. Deacon truly served as the inspiration for this project.

Finally, I would like to thank the remaining members of my thesis committee, Dr. David James and Dr. David Hassenzahl, for their patience and guidance.
CHAPTER 1

PROBLEM STATEMENT

An Endangered Species

This thesis describes the development and use of a system dynamics simulation model to understand the recent decline in the population of the Devil's Hole Pupfish and to identify and test potential strategies and policies to reverse or stop the decline. Devil's Hole, a water-filled cavern that forms a skylight into the regional aquifer of Ash Meadows, Nevada, was designated as part of the Death Valley National Monument in 1952. Large-scale land development and aquifer pumping in the area surrounding Devil's Hole in the 1950s and 60s led to declining water levels in Devil's Hole in the late 60s reaching its lowest level in September 1972. This decline in water level corresponded to a dramatic decrease in the Devil's Hole Pupfish population. In 1970, a Pupfish Task Force and the Desert Fishes Council were established to address issues related to the endangerment of the Devil's Hole Pupfish. Successive decisions by the U.S. District Court of Nevada,
the 9th Circuit Court of Appeals, and the U.S. Supreme Court resulted in the designation of a minimum water level in Devil's Hole. These efforts not only stabilized the population of the Devil's Hole Pupfish, but also helped build support for the Endangered Species Act of 1973. The Devil's Hole Pupfish was one of the first fishes to be listed as an endangered species (Anderson & Deacon, 2001). Based on these early and intensive habitat protection efforts, the pupfish population showed a slight but steady increase from the 1970s until the mid-1990s.

The Devil's Hole Pupfish has again become a focal point for policy managers, however. Since 1995, the population has seen a sharp and sustained decline (Figure 1). While the risk of extinction has been lowered by a successful refuge program, the protection of the native population in its native habitat is essential to long-term survival, since the long-term effects of refuge environment on the evolutionary trajectory of the species is not entirely understood (Baugh and Deacon, 1988), and would almost certainly be different than the trajectory occurring in Devil's Hole. The U.S. Fish and Wildlife Service, under provisions of the Endangered Species Act, has appointed a Recovery Team consisting of federal, state and educational agency representatives charged with formulating management
Figure 1: Reference mode for Devil's Hole Pupfish population 1972-2003. Trends show a gradual increase from 1972 until the mid-1990s when a steep decline in the population begins. Data points represent annual maxima and minima.

recommendations likely to reverse the downward trend in the population. The Team has limited information about the system as well as limited resources for data collection. Their monitoring and management efforts must be carefully
targeted. The Team needs to answer the following questions:

What, if any management actions might be effective in reversing the recent population decline?

Given limited resources, what would be the most important focus for data collection to help understand the system better?

The team requested help in answering these questions. A subgroup of the Recovery Team, the Pupfish Modeling Group, was created to serve as expert advisors on this project. The group is composed of members from the University of Nevada, Las Vegas, Southern Oregon University, the U.S. Fish and Wildlife Service, the National Park Service and the Nevada Division of Wildlife. The focus of this group, and my study, is the development and use of a system dynamics model to help the Modeling Group and Recovery Team:

1) understand the reasons for the population decline,
2) help find habitat management levers that can reverse the population decline, and
3) identify critical parameters that should be monitored to anticipate future population changes.
CHAPTER 2

APPROACH

Appropriateness of System Dynamics

System dynamics modeling is the tool I have chosen to help understand the causes of population decline of the Devil's Hole Pupfish and to test potential management strategies. System dynamics is a methodology for addressing dynamic problems. Unlike other computer models that may focus on optimization issues, system dynamics addresses a specific, problematic behavior that changes over time (Richardson and Pugh, 1999). It focuses on causal relationships and examines feedback in complex systems where one attribute not only affects other attributes but is itself, affected by those other attributes (Sterman, 2000).

In most cases, one cannot perform tests on actual systems because of potential negative effects on that system. It is therefore useful to be able to conduct tests on a system through a system dynamics model. Once causal relationships between variables that represent real-world
components of the system are established, mathematical
equations are formulated and entered into the model. This
mathematically-based computer simulation model is then used
to try to replicate the behavior of the real-world system
(Ford, 1999). It can then be used to test different
hypotheses for rectifying the problematic behavior without
any risk to the actual system.

A fundamental principle of system dynamics is that the
structure of the system, whether it is industrial,
biological, etc., determines the behavior of the system
(Ford, 1999). This premise requires that modelers extract
the essential components of the real world system and
include them in a system dynamics model. This
understanding of components can be developed through
consultation with interdisciplinary stakeholders. System
dynamics models can appeal to a wide range of stakeholders
because of the interaction required to develop most models.
The result is an increase in knowledge of the system and
better understanding of feedback and variable relationships
by all. These models reduce the necessity of constraints
on assumptions, and introduce the important aspect of
feedback and nonlinearity which are inherent in many
ecological systems (Ford, 1999). Ecologists, and others,
can represent the behavior of a system and begin to
understand how variables and other parameters effect change within the system. Furthermore, even when values of parameters are unknown or uncertain, the ecologist can test a range of values or approximations within the model.

Each model has boundaries and for some projects those boundaries restrict the nature of the model to the question at hand. A modeler may want to address a particular problem related to a specific species but some variables will not be included because they are not directly involved in answering the final question. The model is created to address a specific problem or question. It is that question that determines the boundaries of the model.

System Dynamics models seem to lend themselves very well to ecological problems. Biological systems and entities have many intertwined mechanisms that are not easily discernable. System dynamics allows ecologists, biologists and resource managers to increase their understanding of a biological system and its related ecological problem. System Dynamics is a structured framework for defining variables and processes within the system (Richardson and Pugh, 1999). The modeling process will inevitably lead to a better understanding of the system and to potential feedback mechanisms within the system. This sharing of knowledge and expertise can only
improve the overall modeling process. This process also helps to develop and test hypotheses about management strategies and potential policy decisions prior to actual implementation. The main drawback is that it takes time to engage stakeholders and develop and use the model. Some stakeholders may be directly opposed in their ideas or mandates for management which can also present challenges.

System Dynamics for this project

The variables and relationships related to the population decline of the Devil’s Hole Pupfish are well-suited for a system dynamics model. There are some aspects of the Devil’s Hole Pupfish that are relatively well understood such as egg viability, egg development and the maturation process. Other variables such as algae, pore space and dissolved oxygen are not as well understood but can be represented in a system dynamics model because their causal relationships are known. Values for these uncertain variables can be tested over a wide range in an attempt to replicate the behavior of the actual system and better understand the specific variable.

Previous models of aquatic species have shown some success in defining complex biological problems. Aggarwal (1991) successfully modeled an aquatic species that had
similar assumptions and basic concerns related to the
dlarval life stage. This study focuses on the egg and larval
stages as potential determinants of adult populations
through habitat changes. Steinberg (1986) represents the
essence of successful modeling where established methods
and paradigms are verified or are cast aside when
counterintuitive methods prove to be viable solutions.

Systems dynamics also lends itself well to this
stakeholder project. It provides a forum for discussion,
confirmation of data and insights into the system that will
help focus future research and monitoring.

System Dynamics

System Dynamics was conceptualized by Jay Forrester
and first described in his landmark publication entitled
Industrial Dynamics (1961). Forrester began to examine the
effects of non-linear relationships and feedback loops to
address problems in industrial systems. Forrester (1969)
continued his application of system dynamics in Urban
Dynamics where he applied his modeling techniques to the
problem of low-income housing and population fluctuations
within major cities. System dynamics began to be applied
to environmental concerns with the publication of The
Limits to Growth (Meadows et al., 1972) which addressed the
problems of pollution, population growth, natural resource usage and food production in a "World Model." Limits to Growth sparked major debate around the world regarding our attempts to reach equilibrium between the costs of development and ecological sustainability.

System dynamics has grown from Forrester's original concept to a broad international discipline that is applied to a spectrum of topics. It is taught from kindergarten to college level and beyond. The key to system dynamics is the idea that people often try to fix systems using "leverage points" (Meadows et al. 1972) that are seemingly readily apparent. The problem is that most of those leverage points are not the components that effect positive change on the system. "All too often, well intentioned efforts to solve pressing problems lead to policy resistance, where our policies are delayed, diluted or defeated by the unforeseen reactions of other people or nature. Many times our best efforts to solve a problem actually make it worse" (Sterman, 2000). Sometimes the most effective leverage points are counterintuitive and may only be understood once a problem is represented in a system dynamics model.

Rowell et al (1997), describe system dynamics as the study of dynamic or time-varying behavior of a system.
through the development and use of a computer simulation model. Ford (1999) describes eight steps to the modeling process. The first step is to "get acquainted with the system" and the people that will be involved in the process. You must know the stakeholders and the real decision-makers and whether system dynamics is applicable to the problem.

The second step is to "be specific about the dynamic problem." You must be able to draw a graph of the problematic behavior of your variable of interest as it changes over time. This is known as the "reference mode." This shows the problem that you are attempting to address and is arguably the most essential step in the modeling process.

Steps 3 and 4 are interchangeable and the order is determined by the preference of the modeler. In step 3 the modeler constructs a "stock and flow diagram" which outlines your variable of interest and other associated variables and describes their relationships. Some are stocks, or accumulations, and some are flows, which represent inflows and outflows to the stocks. Other variables, called constants, or auxiliaries, connect to stocks and flows.
Step 4 is "drawing the causal loop." This requires a conversion of the stock and flow model to a representation of the system as positive and negative feedback loops. Step 5, "estimating the parameter values", requires the modeler to use "all sources of information at your disposal." This may involve intense research of professional publications, previous lab experiments, government studies, and consultation with experts/stakeholders.

Step 6, "running the model to get the reference mode" is the initial "test" of the model and whether it represents the actual behavior of the system as described in the reference mode (step 2). Conducting sensitivity analysis, step 7, involves running the model and determining which variables, when changed, alter the output of the model. The model will be more "sensitive" to some variables, especially those that may have some uncertainty as to their value, and less sensitive to others. A model is more robust when it generates the same general pattern despite the great uncertainty in parameter values.

