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

Yuri V. Graves and Krystyna A. Stave
Graduate Student and Associate Professor, respectively.
Department of Environmental Studies, University of Nevada Las Vegas,
4505 Maryland Parkway, Las Vegas Nevada 89154-4030
(702) 450-8833, (702) 895-4833
(E-mail for corresponding author Graves: YURGGIE@aol.com)

Abstract

This paper describes a system dynamics simulation model created to help the Devil's Hole Pupfish Recovery Team understand reasons for population decline since the mid-1990s and to evaluate potential interventions to reverse the population decline. 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. The Team is seeking ways to reverse the recent population decline in the native habitat, but has limited information about the system as well as limited resources for data collection. The focus of this study is the development of a system dynamics model that can help the Team understand the reasons for the population decline, identify critical parameters that should be monitored to anticipate future population changes, and help find habitat management levers that can reverse the population decline.

Keywords: Devil's Hole Pupfish, Devil's Hole, population, *Cyprinodon diabolis*, habitat management

Introduction

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, a water- filled cavern forming a skylight into the regional aquifer is a “disjunct part of the Death Valley National Park” in Ash Meadows, NV. The Hole was created about 60,000 years ago when the roof of an underground fissure collapsed, creating an opening to the surface (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. It is the only natural habitat for the Devil’s Hole Pupfish *(Cyprinodon diaboli*s).

Devil’s Hole 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 and a dramatic decrease in the 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 from the U.S. Supreme Court and District 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 (Figure 1).

The Devil’s Hole Pupfish has again become a focal point for policy managers, however. Since 1994, the population has seen a sharp and sustained decline. While the risk of extinction has been lowered by a successful refugium program, the protection of the native population in its native habitat is essential to long-term survival, since the long-term effects of refugium environment on the evolutionary trajectory of the species is not entirely understood (Baugh and Deacon, 1988). 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 recommendations likely to reverse the downward trend in the population. The group has limited information about the system as well as limited resources for data collection. Their monitoring and management efforts must be carefully targeted. The focus of this study is the development of a system dynamics model that can help the group understand the reasons for the population decline, identify critical parameters that should be monitored to anticipate future population changes, and help find habitat management levers that can reverse the population decline. Figure 2, illustrating annual maximum and minimum population sizes recorded in Devil’s Hole since 1972, represents the reference mode for the model. This paper describes the first four steps of a system dynamics approach to understanding this problem: problem definition, system description, model development, building confidence in the model, using the model and initial conclusions.

Problem Definition

The behavior over time graph (Figures 1 and 2) depicts the annual maximum (summer) and minimum (winter) population sizes of mature Devil's Hole pupfish from 1972 to the present. 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 then levels off at a slight growth rate for nearly 20 years. The decline that inspired this analysis appears to have started about 1994.

System Description

The system generating the Devils Hole Pupfish population pattern of change has its basis in a generic population model. The model is dominated by one positive and one negative loop (Figure 3). 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 expire.

This typical population model was a starting point for explaining what was causing the number of mature pupfish to expire at higher than normal rates. Through discussions with pupfish experts, it became apparent that the cause of the decline was not likely related to a higher mortality rate of mature fish. Rather, it was the hypothesis of the experts that the population was declining because of a greater mortality rate of eggs and larvae. Accordingly, the focus turned in the direction of understanding what variables affected the hatch and survival rates. Some of the variables to be defined further are the effects of filamentous algal growth (cyanobacteria and green algae) on larvae and eggs, the effect of seismic activity and sedimentation on available interstitial space in the substrate of the spawning shelf, and the effects of predation and possibly cannibalism on larvae and eggs. All of these variables would directly impact the existing variable, *Hatch Rate Modifier due to Habitat Change*, on all three areas of the spawning shelf.

Model Development

The stock and flow diagram (Figure 4), 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 were added. The number of mature pupfish multiplied by the egg production rate determines the rate of egg production. 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 that are affecting the population negatively were explored and added to the model structure.

Subsequent iterations of this process and consultation with a newly established Pupfish Modeling Group, a sub-group of the Pupfish Recovery Team, have produced a more detailed model (Figure 5) that represents more variables and processes within the system. The importance of spatial distributions in the critical habitat known as the "spawning shelf" was introduced into the model. These divisions were based upon substrate characteristics and potential productivity established by Gustafson et al, (1998) and the consultations mentioned above. 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 three 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.