The final step, step 8, is "testing the impact of policies." Variables that can be changed by decision-makers and implemented through changes in policy should be tested through numerous runs of the model. The purpose is
to determine whether the policies being tested result in the "desired changes" in the behavior of the system.

Stave (2002) examined the potential for a system dynamics model to facilitate public understanding and stakeholder participation in a project related to water management options in Las Vegas, Nevada. Stave described six steps to the system dynamics modeling process: 1) Define the problem, 2) describe the system, 3) develop the model, 4) build confidence in the model, 5) use the model for policy analysis and 6) use the model for public outreach. This study incorporates the first five steps of this process and iterates between steps two and five as stakeholder participation and knowledge of the system increased.

Literature Review

System Dynamics has been applied to several aquatic organisms including zebra mussels, cod, clams, and salmon. Zebra mussels are an aquatic nuisance species that were introduced into the Great Lakes through ballast water from large commercial ships. Aggarwal (1991) used system dynamics to model the population of the zebra mussel in the Illinois River and assess the future survivability of the species through distribution of larvae. This study enabled
decision makers to understand many aspects of this growing problem such as movement of larvae and potential survival rates in new areas. The study showed that initial populations of zebra mussels and larvae had no significant impact on long-term populations. Larvae movement due to biological and hydrological processes was a key component in understanding long-term population trends. This study also determined that lack of information regarding dissolved oxygen, water velocities and water chemistry needed to be addressed by future research. Gaps in the data and variable relationships became readily apparent and focused future research.

Similarly, Hannon et al (2001) used a system dynamics model to understand the population dynamics of the zebra mussel in an attempt to better understand this aquatic nuisance species. The system dynamics modeling process brought together numerous stakeholders and focused them on the specific problem of zebra mussels. This process also helped managers gain consensus on potentially key information that was needed for future evaluation but was not available at the time of the study.

Steinberg (1986) addressed the sharp decline in New York’s hard clam fishery by developing a system dynamics model. Her model, CLAM4, consisted of three sectors:
clams, natural predators, and the baymen who harvest the clams. Six management alternatives, based upon current shellfish management practices, were evaluated using the model resulting in "largely unanticipated" results. Current practices, which include hatchery manipulations and restrictions on time and amount of catch, did not resolve the problem. However, the model showed that an increase on the allowed catch and bounty of predators proved to stabilize the population. This practice is not typically used by fishery managers but proved effective in this case. Without the feedback from the system dynamics model, this management action would not have been considered.

Olson (1985) used a system dynamics model to assess the harvesting of Atlantic salmon with respect to distant and home water fishing areas near Greenland and the Faroe Islands and its impact on the overall fish population. The model encompassed the complex life cycle of the salmon and economic influences. Olson (1985) tested potential management practices such as catch limits and gear restrictions and found them to be adequate for preserving the home fisheries at least in the short term. It was also shown that both home and distant fisheries could be maintained if severe catch restrictions were put in place until the species numbers grew to five times the size of
the present population. Previously, it was thought that both fisheries could not be maintained because of the cost to home fishery populations. If managers and fishermen could sacrifice during the short term, the result would be a sustained, greater catch and long-term revenues.

Ruth and Wormley (1996) developed a system dynamics model that investigated the interactions of three demersal fish species (Atlantic Cod, Haddock and Pollack) on the Georges Bank. Ruth’s (1996) study tested proposed management options such as quotas and seasonal restrictions, and has shown that alternative, or uncommon, management strategies, such as fishing “effort” controls, net mesh size reductions and advances in technology (boats, gear, etc.), seem to be necessary to prevent collapse of the fisheries. System dynamics modeling was again the key component in understanding the dynamic population problem and when necessary, being able to step outside firmly established paradigms and test hypothetical strategies.

Stakeholder Involvement

An important decision modelers have to make is to what extent to involve stakeholders. Being an interdisciplinary endeavor, system dynamics modeling could include stakeholders such as resource managers from various
government agencies, politicians, scientists, and private citizens. The modeler can involve stakeholders in the actual development of the model or they could act as consultants to the overall project. In order to increase confidence in the model, stakeholders could be involved early in the process. Stakeholders who do not participate in the early stages may not fully trust the model and its assumptions or its results (Ruth and Lindholm, 1996). They may not buy into management practices or policies developed with the model. Participatory and transparent modeling approaches are essential and result in improved science and policy decisions (Ruth and Lindholm, 1996). Stakeholder participation provides a method for bridging the gaps between various interdisciplinary experts or scientists and policy makers and the general public (Costanza and Ruth, 1998). Consensus building and continued dialog between participants is inherent in the modeling process and serves as a key component to the overall success of the modeling effort and the solution to the problematic behavior.
CHAPTER 3

SITE/SPECIES DESCRIPTION

Study Area

Approximately 100 miles northwest of Las Vegas, Nevada, exists "the smallest vertebrate habitat known to contain the entire population of a species" (Riggs and Deacon, 2003). Devil's Hole is a "disjunct part of the Death Valley National Park" in Ash Meadows, NV (Figure 2). The cavern was created about 60,000 years ago when the roof of an underground fissure collapsed, creating an opening to the surface (Figure 3) (Riggs and Deacon, 2003). The opening is approximately 15 feet wide and 40 feet long and the water depth is unknown, but greater than 400 feet (Figure 4). It is the only natural habitat for the Devil's Hole Pupfish (Cyprinodon diabolis). The Devil's Hole Pupfish exist in the uppermost reaches of the cavern and spawn on a shallow limestone shelf. Scuba divers, conducting pupfish fish counts, have witnessed pupfish to a depth of 100 feet.
Figure 2: Ash Meadows, NV and Devil’s Hole (Courtesy of Devil’s Hole Pupfish Recovery Team).
Figure 3: View of Devil’s Hole (Courtesy of Devil’s Hole Pupfish Recovery Team).
Figure 4: Profile of Devil’s Hole complex with location of spawning shelf (Adapted from Soltz and Naiman, 1978). The dotted area represents the maximum range of the Devil’s Hole Pupfish within the cavern (approximately 26 meters from the surface and spawning shelf).
The spawning shelf is a block of bedrock that has collapsed into Devils' Hole and covers an area approximately 2.8 meters wide and 5.8 meters long. Its submerged area is the only known spawning area for the Devil's Hole Pupfish (Figure 5). The inner shelf, as defined by Gustafson (1998) is the most productive area. Productivity decreases from the inner to outer shelf areas.

![Figure 5: View of the spawning shelf (Courtesy of Devil's Hole Pupfish Recovery Team).](image-url)
Morphology and Biology

According to Soltz and Naiman (1978), the Devil’s Hole pupfish probably has been isolated longer than any other Death Valley System pupfish. A reasonable estimate is 10,000 to 20,000 years, though Riggs and Deacon (2003) suggest that isolation could have been as much as 60,000 years ago. They demonstrate that there has been no known surface water connection throughout the intervening 60,000 years that would have allowed colonization. Riggs and Deacon (2003) further state that the Devil’s Hole Pupfish has undergone significant evolutionary change during this long period of isolation and is remarkably distinct from its closest relative, the Amargosa pupfish. It is the smallest of some 25 species of pupfish, rarely exceeding 2.5 cm in length, and has retained a number of features (large head and eye, long anal fin, reduced pigmentation) characteristic of juvenile pupfish. Pelvic fins are completely lacking, as are vertical bars in either males or females (Figure 6). Females lack the ocellus on the dorsal fin. Breeding males become solid silver-blue and show the characteristic black terminal band on the caudal fin (Soltz and Naiman, 1978). Younger fish tend to look like females.

Dr. Kodic-Brown of the University of New Mexico, reports that Devil’s Hole Pupfish uses a consort-pair
breeding system in one male will follow closely behind an egg-bearing female. The two will stay paired for up to an hour with aperiodic descents to the bottom for spawning. Peak spawning occurs between the months of April and June but can occur all year long due to the near constant environment of Devil’s Hole. The males do not exhibit territorial behavior or aggressive tendencies. This is in contrast to other pupfish. The Devil’s Hole pupfish is omnivorous. It eats algae and detritus in the substrate.
Figure 6. Drawing of the Devil's Hole Pupfish, Male above (2.7 cm), female below (2.3 cm) (adapted from Soltz and Naiman, 1978).
Problem Definition

The first step in the system dynamics modeling process is to identify one or more key variables whose behavior over time defines the problem. Figure 1 shows the annual maximum (summer) and minimum (winter) population sizes of mature Devil's Hole pupfish from 1972 to the present. The numbers were generated from actual counts by divers in Devil's Hole. These counts attempt to include all adult pupfish greater than twelve millimeters in length. The data were provided by the U.S. Fish and Wildlife Service, the National Park Service and Dr. James Deacon, University of Nevada, Las Vegas. From 1972 to approximately 1995, trend lines fitted to the data show a steady population increase and then a sharp decline.

The result of intensive habitat management can be seen on the graph as the population increases in the first few years after implementation of legally imposed controls on groundwater pumping. The population grows slowly but
steadily for nearly 20 years. The decline that inspired this analysis appears to have started in the mid-1990s. Figure 1 serves as the problem description, or reference mode graph for this modeling project. The purpose of the project is to explain why the population decline occurred and to identify and test policy and management options for reversing the decline.

System Description

The system generating the dynamics of the Devil’s Hole Pupfish population has its basis in a generic population model in which population increases by births and decreases by deaths. The generic model, or causal loop diagram, represents the hypothesis about what is causing the problematic behavior. It is dominated by one positive and one negative loop. The positive loop portrays the reproductive and maturation process, ultimately ‘producing’ more mature pupfish. Absent any stabilizing forces, this loop would result in exponential growth of the pupfish population. As in other population models, the negative loop causes the stabilization of the population as mature fish die. Figure 7 shows the generic model adapted to represent pupfish.
This model was a starting point for explaining the decline in the adult pupfish population. Pupfish experts believe the cause of the decline was not likely related to a higher mortality rate of mature fish. Rather, their working hypothesis had been that the population was declining because of an increase in mortality rate of eggs.
and larvae. Accordingly, the focus turned in the direction of understanding what variables affected the hatch and survival rates of eggs and larvae. It is thought that habitat-related variables are the key to understanding the problem and require further explanation. Some of these habitat variables (Figure 8) that have been further defined are: (1) the effects of algal growth on larvae and eggs, (2) the effects of temperature and dissolved oxygen on eggs and larvae, and (3) the effects of sedimentation on available interstitial space in the substrate of the spawning shelf on eggs and larvae. Most of these variables directly impact the hatch rate on all areas of the spawning shelf and affect hatch rate in the model.

Figure 8: Habitat variables that change hatch rate.

Hatch Rate = f (algae, water temperature, dissolved oxygen and pore space).

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Figure 9 (in pocket) represents the final causal loop diagram. Its basis is the generic causal loop diagram representing pupfish births and deaths (Figure 7). In this final version, changes in hatch rate are examined through habitat changes. The spawning shelf within Devil's Hole can be affected by algae coverage, water temperature in relation to dissolved oxygen, and the amount of pore space available to eggs and larvae in the substrate. All of these factors can either decrease or increase the habitat available to eggs and larvae.

Algae, specifically Spirogyra spp and Oscillatoria spp, can reduce the amount of the shelf available for spawning. Spirogyra spp, in its most extreme form, creates a barrier in the water column that prevents adult pupfish from entering that area while spawning. Oscillatoria spp is believed to create a "shrinkwrap" over the substrate of the spawning shelf. This "shrinkwrap" layer creates an anoxic environment below it which would dramatically decrease the survival rates of those eggs and larvae beneath it. This layer also prevents eggs from being deposited in the protective interstices of the rocks in the substrate which could make them more susceptible to predation or temperature variations.
Available pore space can also be reduced by the amount of silt deposited into these spaces. This reduction in available pore space reduces the protective area available to eggs and larvae.

The relationship between water temperature and dissolved oxygen play a critical role in habitat of eggs and larvae, as well as juveniles and adults. Eggs and larvae develop and grow in the substrate of the spawning shelf. Dissolved oxygen has to reach certain levels at certain temperatures in order for egg and larvae development to occur. If the dissolved oxygen level does not reach this minimum requirement then eggs and larvae cannot survive. Eggs and larvae will also not survive water temperatures greater than 37 degrees Celsius regardless of dissolved oxygen levels. Devil's Hole remains at virtually constant temperature and dissolved oxygen level. These aspects change with the increase in algae and direct sunlight (Deacon et al, 2003).

Stock and Flow Model

The stock and flow model is developed using VENSIM PLE version 3.0 software (Ventana Systems, Inc., 1998) on a Microsoft Windows XP platform. The modeler enters in the stock, flow and auxiliary variables and develops the
structure of the model within the software. The modeler
then enters corresponding equations for each variable to
represent processes and interactions between the variables.
The equations are based upon the modeler’s understanding of
system processes. The model is then used to produce an
output. See appendix for representation of a model run.

The first sector of the model is the original stock
and flow model (Figure 10). The second sector of the model
relates to the habitat of the Devil’s Hole Pupfish. It
includes changes in the habitat due to algal coverage,
relationships of water temperature and dissolved oxygen and
available pore space.

Population Sector

The first sector, or population sector, represents a
simple aging chain, in which pupfish begin as eggs, eggs
hatch to produce larvae, larvae mature to become juveniles
and finally, adult pupfish. Flows representing the rate at
which eggs become larvae, and the rate at which larvae
become mature pupfish control the movement of pupfish along
the chain. For example, the number of mature pupfish
multiplied by the egg production rate determines the total
number of eggs produced. This stock and flow structure
forms the backbone of the model. Once the relationships
comprising the reproductive cycle of mature pupfish were established, the relationships affecting the population negatively were explored and added to the model structure. Subsequent iterations of this process and consultation with the Pupfish Modeling Group, a sub-group of the Pupfish Recovery Team, have produced a more detailed model (Figure 11 - in pocket) that represents more variables and processes within the system. It includes the original stock and flow model and expands on changes which affect the hatch rate through changes in habitat. This second section of the stock and flow model includes three major sectors related to Algae, available pore space, and water temperature related to dissolved oxygen. All are thought to reduce the areas of the spawning shelf that are available to eggs and larvae for survival. This is the version of the model that was used for final determinations within this thesis.

The population sector represents the initial stock and flow model. Spatial differences in the critical habitat known as the "spawning shelf" (Figure 5) were then introduced into the model by dividing the early stages of the population into two groups based upon where they began.
development. Gustafson and Deacon (1998) had previously divided the spawning shelf into three distinct areas. This study includes only two of those areas, the inner and middle parts of the shelf, because these areas are known to have the highest production rates of eggs and larvae. The outer shelf is not included because of its lack of productivity and its substrate characteristics. The stock for juvenile pupfish was added because it is an established stage of life for the pupfish that represents the ability of the pupfish to become mobile for the first time and, therefore, avoid most of the losses that occur during earlier life stages. It is also an important part of the
model because it represents a convergence of the two separate areas of the spawning shelf into one single stock variable derived from larval maturation rate. Variables for initial numbers of eggs, larvae, juveniles and adults also had to be added to account for initial populations in each stage of life (Table 1).

The original variables for Pupfish eggs and larvae were divided into two paths in the model each representing areas of the spawning shelf with different habitat characteristics. The eggs stock was divided into Eggs on middle shelf and Eggs on inner shelf. Based on observations by Gustafson and Deacon (1998), the middle shelf was given 1/3 the total number of eggs and the inner shelf given 2/3 the total number of eggs. A new variable, Total Number of Eggs, linked the Egg Production on each part of the shelf to the actual determining variables for production including Egg Production LOOKUP, Normal Production Rate, Month Number and Percent Female. The Egg Production LOOKUP variable represents differences in the number of eggs produced per female over the course of the year. It is based upon an estimation of the number of eggs produced per female in each month of the year (Chernoff, 1985). Changes in the number of eggs may reflect the relationship between food availability and variability of
Table 1: Variables related to the population sector.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Formula</th>
<th>Initial value</th>
<th>Level of Uncertainty</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg Production</td>
<td>normal production rate X percent female</td>
<td>Calc.</td>
<td>medium</td>
<td>pupfish/month</td>
</tr>
<tr>
<td>Eggs</td>
<td>intg(initial eggs - eggs hatched + eggs produced)</td>
<td>60</td>
<td>medium</td>
<td>pupfish</td>
</tr>
<tr>
<td>hatch</td>
<td>normal hatch rate X hatch rate modifier</td>
<td>Calc.</td>
<td>medium</td>
<td>pupfish/month</td>
</tr>
<tr>
<td>Larvae</td>
<td>intg(initial larvae - larvae matured + eggs hatched)</td>
<td>6</td>
<td>medium</td>
<td>pupfish</td>
</tr>
<tr>
<td>larvae maturation</td>
<td>larvae/time to mature larvae to juvenile</td>
<td>Calc.</td>
<td>medium</td>
<td>pupfish/month</td>
</tr>
<tr>
<td>Juveniles</td>
<td>intg(initial juveniles - juveniles matured + larvae matured)</td>
<td>200</td>
<td>medium</td>
<td>pupfish</td>
</tr>
<tr>
<td>juvenile maturation</td>
<td>juvenile/time to mature juvenile to adult</td>
<td>Calc.</td>
<td>medium</td>
<td>pupfish/month</td>
</tr>
<tr>
<td>Pupfish</td>
<td>Pupfish X adult lifespan</td>
<td>200</td>
<td>medium</td>
<td>pupfish</td>
</tr>
<tr>
<td>normal hatch rate</td>
<td>constant</td>
<td>6.5</td>
<td>high</td>
<td>dmnl</td>
</tr>
<tr>
<td>time to incubate</td>
<td>constant</td>
<td>0.25</td>
<td>low</td>
<td>month</td>
</tr>
<tr>
<td>time to mature larvae to juvenile</td>
<td>constant</td>
<td>1</td>
<td>low</td>
<td>month</td>
</tr>
</tbody>
</table>
water temperature and dissolved oxygen, as related to time of year, and egg production. Highest rates of egg production occur in the spring and summer and the lowest rates occur in the fall and winter. Percent Female is also a sensitive variable that will significantly skew the population even with the slightest increase or decrease in percentage. It is thought that the actual percent female changes throughout the year, but because there is little information, Percent Female is assumed to be constant at 50%.

Egg losses on each part of the shelf are affected by a number of processes. The Normal Hatch Rate may vary but is assumed to be 6.5% for both areas of the shelf. Egg Loss is modified due to habitat changes and the timing of this change. Actual egg loss could be the result of many different factors relating to dissolved oxygen, water temperature, algal coverage and protective interstitial space. Changes in these environmental conditions could have positive and negative effects on actual pupfish populations. The (inner and middle) Hatch rate modifier due to habitat change variable is used to represent these changes and may provide insight into understanding the recent decline in the adult pupfish population and
evaluating any causes related to a reduction in eggs or larvae.

Larvae loss on each part of the shelf is determined by the same environmental factors that affect eggs. Larvae loss in the model is related Normal Larvae loss. This value is assumed to be 66.6% for the middle shelf and 33.3% for the inner shelf. These percentages are based upon productivity (Gustafson and Deacon, 1998). The variables Time to Incubate, Time to Mature Larvae to Juvenile (larval development) and Time to Mature Juvenile to Adult (juvenile maturation) represent scientific data gathered in these areas. The Time to Incubate varies in reality but is assumed to be consistent on all areas of the shelf and is set at 1 week (.25 months) (Gustafson and Deacon, 1998) in the model. The Time to Mature Larvae to Juvenile (larval development) is also assumed to be constant on all areas of the shelf and is set at 1 month (Deacon et al, 2003). The Time to Mature Juvenile to Adult (juvenile maturation) is set at 2 months (James, 1969).