The original variables for Pupfish eggs and larvae were divided into three paths in the model each representing areas of the spawning shelf with different habitat characteristics. The *Eggs* stock became *Eggs on outer shelf*, *Eggs on middle shelf* and *Eggs on inner shelf*. Until further defined, each area of the shelf is assumed to have 1/3 of the carrying capacity of the total shelf. A new variable, *Total Number of Eggs*, linked the *Egg Production* on each part of the shelf to the actual determinant variables for production including *Egg Production LOOKUP*, *Normal Production Rate*, *Month Number* and *Percent Female*. The *Egg Production LOOKUP* variable is based upon a 12-month measurement of the number of eggs produced per female (Chernoff, 1985). This distribution may reflect the relationship between food availability and diel variability of water temperature, as related to time of year, and egg production. Fluctuations in egg production on the spawning shelf throughout the year result in the highest rates occurring in the spring and summer and the lowest rates occurring in the fall and winter. This variable is critical to the overall hypothesis that the recent decline in population is due to reduced egg and larval survival rates. *Percent Female* is also a sensitive variable that will significantly skew the population even with the slightest increase or decrease in percentage. *Percent Female* is presently set at 50%.

Egg losses on each part of the shelf are affected by a number of variables. The *Normal Hatch Rate* that varies from a high of 7% on the inner shelf to a low of 5.5% on the outer shelf (Deacon, 2003). *Egg Loss* is modified due to habitat changes and the timing of this change. They are presently assumed to be a default value of 1. The (inner, middle, outer shelf) *Hatch rate modifier due to habitat change* is critical to 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 a function of *Normal Larvae loss*. This value is assumed to be equal for each part of the shelf and formulated using 33.3% for each. The variables *Time to Incubate*, *Time to Mature Larvae to Juvenile* and *Time to Mature Juvenile to Adult* are representative of scientific data gathered in these areas. The *Time to Incubate* is consistent on all areas of the shelf and is expressed as 1 week (.25 months) (Gustafson et al, 1998). The *Time to Mature Larvae to Juvenile* is also consistent on all areas of the shelf and is expressed as 1 month (Deacon et al, 2003). The *Time to Mature Juvenile to Adult* is expressed as 2 months (James, 1969). The *Average Lifespan* is 10 months (Chernoff, 1985) but is expressed as 8 months when time spent in previous life stages are accounted for.

Building Confidence in the Model

In order to gain confidence in the results, the model must be shown to replicate the reference mode. Figure 6 shows that the model output does replicate the population trend witnessed by actual adult population counts from 1972-1994 (Figures 1 and 2). This is represented by the "base" run of the model. Figure 6 also shows that a 10% increase in egg loss replicates the decline in population from 1994-2002. This indicates that the model does replicate the overall trend shown in figure 6 and supports the hypothesis that egg loss, and possibly larvae loss, are significant contributors to the declining population trend. Figure 7 represents the next iteration of the causal loop diagram. It builds upon the initial diagram and builds into the model factors such as predation, cannibalism, effects of water level and substrate porosity. All of these factors need to be defined in order to understand their potential relationship to reduced egg and larvae populations that may have contributed to the recent decline in the adult pupfish population.

Using the Model

Intensive group modeling sessions were held with members of the Pupfish Recovery Team between January and May 2003. Modeling group members have specified model parameters, helped to refine the model, and use the model to design monitoring and management strategies. In February, Pupfish populations fell to their lowest recorded level. This has intensified the group's use of the model. The group is aiming to have another revised version of the model completed by August 2003, but to use preliminary versions of the model in March, April and May to test potential emergency management options in the meantime.

The Pupfish Modeling Group has made several recent runs on the model to determine areas of emphasis for research and management strategies. One of the early runs (Figure 8) represented an attempt to understand how all the stages of life of a pupfish are related temporally. It showed the expected lag time between maximum population types. A maximum in adult pupfish followed by a maximum in eggs, then larvae and juveniles.

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 (Figure 9) showed that an increase of 8% to 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 (Figure 9) showed that adding to the number of initial adults did not have a significant impact on the long-term population. This run was actually very similar to a decline in the initial adult population (Figure 9) thereby disproving a theory that initial populations could play an important role in overall model effectiveness.