The Shelf Hatch Rate Modifier Due to Habitat Change represents environmental factors that affect the hatch rate on all areas of the spawning shelf. It is the product of the Temperature/Oxygen Concentration Modifier, the Pore
Space Modifier and the Algae Modifier. These processes are represented as three separate sectors within the model.

**Water Temperature/Dissolved Oxygen Subsector**

The relationship between water temperature and dissolved oxygen can determine the viability of eggs and larvae in the substrate. If the water temperature increases there must also be a corresponding increase in dissolved oxygen, otherwise, egg and larvae survival rates will be reduced. See Table 2 for variable descriptions.

The Water Temperature LOOKUP represents fluctuations in water temperature over the year. It was developed by averaging recorded daily temperature readings (see Appendix for data Table #2) into monthly values for use in the model. Water Temperature is the average monthly temperature for the month. The Minimum Oxygen Concentration LOOKUP represents the minimum oxygen required for egg and larvae survival at given temperatures. Eggs and larvae can only survive if this minimum oxygen level is attained. These values are estimates based upon observations by Deacon et al (2003). The Oxygen Concentration Requirement is calculated by reading the Water Temperature LOOKUP and corresponding oxygen
requirement. The Maximum temperature is defined as 37 degrees Celsius at which no level of dissolved oxygen will allow for successful hatching (Deacon et al, 1995, Deacon et al, 2003). Dissolved oxygen within Devil's Hole varies from 2.3 to about 4.3 mg/l and is increased by higher sunlight levels during the summer months (Deacon et al, 1995). The Oxygen Concentration variable represents the actual oxygen concentrations on the shelf. It is

Table 2. Variables for the water temperature and dissolved oxygen subsector.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Formula</th>
<th>Initial value</th>
<th>Level of Uncertainty</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>water temperature</td>
<td>water temperature LOOKUP(Month number)</td>
<td>Calc.</td>
<td>low</td>
<td>degrees C</td>
</tr>
<tr>
<td>dissolved oxygen</td>
<td>dissolved oxygen LOOKUP(Month number)</td>
<td>Calc.</td>
<td>low</td>
<td>mg/l</td>
</tr>
<tr>
<td>temp/DO modifier</td>
<td>IF THEN ELSE (water temperature,maximum temperature for hatching and dissolved oxygen&gt;=Oxygen concentration requirement, 1, 0)</td>
<td>Calc.</td>
<td>low</td>
<td>dmnl</td>
</tr>
<tr>
<td>maximum temperature for hatching</td>
<td>constant</td>
<td>37</td>
<td>low</td>
<td>degrees C</td>
</tr>
</tbody>
</table>
determined by the Oxygen Concentration LOOKUP which represents estimates of actual dissolved oxygen throughout the year (Deacon et al, 2003). The Temperature/Oxygen Concentration modifier attempts to relate known processes into the model through an IF THEN ELSE function. This function requires dissolved oxygen levels for certain temperatures to be attained in order to have successful hatching, otherwise, there is no hatching of eggs to larvae within the model.

Available Pore Space Subsector

The amount of available pore space is another important factor regarding the survival of eggs and larvae. Pore space in the substrate helps protect eggs and larvae against temperature fluctuations and predation. As the available pore space is reduced by silt deposition, survivability of eggs and larvae is reduced. See Table 3 for variable descriptions.

The Area Available (on the spawning shelf) is calculated by multiplying the Length of Substrate by the Width of Substrate. Gustafson and Deacon (1998) gives the length of the substrate of the spawning shelf as approximately 5.8 meters and the width as 2.8 meters (Gustafson and Deacon, 1998). The % Pore Space variable
represents actual percentage of pore space. Pore space is primarily determined by packing of different particles. Homogeneous sediments have a porosity ranging from 47.64% (cubic packing) to 26.95 (rhombohedral packing) (Selley, 2000).

Table 3. Variables related to the pore space subsector.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Formula</th>
<th>Initial value</th>
<th>Level of Uncertainty</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>% pore space</td>
<td>constant</td>
<td>47%</td>
<td>high</td>
<td>dmnl</td>
</tr>
<tr>
<td>depth of substrate</td>
<td>constant</td>
<td>15</td>
<td>low</td>
<td>cm</td>
</tr>
<tr>
<td>width of substrate</td>
<td>constant</td>
<td>280</td>
<td>low</td>
<td>cm</td>
</tr>
<tr>
<td>length of substrate</td>
<td>constant</td>
<td>193</td>
<td>low</td>
<td>cm</td>
</tr>
<tr>
<td>total functional volume</td>
<td>depth X width X length X % pore space</td>
<td>Calc.</td>
<td>medium</td>
<td>cm(^{3})</td>
</tr>
<tr>
<td>amount of silt</td>
<td>constant</td>
<td>0</td>
<td>low</td>
<td>cm(^{3})</td>
</tr>
<tr>
<td>amount of detritus</td>
<td>constant</td>
<td>0</td>
<td>low</td>
<td>cm(^{3})</td>
</tr>
<tr>
<td>occupied pore space</td>
<td>amount of silt + amount of detritus</td>
<td>0</td>
<td>low</td>
<td>cm(^{3})</td>
</tr>
<tr>
<td>pore space modifier</td>
<td>unoccupied pore space/total functional volume</td>
<td>Calc.</td>
<td>medium</td>
<td>dmnl</td>
</tr>
</tbody>
</table>

The inner shelf is predominately gravel (particles larger than silt but smaller than cobble, USDA soil classification system, coarse gravels are 1.9-7.6 cm). The
middle shelf is predominately cobble (particles larger than gravel, USDA soil classification system, small cobbles are 7.6-15.2 cm) Both areas would have a percentage of pore space somewhat less than the above estimates because of their heterogeneity where smaller sediments would fill in larger pore spaces. The Total Functional Volume variable is calculated by multiplying the Area Available by the Depth of Substrate and then multiplying this total volume by the % Pore Space. This value represents the amount of space available to pupfish larvae and eggs to grow and mature. Silt and detritus fill in the available pore space on the spawning shelf and reduce the amount of protective space available to eggs and larvae. The Occupied Pore Space variable is the sum of the Amount of Detritus and Amount of Silt and represents the amount of pore space unavailable to eggs and larvae. Available Pore Space is the Total Functional Volume minus the Occupied Pore Space. The Pore Space Modifier is the ratio of Unoccupied Pore Space divided by Total Functional Volume. This value is a part of a multiplicative modifier which determines the hatch rate modifier for each part of the shelf and attempts to replicate the effects of a reduction or addition of pore space to the spawning shelf.
Algae Subsector

Algal coverage is thought to play a crucial role in the survival of eggs and larvae. A genus of algae called Oscillatoria spp forms a cover that has been called "shrinkwrap." This cover creates an anoxic environment below it which becomes unsuitable for egg and larval development. The most extreme stage of Spirogyra spp algae forms a barrier that prevents spawning and the deposition of eggs on the shelf. The Algae modifier represents these effects in the model. The Algal Coverage variable is the sum of the Area Covered by Oscillatoria and the Area Covered by Spirogyra. Uncovered Area is determined by subtracting Algal Coverage from the Area Available. The Algae Modifier is the ratio of Uncovered Area divided by Area Available. See Table 4 for variable descriptions.

Table 4: Variables related to the algae subsector.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Formula</th>
<th>Initial value</th>
<th>Level of Uncertainty</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>area covered by Spirogyra spp</td>
<td>constant</td>
<td>Calc.</td>
<td>low</td>
<td>cm^2</td>
</tr>
<tr>
<td>area covered by Oscillatoria spp</td>
<td>constant</td>
<td>Calc.</td>
<td>low</td>
<td>cm^2</td>
</tr>
<tr>
<td>Algal coverage</td>
<td>area covered by Spirogyra spp + area covered by Oscillatoria spp</td>
<td>Calc.</td>
<td>low</td>
<td>cm^2</td>
</tr>
</tbody>
</table>
Chernoff (1985) reports the total lifespan of a Devil’s Hole Pupfish to be on the order of 10-11 months. Pupfish spend approximately 2 months in earlier life stages. The model represents the Average Lifespan as 8 months which corresponds to total time spent as an adult. The Adult Carrying Capacity is presently thought to be 600 adult pupfish (Deacon et al, 2003). Adult Density is determined by dividing the number Pupfish by the Adult Carrying Capacity. When this ratio exceeds one then the model uses the Lifespan determinant instead of Average Lifespan to determine longevity of adults thereby reducing the population to below the carrying capacity. The Food Limitation LOOKUP represents food availability throughout the year and is derived from available phytobenthic biomass (food) measurements (Wilson et al, 2001).

Assumptions in the Model

There are many aspects of the Devil’s Hole Pupfish population that are still under investigation or have minimal data available. Some of these undocumented processes or variables are included in the model. Each of these variables was given a value or range of values that is based on the best available information provided by stakeholders. The assumptions are as follows:
1) Percent Female is assumed to be 50% for this baseline study and is based upon consultation with experts.

2) Initial eggs, larvae, juveniles, adults are given values based upon consultation with members of the modeling group. These variables have not been measured.

3) Normal Hatch Rate is assumed to be same for both areas (middle and inner) of the shelf. This measurement has never been taken in Devil’s Hole and is based on consultation with experts.

4) Average Water temperatures represent average monthly temperatures as derived from daily maximum temperature measurements.

5) Rock composition (particle size) on the inner and middle shelf is assumed to be homogenous. The inner shelf being gravel and the middle shelf being cobble.

6) Carrying capacity is assumed to be 600 adults based on consultation with experts. Actual carrying capacity is unknown.

7) Larvae and Juvenile maturation rates are considered to be the same on the inner and middle areas of the shelf and not affected by habitat differences.

8) Oxygen Concentrations are considered to be representative of a typical year.
9) Hatch rate is assumed to be higher in Devil's Hole than witnessed in lab. Deacon et al (1995) determined a 4% hatch rate in the lab but it is thought that the normal hatch rate in Devil's Hole would be somewhat higher. It is estimated to be 6.5% in the model.

10) The spawning shelf is assumed to be the only place that pupfish spawn.

11) Oscillatoria spp and Spirogyra spp have different effects on the spawning shelf in Devil's Hole but both are represented as negative influences on available spawning area. Oscillatoria spp creates a "shrinkwrap" layer that prevents eggs and larvae from entering protective pore spaces and creating an anoxic environment below which eggs and larvae may not survive. Spirogyra spp, in its extreme form, acts as a barrier in the water column preventing fish from spawning in areas above the spawning shelf.

12) The spawning shelf is assumed to be covered in its entirety by water as a result of legal mandates for minimum water level with Devil's Hole. If there were a serious drought or significant build up of sediments then parts of the shelf may become exposed and unavailable for spawning.
Building Confidence in the Model

In order to gain confidence that the model accurately represents the structure of the system generating the problematic behavior, the model must, at a minimum, replicate the reference mode. If the model can replicate the problematic trend and stakeholders have helped to represent the system as they believe it to exist, then it supports the hypothesis that essential pieces of the system that are generating the behavior have been represented (Stave, 2002). If it does not reproduce the reference mode then one must either revise the model or change the working hypothesis. In this study, there were three potential sources for egg and larvae reduction all of which were related to habitat changes. A reduction caused by algal coverage, an increase in silt in pore spaces and an increase in temperature were examined in attempts to replicate the reference mode.

Figure 13, the base model run, shows that the model output does replicate the population trend in actual adult population counts from 1972-1994 (Figure 1). Figure 12 also shows that a decrease in hatch rate due to habitat conditions, specifically a 35% reduction in area available (due to Oscillatoria spp) on the inner shelf, shows a similar downward trend as the decline in the actual
population from approximately 1995-2003. This indicates that the model can be shown to replicate the overall trend shown in the reference mode (Figure 1). The reason that Oscillatoria algae is shown first is that Oscillatoria spp, referred to as brown algae by those that conducted actual pupfish counts, appeared just about the time that the decline began and seems like the most likely candidate for causing the population decline.

Similarly, however, an increase in silt from 0 to 35% on the inner shelf (Figure 13) (pore space filled) results in a decline similar to that stated in the first replication of the reference mode (Figure 12). This output suggests that there may be at least two ways to replicate the reference mode using variables that were hypothesized to be causes of the problematic behavior.
Figure 12. Model output: Base run and a run with 35% reduction in area available, by Oscillatoria spp on the inner shelf in 1995 shows the same general trend as the reference mode (Figure 1).
Figure 13: Model output: Base run and a run with 35% reduction in available pore space by silt on the inner shelf in 1995 also show the same general trend as the reference mode.

Figure 14 shows a third possibility for the decline in adult pupfish populations via a reduction in hatch rate. Temperatures were set to exceed the maximum allowable temperature (37 degrees Celsius) in August and September in relation to dissolved oxygen. This increase in temperature produces a similar downward trend shown in figures 11 and 12.
Figure 14: Model output: Base run and a run with an average temperature of 38 degrees Celsius in August and September on the inner and middle shelf beginning in 1995 also shows the same general trend as the reference mode.

Figure 15 represents a combination of potential causes for a decrease in hatch rate due to habitat changes. It shows that a reduction of 15% in area available by Oscillatoria spp and a 20% reduction in available pore space by silt in 1995 also produces a similar downward trend when compared to the reference mode.
Figure 15: Model output: Base run and a run with 15% reduction in area available by Oscillatoria spp and a 20% reduction in available pore space by silt on the inner shelf in 1995 also shows the same general trend as the reference mode.

Replication of the reference mode can be accomplished by changing parameters for algae, water temperature/dissolved oxygen, and pore space. This multiple replication of the reference seems to support the original theory that a reduction in hatch rate due to habitat changes due to algae coverage, reduction of pore space by silt and changes in water temperature and
dissolved oxygen may be related to the cause of the population decline and provides confidence in the structure of the model.
CHAPTER 5

MODEL USE

Understanding the system

Upon replication of the reference mode, the model was used to conduct an examination of the effects of different variables on the system. Model parameters were changed to reflect actual concerns related to potential changes to the system. The model was initially used to examine the following questions in order to better understand the system and its natural processes:

What variables is the model most sensitive to?

Slight increases or decreases to Average Lifespan (adult) (Figure 16) and larvae and juvenile maturation rates (Figure 17) caused significant growth of the population in the first few years. At 48 months (four years) the population decreased from nearly 600 for a 9-month average lifespan to approximately 170 for a 7-month average lifespan.

Increasing or decreasing larvae and juvenile maturation rates would also result in marked changes
in the adult population over the short term (4.5 years). Group members recognized the importance of having comprehensive data related to these important variables and established a need for improved data collection and monitoring.

![Pupfish graph](image)

**Figure 16:** Comparison of different average lifespans.
How are the life stages of the Devil's Hole Pupfish related? Are there significant lag times in maximum population types?

Figure 18 represents the predicted relationships of life stages temporally. It showed the expected lag time between maxima in age classes. A maximum in adult pupfish was followed by a maximum in eggs, then a larval maximum and juveniles. The maxima for larvae and juveniles seem to be lower than adults, but due to the integration for these stocks in the model and different times spent in each life stage, more
adults would result from seemingly lower number of larvae and juveniles. This graph further confirms the need for managers to monitor stages other than adults, and emphasized that the egg stage is much more volatile than other life stages.

Figure 18: Life stages of the Devil's Hole Pupfish.

What effects might spikes in water temperature have on the population if they occurred in mid-summer?

If the average water temperature on the spawning shelf for the months of July and August were increased to 38 degrees Celsius (Figure 19), which is above the
temperature threshold for pupfish eggs and larvae. As a result, the adult pupfish population begins a fairly steep decline within 2 years. It shows that even with just 2 months of adverse temperatures, the effect could be significant.

![Graph showing pupfish population decline](image)

38 degrees Jul_Aug 
Base Run

Figure 19: Increased temperatures for July-August.

What is the effect of reduced dissolved oxygen on the long-term population?

Figure 20 shows that if the level of dissolved oxygen is set at 4 mg/l, which is below the minimum required (5 mg/l) for the average monthly temperature for the month of July, then there will be a slight decrease in the adult
population but is not as significant as the decline caused by increased temperatures.

![Graph showing changes in dissolved oxygen](image)

Figure 20: Changes in dissolved oxygen. Starting in 1995, dissolved oxygen does not meet the minimum requirement in the month of July.

Testing Management Strategies

The previous model runs have been associated more with natural processes, understanding the relationships and sensitivities of variables and testing the robustness of the model. This study included four specific tests of management strategies: 1) removal of algae, 2) introduction of fish from refugia populations into Devil's Hole, 3)
introduction of female fish from refugia populations into Devil’s Hole and 4) shading the spawning shelf to reduce water temperatures. In order to test the first management strategy, the parameters, specifically increasing Oscillatoria spp coverage from to 35%, used to replicate the decline in the reference mode were implemented. Strategies were then tested to attempt to reverse the decline.

Figure 21: Base run from 1995 with a 10% decrease (from 35% to 25%) in Oscillatoria algae at month number 96.
Figure 21 indicates that a reduction in Oscillatoria spp from 35% to 25%, a prime suspect for the cause of the decline, would begin to slow the decline of the population, especially over the short term. Management strategies might include increasing indirect sunlight onto the shelf as Oscillatoria spp seems to produce better in the shade. Another management option is to physically remove the algae from the spawning shelf to reduce coverage. Physical removal is a possibility, however, effects of human removal such as physically manipulating shelf materials, churning up water, etc. are unknown. There is the potential to cause more damage than assistance.

Another management possibility is that of adding refugia fish to the in situ population thereby increasing the adult population. Contrary to the expectations of the group, changing the initial adult pupfish population from 200 to 400 and increasing the initial egg population from 30 to 60, produced no significant change to the long-term population other than the initial jump represented by the initial increase (Figure 22).
A third management strategy, similar to the second, is the introduction of refugia females to increase the total female population from 50% to 51%, or possibly a reduction of females in the in-situ population from 50% to 49%. Figure 23 shows that both of these options would have little effect in the first 4 years and only result in minor changes to the adult population beyond 4 years.
Since there are potentially multiple reasons for habitat changes on the spawning shelf and an increase in *oscillatoria* and water temperature could result in a population decline, figure 24 shows the effect of reducing these negative effects. Specifically, algae is completely removed from the substrate and shade is applied in August, but not September, in order to maintain egg and larvae viability by reducing water temperature below the maximum threshold. With these positive changes, you can expect to start seeing a population increase from the base population in the first 24 months.
Specification of model parameters, refinements within the model, and use of the model to design monitoring and management strategies were the leading principles in model runs. Modeling Group members had thought that human intervention in the hatch rate, perhaps through temperature modification through shading or substrate porosity changes could significantly increase the adult population. Subsequent runs on an earlier version of the model (Figure 9) showed that an increase from 6.5 to 8% in the middle
shelf hatch rate raised the overall adult population when compared to the base run, but did not warrant a management action at this point. Another run using the present model (Figure 22) showed that adding to the number of initial adults did not have a significant effect on the long-term population. This run was actually very similar to a decline in the initial adult population thereby casting doubt on the hypothesis that initial populations could play an important role in overall adult population.