Another critical factor that was determined by model development and use was the determination of gaps in existing data. Seismic activity, flushing events and algal growth 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 substrate on the shelf. Algal growth, depending on the species, may become so extreme as to form "shrink wrap" on top of the substrate. This coverage produces an anoxic environment in the substrate that could be fatal to both eggs and larvae. Predation of 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 also caused members of the Pupfish Recovery Team and the Modeling Group on variables included in the model and the assumptions that have been made. The Percent Female is assumed to be 50% but we do not know if this is consistent throughout the year. This may be a variable better represented by a LOOKUP table to show the distribution of females throughout the year when this can be quantified. The hatch rates on all three areas of the shelf are estimates based upon results from one experiment (Deacon et al, 1995) conducted under laboratory conditions. Members of the Modeling Group then incorporated the results into the model. Initial values for all stocks are established from several previous works and then extrapolated by members of the Modeling Group.

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 eggs and larvae has caused the adult population decline. These counts would help determine whether the pupfish had reached a critical population point in regards to potential extinction as the number of larvae are thought to represent the overall success of the population. 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 eggs and larvae. Flatworm or algal coverage estimates and spreading rates would assist in determining potential effects through predation and "shrink wrap." The effect of seismic activity on substrate porosity needs to be understood to establish potential relationships between available pore space, which serves as protection against predation, and egg and larvae survivability. The presence of sediments that could potentially reduce substrate porosity need to be examined further.

Initial Conclusions

The model has proven useful to the Pupfish Recovery Group. Initial runs have provided insight into potential leverage points within the system. Some variables, such as initial populations, which were thought to be sensitive leverage points, have been reevaluated as to overall significance. Other variables, such as *hatch rate modifier due to habitat change*, are now known to be potential leverage points in the system and require more research to define their role. The model will continue to be modified as research and professional consultation provide more information about this tiny, yet complex, ecosystem and it unusually "charismatic mini-fauna" (Deacon, 2003).

Acknowledgments

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Figure Captions

Figure 1: Reference mode for Devil’s Hole Pupfish population 1972-2002.

Figure 2: Reference mode including trend line.

Figure 3: Initial Causal Loop Diagram.

Figure 4: Original Stock and Flow Diagram.

Figure 5: Updated Stock and Flow Diagram

Figure 6: Model output showing replication of reference mode and the results of a 10% increase in egg loss and trend lines.

Figure 7: Second iteration of Causal Loop Diagram.

Figure 8: Comparison of Life Stages

Figure 9: Results of various runs as compared to base run.

Figures

SYSTEM BEHAVIOR

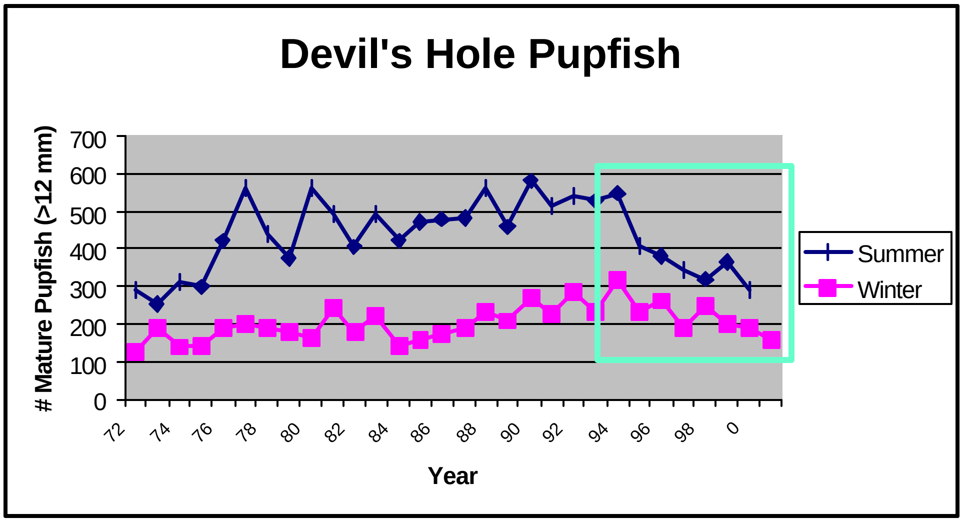


Figure 1.