This study has shown that management strategies can be employed that have a positive effect on the overall population; however, none of the strategies tested in this study provided substantial increase to the population in the short term. Quick, short-term changes may be necessary if the Devil's Hole Pupfish continues to decline in population. Long-term strategies such as adding refugia fish or increasing females through refugia, could have a positive effect on the long-term population but may not be a quick fix.
CHAPTER 6

DISCUSSION

This purpose of this thesis was to develop a system dynamics model to help understand the recent decline in the Devil's Hole Pupfish population and to test management strategies that would slow or reverse the decline. Did the model help increase understanding of the recent decline? Yes, the process of model development and testing engaged interagency/interdisciplinary stakeholders and decision makers in the process of developing understanding of the relevant variables and processes. Affects of variables such as maturation, egg production rates, water temperature, substrate porosity and algal coverage had not been previously evaluated.

Could the model be used to test potential management strategies for reversing the decline? Yes, tests of management strategies such as removal of algae, introduction of refugia fish and shading the spawning shelf were shown to slow the decline over the long-term but none were quick fixes to the problem.
The modeling process has also helped understand the gaps in existing data and outline future academic research and federal monitoring needs such as: seismic activity, available pore space, flushing events, algal growth, predation by flatworms and potential cannibalism. For example, results of model runs have helped clarify and test assumptions, on the basis of past research and expert consultation, regarding normal hatch rates on different areas of the shelf, percent female, and maturation rates of larvae and juveniles.

Using the model to evaluate variables and processes has provided insight into potential leverage points within the system that may be manipulated by resource managers. Some variables, such as initial populations, which were thought to be sensitive leverage points, have been shown to be insignificant. Other variables, such as hatch rate modifier due to habitat change, have been expanded to include process variables and have helped determine potential leverage points in the system but require more research to further define the role of these variables.

The version of the model described and used in this thesis begins to describe the complex ecosystem associated with the Devil's Hole Pupfish. Findings as a result of using this version of the model are only preliminary.
because so many variables are not yet well documented. If one physically removes algae and if algae are the presumed cause of the problem, the problem will be reduced. However, the time for this change to affect the system according to processes in the real world, and as established in the model, become very important.

The current version of the model is somewhat limited due to the lack of understanding of some of the natural processes within Devil's Hole. Seismic activity could play a vital role in resetting the entire spawning shelf substrate. The timing of these events and the actual effects on the spawning shelf still need to be investigated further.

Another critical factor that was determined by model development and stakeholder participation was the determination of gaps in existing data. Seismic activity, flushing events, and predation/cannibalism may play critical roles in the overall success or failure of eggs and larvae.

Seismic activity may cause the porosity of the substrate on the spawning shelf to be minimized resulting in less space for eggs and larvae to safely grow. Flushing events may wash some or all of the existing substrate from the shelf, while also depositing a new, more porous,
substrate on the shelf. Predation on eggs and larvae by flatworms (*Dugesia dorotocephala*) and other invertebrates is known to occur but the rate at which this occurs is unknown and difficult to quantify. Cannibalism of eggs and larvae is thought to occur but, again, is difficult to quantify and include in the model until further research is conducted.

The development of the model has focused this study and members of the Pupfish Recovery Team and the Modeling Group on several variables included in the model and the assumed values for those variables. For example, the Percent Female is assumed to be 50% but it is believed that this variable fluctuates throughout the year (James, 1969). This may be better represented by a LOOKUP table to show the distribution of females throughout the year when this can be quantified. The processes which cause this change in percent female are unknown at this point. The normal hatch rates on all areas of the shelf are estimates based upon results from one experiment (Deacon et al, 1995) conducted under laboratory conditions. It is thought that conditions in Devil’s Hole, the natural environment, would be somewhat better than in the lab. Therefore, the values given in the model for normal hatch are somewhat higher (6.5% instead of 4%). The actual hatch rate is unknown.
Initial values for all stocks are established through consultations with members of the Modeling Group. Actual numbers depend upon what date the model has for a beginning point. There is severe lack of data regarding stages of life other than adult pupfish.

Further monitoring efforts, some of which may be implemented in a new long-term monitoring plan, would increase the effectiveness of the model to replicate the behavior of the actual pupfish ecosystem. For example, there are no counts currently being conducted of eggs and larvae. This information could prove useful in validating whether a reduction in hatching success of eggs and/or a change in survival of larvae has caused the adult population decline. Measurement of these parameters would help determine whether the pupfish had reached a critical population point in regards to potential extinction as the number of larvae provides an index that would permit prediction of numbers of adults a few months into the future. The general results of this model seem to indicate that this could very well be a plausible theory worthy of investigation.

Monitoring of water temperature, water chemistry and available pore space in the substrate of the spawning shelf would help discern whether these have a significant impact.
on egg and larval survival. The present model only begins to address issues related to substrate. Until further substrate information related to composition, sorting and actual use of pore space is determined, there are limits to which the model can be developed with confidence.

Flatworm populations and dispersal, algal coverage estimates over time and spreading rates would assist in determining potential effects of predation and "shrink wrap." Information on flatworm population density and feeding habits is necessary to further assess the original theory that the recent decline in the pupfish populations is the result of a loss of eggs and larvae. Predation by flatworms is thought to occur but is not included in this study. Improved data regarding algal coverage is important because it is an essential variable used to determine the viability of the habitat for eggs and larvae. Algal coverage of the shelf has been noted in the past during pupfish counts but only as a percentage of shelf coverage with estimates of species. The lack of algal information makes it difficult to render any real conclusions about the effects of specific changes in coverage over the last 30 years.

The effect of seismic activity on substrate porosity needs to be understood. Notes from pupfish counts indicate
that seismic activity may have had a tremendous effect on substrate and some instances have wiped the shelf completely clean of gravel. Seismic activity is difficult to measure as one would have to be present during the seismic event or shortly thereafter. This has occurred and removal of gravel and algae has been witnessed but the intensity of a seismic event to accomplish this has never been determined. There is also a need to establish potential relationships between seismic activity and available pore space, which serves as protection against predation, and egg and larvae survivability. Compaction of sediments due to seismic activity has not been examined and could be a critical factor especially if these events occur often.

The effects of flushing events are crucial to a more effective model and subsequent understanding of the system. Rain events, or lack thereof due to drought, could have a profound effect on available substrate. Smaller storms may wash in silt, significantly reducing substrate porosity. Larger storms may wash away the existing substrate but then deposit a new bed of gravel and cobble. These effects also need to be monitored and are subject for future research.

The process of developing a system dynamics model provided a framework for the Modeling Group to assess
effects of changes in system variables. The current version of the model allows testing of scenarios that can simulate the recent decline in the Devil's Hole Pupfish population.

Important data gaps were recognized. The question now becomes "where do we go from here?" An effort has already been made to address many of the data gaps through academic research and federal monitoring plans. In order to construct a more accurate model, the following research could be considered:

1) An active weather monitoring station on site to capture rainfall and potential flushing events so that the effects and occurrence rates of these events can be better understood,

2) Monitoring of larvae, eggs and juveniles during adult pupfish counts to determine growth rates and actual normal loss rates in Devil's Hole,

3) Monitoring of algal coverage of spawning shelf and species identification to understand the growth rates of algae and their specific effects on the substrate,
4) Monitoring of flatworm populations to understand potential predation of eggs and larvae,

5) Continue to track seismic events and monitor effects in Devil’s Hole so that these events and their effects can be considered in the model,

6) Monitoring of substrate composition and water temperature to provide updated data on these specific variables,

7) Continue to monitor autochthonous (from inside Devil’s Hole) and allochthonous (from outside Devil’s Hole) biomass input into Devil’s Hole for better food availability data,

8) Monitor percent female of the population to understand its relationship to overall productivity throughout the year.

More information related to the above processes would improve this initial model and could lead to new theories about the pupfish population decline and allow for a better understanding of potential management strategies.
This project has accomplished the primary goal of achieving a better understanding of the Devil's Hole Pupfish system and its problematic behavior. It became clear that it had also reached the current limits of understanding and that further supposition only increased the uncertainty in the model. Uncertainty is inherent in any model where even values that we think are well known may change as result of some exterior catalyst in some given situation. The use of Monte Carlo Analysis in conjunction with system dynamics could help reduce the uncertainty. Monte Carlo analysis allows for testing extreme ranges of values of variables to help determine their probability of occurrence. This is could be a worthwhile endeavor given what we actually know about the system.

Figure 25 (in pocket) is a conceptual framework for a more detailed model including dynamic changes in gravel, algae and seismic activity. It, along with the present model, can serve as starting point for future modeling efforts. The model will eventually be in the custody of the Pupfish Recovery Team. Members of the team, have received introductory training in VENSIM and will continue to modify the model as research and monitoring provide more
information about this tiny, yet complex, ecosystem and its unusually "charismatic mini-fauna" (Riggs and Deacon, 2003).
APPENDIX

Table 1. Raw data for fish counts (adult pupfish) used in reference mode.

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</tbody>
</table>
Table 4. List of variables

(001) "% Pore Space inner shelf" = 0.47
Units: Dmnl
Mostly gravel = 4.75 cm. (USDA soil classification system, avg. of coarse gravel 1.9-7.6 cm) Pore Space % depends upon packing of particles and ranges from 47.64% (cubic packing) to 26.95% (rhombohedral packing) (Selley, 2000).

(002) "% Pore Space middle shelf" = 0.47
Units: Dmnl
Mostly cobbles = 11.4 cm (USDA soil classification system, avg. of small cobbles 7.6-15.2 cm) Pore Space % depends upon packing of particles and ranges from 47.64% (cubic packing) to 26.95% (rhombohedral packing) (Selley, 2000).

(003) Adult Carrying Capacity = 600
Units: pupfish
Provided by Dr. Deacon, mtg 12 Nov 03, citing recent study by Blinn, carrying capacity is 600.

(004) Adult Density = Pupfish/Adult Carrying Capacity
Units: Dmnl

(005) Adult Lifespan = Lifespan determinant
Units: Month

(006) Algae modifier inner shelf = Uncovered Area inner shelf/Area Available inner shelf
Units: Dmnl
Algal coverage will be determined by the % of the area of the shelf covered by Oscillatoria and Spirogyra algaes. *Oscillatoria* creates "shrinkwrap" which produces an anoxic environment below it in the substrate killing eggs and larvae. *Spirogyra* blockage prevents adult fish from entering areas above the shelf to spawn.
and therefore prevents eggs from being deposited and eggs and larvae from surviving in those areas.