SYSTEM BEHAVIOR

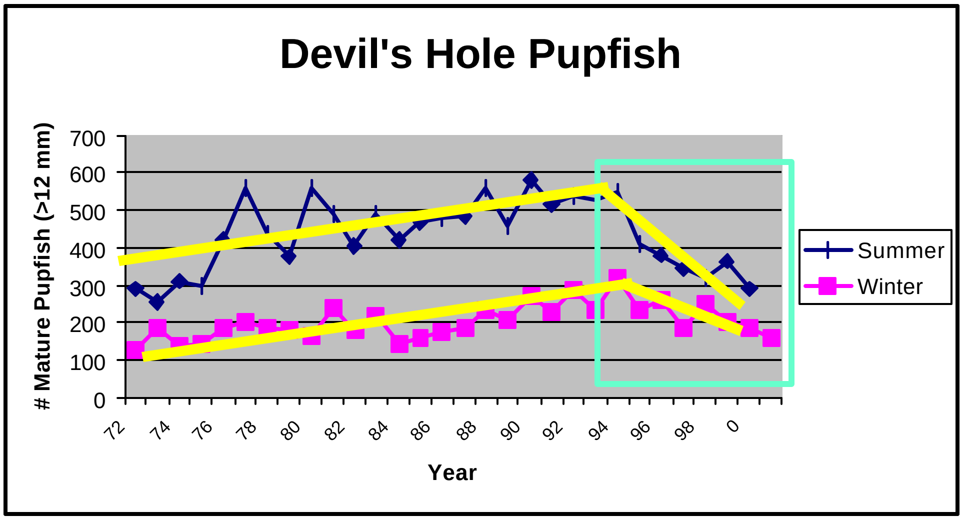


Figure 2.

CAUSAL LOOP DIAGRAM

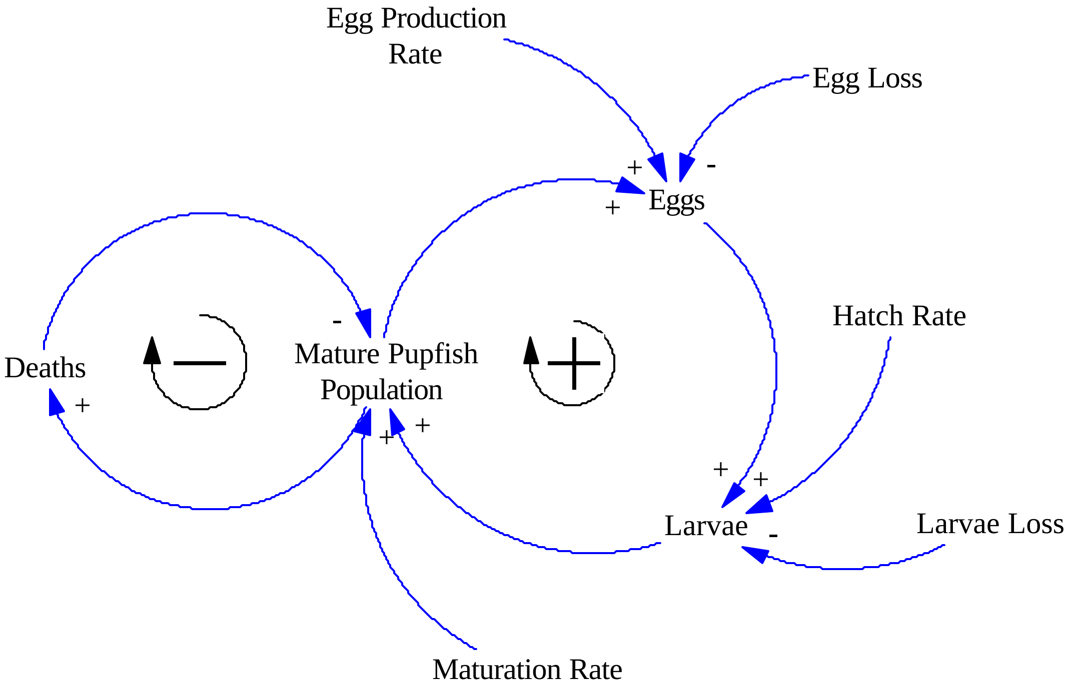


Figure 3.

ORIGINAL STOCK and FLOW MODEL

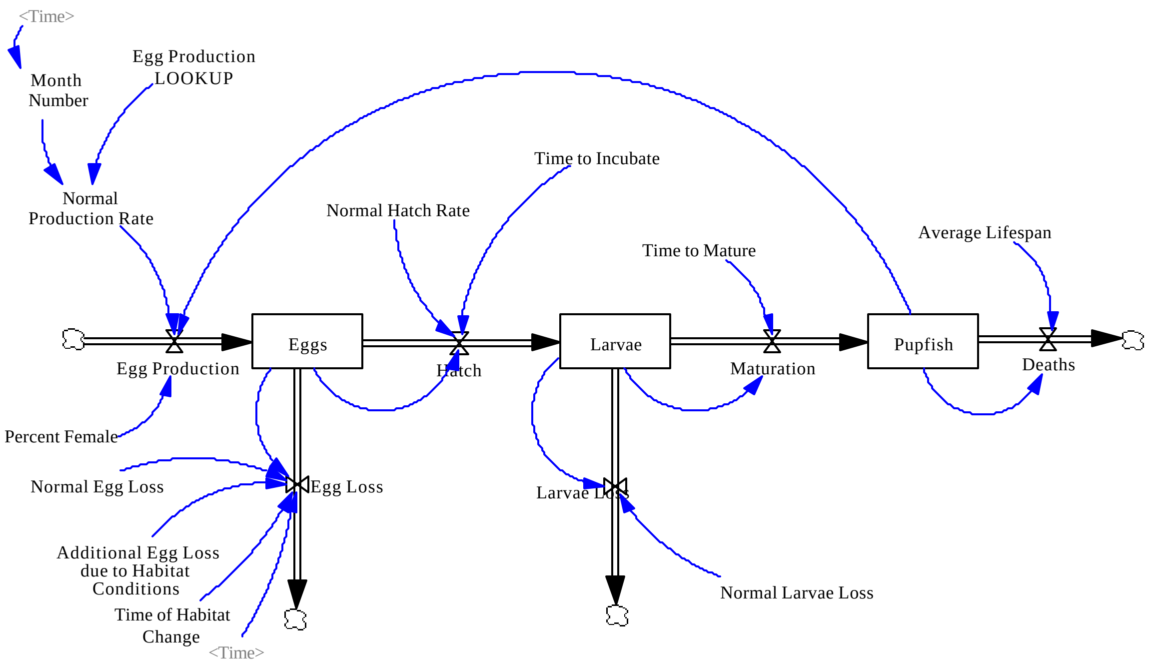


Figure 4.