(007) Algae modifier middle shelf =
Uncovered Area middle shelf/Area Available middle shelf
Units: Dmnl
Algal coverage will be determined by the % of the area of the shelf covered by Oscillatoria and Spirogyra algae. Oscillatoria creates "shrinkwrap" which produces an anoxic environment below it in the substrate killing eggs and larvae. Spirogyra blockage prevents adult fish from entering areas above the shelf to spawn and therefore prevents eggs from being deposited and eggs and larvae from surviving in those areas.

(008) Algal Coverage inner shelf =
Area Covered by Oscillatoria inner shelf + Area Covered by Spirogyra inner shelf
Units: centimeters*centimeters

(009) Algal Coverage middle shelf =
Area Covered by Oscillatoria middle shelf + Area Covered by Spirogyra middle shelf
Units: centimeters*centimeters

(010) Amount of Detritus inner shelf = 0
Units: centimeters*centimeters*centimeters

(011) Amount of Detritus middle shelf = 0
Units: centimeters*centimeters*centimeters

(012) Amount of Silt inner shelf = 0
Units: centimeters*centimeters*centimeters

(013) Amount of Silt middle shelf = 0
Units: centimeters*centimeters*centimeters
Area Available inner shelf = Length substrate inner shelf * Width substrate inner shelf
Units: centimeters * centimeters

Area Available middle shelf = Length substrate middle shelf * Width substrate middle shelf
Units: centimeters * centimeters

Area Covered by Oscillatoria inner shelf = 0
Units: centimeters * centimeters

Area Covered by Oscillatoria middle shelf = 0
Units: centimeters * centimeters

Area Covered by Spirogyra inner shelf = 0
Units: centimeters * centimeters

Area Covered by Spirogyra middle shelf = 0
Units: centimeters * centimeters

Average Lifespan = 8
Units: Month
Chernoff, 1985 give 10 months as ecological life expectancy, so subtracting the 2 months they spend as juveniles gives 8 months average life expectancy in the adult stage.

Deaths = Pupfish/Adult Lifespan
Units: pupfish/Month

Depth of Substrate inner shelf = 10
Units: centimeters
Derived from data collected by Lindsey Treon (2003).
Depth of Substrate middle shelf = 15 units: centimeters
Derived from data collected by Lindsey Treon (2003).

Dissolved Oxygen inner shelf = Dissolved Oxygen LOOKUP inner shelf (Month Number)
Units: milligrams/liter
Dissolved oxygen on the inner shelf per month.

Dissolved Oxygen LOOKUP inner shelf ([(0,0)(20,10)],
(1,4),(2,4),(3,4),(4,5),(5,5),(6,6),(7,6),(8,6),
(9,6),(10,5),(11,4),(12,4))
Units: milligrams/liter
Estimation of dissolved oxygen levels throughout the year, Deacon 2003.

Dissolved Oxygen LOOKUP middle shelf ([(0,2)20,10],
(1,4),(2,4),(3,5),(4,5),(5,6),(6,6),(7,6),(8,6),
(9,6),(10,5),(11,4),(12,4))
Units: milligrams/liter
Estimation of dissolved oxygen levels throughout the year, Deacon 2003.

Dissolved Oxygen middle shelf = Dissolved Oxygen LOOKUP middle shelf (Month Number)
Units: milligrams/liter
Dissolved oxygen on the inner shelf per month.

Egg loss on inner shelf = Eggs on inner shelf * Normal Egg Loss on inner shelf
Units: pupfish/Month

Egg loss on middle shelf = Eggs on middle shelf * Normal Egg Loss on middle shelf
Units: pupfish/Month
Egg Production LOOKUP(
[(0,0)12,5]),
(1,0.5),(2,1.6),(3,4),(4,4.2),(5,4.2),(6,3.2),
(7,2.2),(8,1.6),(9,1),(10,0.5),(11,0.5),(12,0.5))
Units: 1/Month
It is based upon an estimation of the number of eggs produced per female in each month of the year (Chernoff, 1985).

Egg Production on inner shelf= (2/3)*Total Number of Eggs
Units: pupfish/Month
The inner shelf is assumed to receive 2/3 of the total number of eggs deposited based upon sitings by Gustafson (1998).

Egg Production on middle shelf= (1/3)*Total Number of Eggs
Units: pupfish/Month
The middle shelf is assumed to receive 1/3 of the total number of eggs deposited based upon sitings by Gustafson (1998).

Eggs on inner shelf= INTEG ( +Egg Production on inner shelf-Egg loss on inner shelf-Hatch inner shelf,initial eggs on inner shelf)
Units: pupfish

Eggs on middle shelf= INTEG ( +Egg Production on middle shelf-Egg loss on middle shelf-Hatch middle shelf,initial eggs on middle shelf)
Units: pupfish

FINAL TIME = 420
Units: Month
The final time for the simulation.
(036) food limitation LOOKUP(  
\[(0,0)12,1),  
(1,0.33),(2,0.359649),(3,0.377193),(4,0.447368),  
(5,0.697368),(6,0.864035),(7,0.916667),  
(8,0.964912),(9,1),(10,1),(11,0.631579),  
(12,0.33))  
Units: Month  
Derived from total phytobenthic biomass as measured by Wilson et al, 2001. Maximum measurements equals one and the remaining months are represented as a percentage of the maximum values attained.

(037) Hatch inner shelf=  
Eggs on inner shelf*(Normal Hatch Rate on inner shelf*(IF THEN ELSE (Time&gt;time of habitat change on inner shelf, inner shelf hatch rate modifier due habitat change, 1))/Time to Incubate)  
Units: pupfish/Month

(038) Hatch middle shelf=  
Eggs on middle shelf*(Normal Hatch Rate on middle shelf*(IF THEN ELSE(Time&gt;time of habitat change on middle shelf, middle shelf hatch rate modifier due to habitat change, 1))/Time to Incubate)  
Units: pupfish/Month

(039) initial adults=  
200  
Units: pupfish

(040) initial eggs on inner shelf=  
30  
Units: pupfish

(041) initial eggs on middle shelf=  
30  
Units: pupfish

(042) initial juveniles=  
200  
Units: pupfish

(043) initial larvae on inner shelf=  
3  
Units: pupfish

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(044)  initial larvae on middle shelf = 3
Units: pupfish

(045)  INITIAL TIME = 0
Units: Month
The initial time for the simulation.

(46)  inner shelf hatch rate modifier due habitat change =
1 * Algae modifier inner shelf * pore space modifier inner shelf * "Temperature/Dissolved Oxygen modifier inner shelf"
Units: Dmnl
Hatch rate modifier. Is multiplied by normal hatch rate to represent change in hatch rate due to change in habitat conditions. Default value = 1 (no effect).

(047)  juvenile loss =
Juveniles * normal juvenile loss
Units: pupfish/Month

(048)  Juvenile maturation =
Juveniles / Time to Mature Juvenile to Adult
Units: pupfish/Month

(049)  Juveniles = INTEG ( 
+ Larvae maturation inner shelf + Larvae maturation middle shelf - Juvenile maturation - juvenile loss, initial juveniles)
Units: pupfish
Defined as juveniles when they absorb yolk sac, pre-juvenile, at 10 mm (Gustafson and Deacon 1998).

(050)  Larvae loss on inner shelf =
Larvae on inner shelf * Normal Larvae Loss on inner shelf
Units: pupfish/Month

(051)  Larvae loss on middle shelf =
Larvae on middle shelf * Normal Larvae Loss on middle shelf
Units: pupfish/Month
Larvae maturation inner shelf = 
Larvae on inner shelf / Time to Mature Larvae to 
Juvenile 
Units: pupfish / Month

Larvae maturation middle shelf = 
Larvae on middle shelf / Time to Mature Larvae to 
Juvenile 
Units: pupfish / Month

Larvae on inner shelf = INTEG ( 
+ Hatch inner shelf - Larvae loss on inner shelf - 
Larvae maturation inner shelf, initial larvae on 
inner shelf) 
Units: pupfish

Larvae on middle shelf = INTEG ( 
+ Hatch middle shelf - Larvae loss on middle shelf - 
Larvae maturation middle shelf, initial larvae on 
middle shelf) 
Units: pupfish
Defined as larvae as soon as they hatch (approx 4 
mm). Stay as larvae until they absorb yolk sac 
and become 10 mm. (stages prolarva, early 
postlarva, and late postlarva: Gustafson and 
Deacon 1998).

Length substrate inner shelf = 
193 
Units: centimeters
Derived from measurements taken by Gustafson 

Length substrate middle shelf = 
193 
Units: centimeters
Derived from measurements taken by Gustafson 

Lifespan determinant = 
IF THEN ELSE (Adult Density < 1, Average Lifespan, 
(food limitation LOOKUP (Month Number))) 
Units: Month
IF Adult Density is < 1 then average lifespan, 
else lifespan lookup (based upon information 
given at meeting with Dr. Deacon, 11/16/03).
loss time=
1
Units: Month

Maximum Temperature for hatching=
37
Units: degrees Celsius
Above 36 degrees Celsius no egg hatching will occur regardless of Dissolved Oxygen level.

middle shelf hatch rate modifier due to habitat change=
1*Algae modifier middle shelf*pore space modifier middle shelf*"Temperature/Dissolved Oxygen modifier middle shelf"
Units: Dmnl
Multiplier on hatch rate due to habitat change. Default value =1 (no effect).

Minimum Oxygen Concentration LOOKUP((0,0)40,10),
(0,2.5),(32,2.5),(33,3),(34,4),(35,5),(36,6))
Units: milligrams/liter
Amount of Dissolved Oxygen required at certain temperatures to allow hatching. Deacon 10 Dec 03.

Month Number=
INTEGER(MODULO(Time, 12 ))+1
Units: Month

Normal Egg Loss on inner shelf=
(1-Normal Hatch Rate on inner shelf)/loss time
Units: 1/Month

Normal Egg Loss on middle shelf=
(1-Normal Hatch Rate on middle shelf)/loss time
Units: 1/Month

Normal Hatch Rate on inner shelf=
0.065
Units: Dmnl
Deacon (3/5/03). Best on inner shelf.
Normal Hatch Rate on middle shelf = 0.065
Units: Dmnl
Deacon, Taylor Pedretti (1995) found 4% hatch in experimental conditions. Deacon (3/5/03) estimates hatch in natural conditions in Devil's Hole should be higher, based in part on results in James (1969). Worst on outer shelf.

Normal juvenile loss = 0.1
Units: 1/Month
Deacon, Taylor and Pedretti, 1995, p. 218, Of 89 eggs, 3 larvae developed. Of those one died, and two survived to adulthood.

Normal Larvae Loss on inner shelf = 0.33
Units: 1/Month
Deacon, Taylor and Pedretti, 1995, p. 218, Of 89 eggs, 3 larvae developed. Of those one died, and two survived to adulthood.

Normal Larvae Loss on middle shelf = 0.33
Units: 1/Month
Deacon, Taylor and Pedretti, 1995, p. 218, Of 89 eggs, 3 larvae developed. Of those one died, and two survived to adulthood.

Normal Production Rate = Egg Production LOOKUP(Month Number)
Units: 1/Month
Average monthly egg production per female. (Chernoff 1985)

Occupied Pore Space inner shelf = Amount of Detritus inner shelf + Amount of Silt inner shelf
Units: centimeters*centimeters*centimeters

Occupied Pore Space middle shelf = Amount of Detritus middle shelf + Amount of Silt middle shelf
Units: centimeters*centimeters*centimeters
Oxygen Concentration Requirement inner shelf =
Minimum Oxygen Concentration LOOKUP(water
temperature inner shelf)
Units: milligrams/liter

Oxygen Concentration Requirement middle shelf =
Minimum Oxygen Concentration LOOKUP(water
temperature middle shelf)
Units: milligrams/liter
Corresponds the actual water temperature with a
minimum oxygen concentration that would allow
for hatching.

Percent Female =
0.5
Units: Dmnl
Female population is assumed to be 50% throughout
the year. This percentage is thought to vary
but data is inconclusive.

pore space modifier inner shelf =
Unoccupied Pore Space inner shelf/Total
Functional volume inner shelf
Units: Dmnl
Default is 1. Represents the percentage of pore
space available for eggs. No sediment, detritus
or algae. Occupied pore space divided by total
pore space.

pore space modifier middle shelf =
Unoccupied Pore Space middle shelf/Total
Functional Volume middle shelf
Units: Dmnl
Accounts for total pore space available on the
spawning shelf to the pupfish eggs and larvae.

Pupfish = INTEG ( 
+Juvenile maturation - Deaths, initial adults)
Units: pupfish
Defined as adults at 15 mm, when they reach
sexual maturity (James 1969, 3/5/03 mtg).

SAVEPER =
TIME STEP
Units: Month [0, ?]
The frequency with which output is stored.
"Temperature/Dissolved Oxygen modifier inner shelf" = IF THEN ELSE(water temperature inner shelf < Maximum Temperature for hatching AND : Dissolved Oxygen inner shelf >= Oxygen Concentration Requirement inner shelf, 1, 0) Units: Dmnl
If the water temperature does not exceed 37 deg Celsius and the minimum Dissolved Oxygen concentration is met, then hatching can occur.

"Temperature/Dissolved Oxygen modifier middle shelf" = IF THEN ELSE(water temperature middle shelf < Maximum Temperature for hatching AND : Dissolved Oxygen middle shelf >= Oxygen Concentration Requirement middle shelf, 1, 0) Units: Dmnl
If the water temperature does not exceed 37 deg Celsius and the minimum Dissolved Oxygen concentration is met, then hatching can occur.

(time of habitat change on inner shelf = 0 Units: Month
(time of habitat change on middle shelf = 0 Units: Month

TIME STEP = 0.0625 Units: Month [0,?] The time step for the simulation.

Time to Incubate = 0.25 Units: Month One week incubation from eggs to larvae (Gustafson and Deacon 1998, p.2).

Time to Mature Juvenile to Adult = 2 Units: Month Approx 2 months. Time to grow from 5-8 mm to 15 mm, given growth rate of approx 4.7 mm/month for offspring (James 1969).
(088) Time to Mature Larvae to Juvenile = 
1
Units: Month
Approx 1 month. Time to grow from 4 mm to 10 mm, through larval stages. Estimate that larvae grow faster than juveniles, approx 6 mm/month (Deacon estimate, 3/5/03).

(089) total eggs =
Eggs on inner shelf + Eggs on middle shelf
Units: pupfish

(090) Total Functional volume inner shelf =
(Area Available inner shelf * Depth of Substrate inner shelf) * "% Pore Space inner shelf"
Units: centimeters*centimeters*centimeters

(091) Total Functional Volume middle shelf =
(Area Available middle shelf * Depth of Substrate middle shelf) * "% Pore Space middle shelf"
Units: centimeters*centimeters*centimeters

(092) total larvae =
Larvae on inner shelf + Larvae on middle shelf
Units: pupfish

(093) Total Number of Eggs =
Normal Production Rate * (Percent Female * Pupfish)
Units: pupfish/Month
Calculates total number of eggs produced based upon female pupfish population and number of eggs produced per female per month.

(094) Uncovered Area inner shelf =
Area Available inner shelf - Algal Coverage inner shelf
Units: centimeters*centimeters

(095) Uncovered Area middle shelf =
Area Available middle shelf - Algal Coverage middle shelf
Units: centimeters*centimeters

(096) Unoccupied Pore Space inner shelf =
Total Functional volume inner shelf - Occupied Pore Space inner shelf
Units: centimeters*centimeters*centimeters
(097) Unoccupied Pore Space middle shelf =
Total Functional Volume middle shelf - Occupied
Pore Space middle shelf
Units: centimeters*centimeters*centimeters

(098) water temperature inner shelf =
Water Temperature LOOKUP inner shelf (Month
Number)
Units: degrees Celsius
Actual water temperature on the shelf.

(099) Water Temperature LOOKUP inner shelf(
\[ (0,0) (20,40) \],
(1,32.05), (2,31.77), (3,32.36), (4,33.98),
(5,34.63), (6,35.4), (7,35.06), (8,35.28),
(9,34.53), (10,32.06), (11,32.32), (12,32.32)\)
Units: degrees Celsius
Based on average monthly temperatures derived
from daily temperatures in 2001, provided by Dr.
James Deacon.

(100) Water Temperature LOOKUP middle shelf(
\[ (0,0) (20,40) \],
(1,33.01), (2,33.39), (3,34.24), (4,34.92),
(5,35.33), (6,35.58), (7,35.11), (8,35.7),
(9,34.76), (10,33.76), (11,33.47), (12,33.34)\)
Units: degrees Celsius
Based on average monthly temperatures derived
from daily temperatures in 2001, provided by Dr.
James Deacon.

(101) water temperature middle shelf =
Water Temperature LOOKUP middle shelf (Month
Number)
Units: degrees Celsius
Actual water temperature on the shelf.

(102) Width substrate inner shelf =
280
Units: centimeters
Derived from measurements taken by Gustafson

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(103) Width substrate middle shelf = 280
    Units: centimeters
The following graphs represent LOOKUP tables in the model. These graphs show the data that is used by the model when it attempts to calculate monthly values for the related variable.

**Water Temperature**

![Water Temperature Graph](image)

**Dissolved Oxygen**

![Dissolved Oxygen Graph](image)
Simple representation of a run of the
Population sector of the
final stock and flow model.

The model begins in the egg production sector. Eggs are
produced by females which have a production rate that
varies by month. It is assumed that females make up 50% of
the population of adults.

For example:
In early May, there are 200 adult pupfish and, therefore,
100 females. Females produce 4 eggs per fish in May
resulting in $4 \times 100 = 400$ eggs produced.

The model then calculates the hatch rate of eggs into
larvae. The normal hatch rate is 6.5%.

For example:
In May, there are 400 eggs produced. The normal hatch rate
is 6.5%. The result would be $400 \times 0.065 = 26$ larvae.

The model then calculates the number of juveniles produced
from larvae.

For example:
In mid-May, there are 26 larvae produced from eggs. The
normal larvae loss rate is 33%. The result would be $26 \times
0.33 = 8.58$ juveniles lost. There would then be $26 - 8.58 =
17.4$ juveniles.

Finally, the model calculates the number of adults from
juveniles.

For example:
In mid-June, there are 17.4 juveniles. The normal juvenile
loss rate is 10%. The result would be $17.4 \times 0.1 = 1.74$
juveniles lost. There would then be $17.4 - 1.74 = 15.66$
adults produced from juveniles.

These 15.66 one month old adults would then feed back into
the egg production sector in mid-June and will typically
produce eggs for 8 months. Egg production will vary
according to the Egg Production LOOKUP table presented in
the Appendix. Then at 9 months (January of the next year)
these adults are assumed to die.
BIBLIOGRAPHY


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VITA

Graduate College
University of Nevada, Las Vegas

Yuri V. Graves

Home Address:
313 Montcliff Avenue
Henderson, Nevada 89074

Degrees:
Bachelor of Science, 1990
Edinboro University of Pennsylvania

Master of Science, 1993
Ohio University

Thesis Title: A Model to Understand Population Decline of the Devil's Hole Pupfish (Cyprinodon diabolis) and Support Habitat Management Decisions

Thesis Examination Committee:
Chairperson, Dr. Krystyna Stave, Ph. D.
Committee Member, Dr. James Deacon, Ph. D.
Committee Member, Dr. David Hassenzahl, Ph. D.
Graduate Faculty Representative., Dr. David James, Ph. D.