UPDATED STOCK AND FLOW MODEL

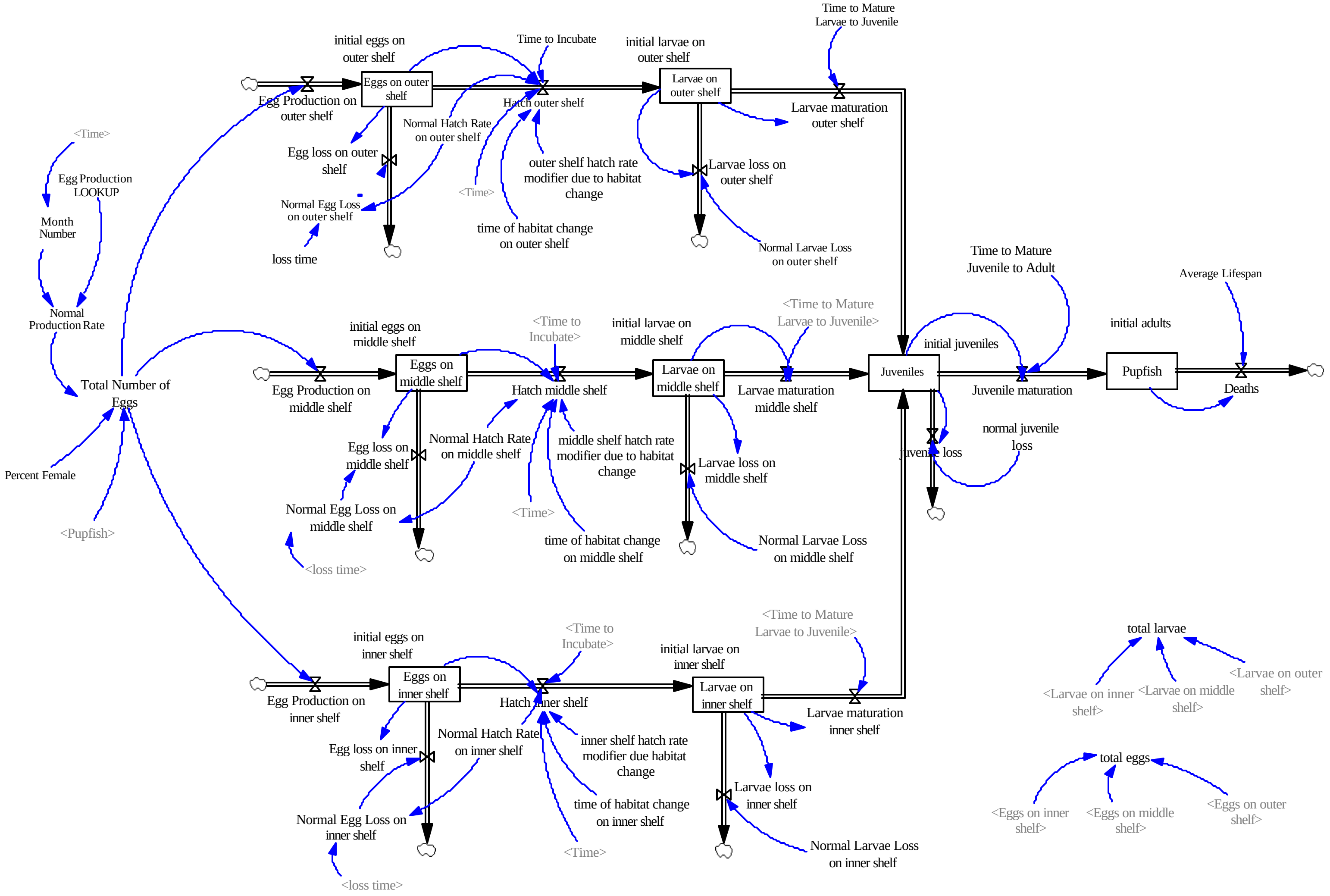
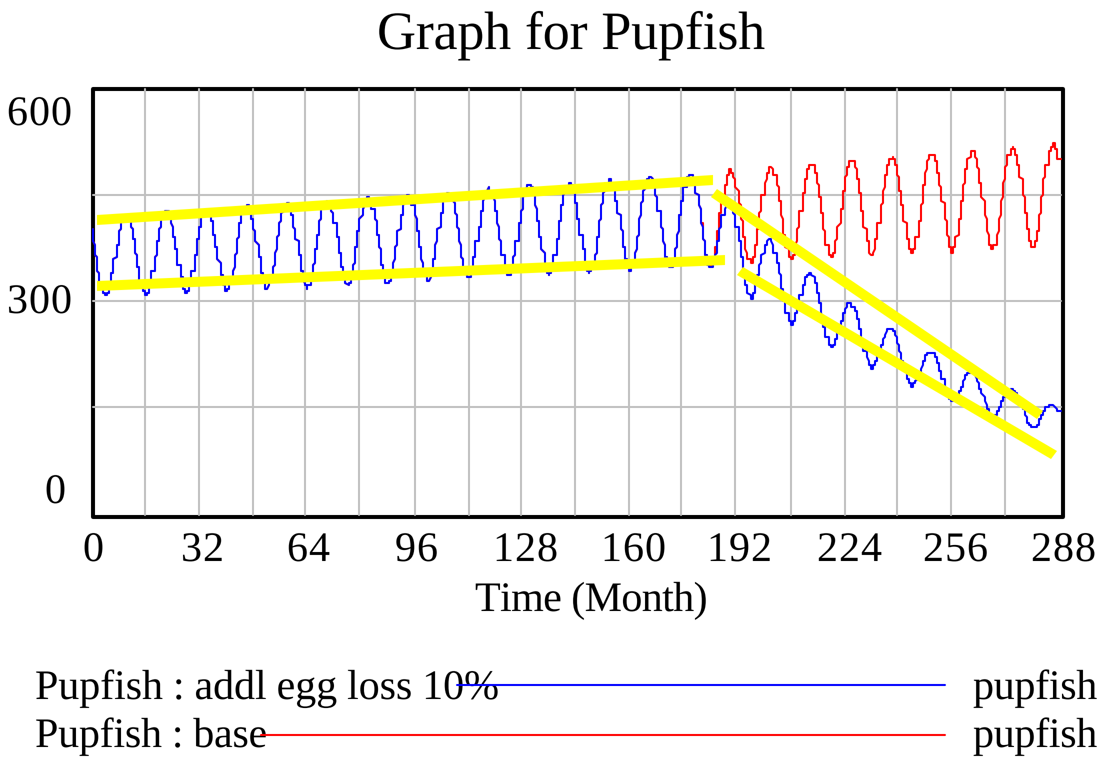


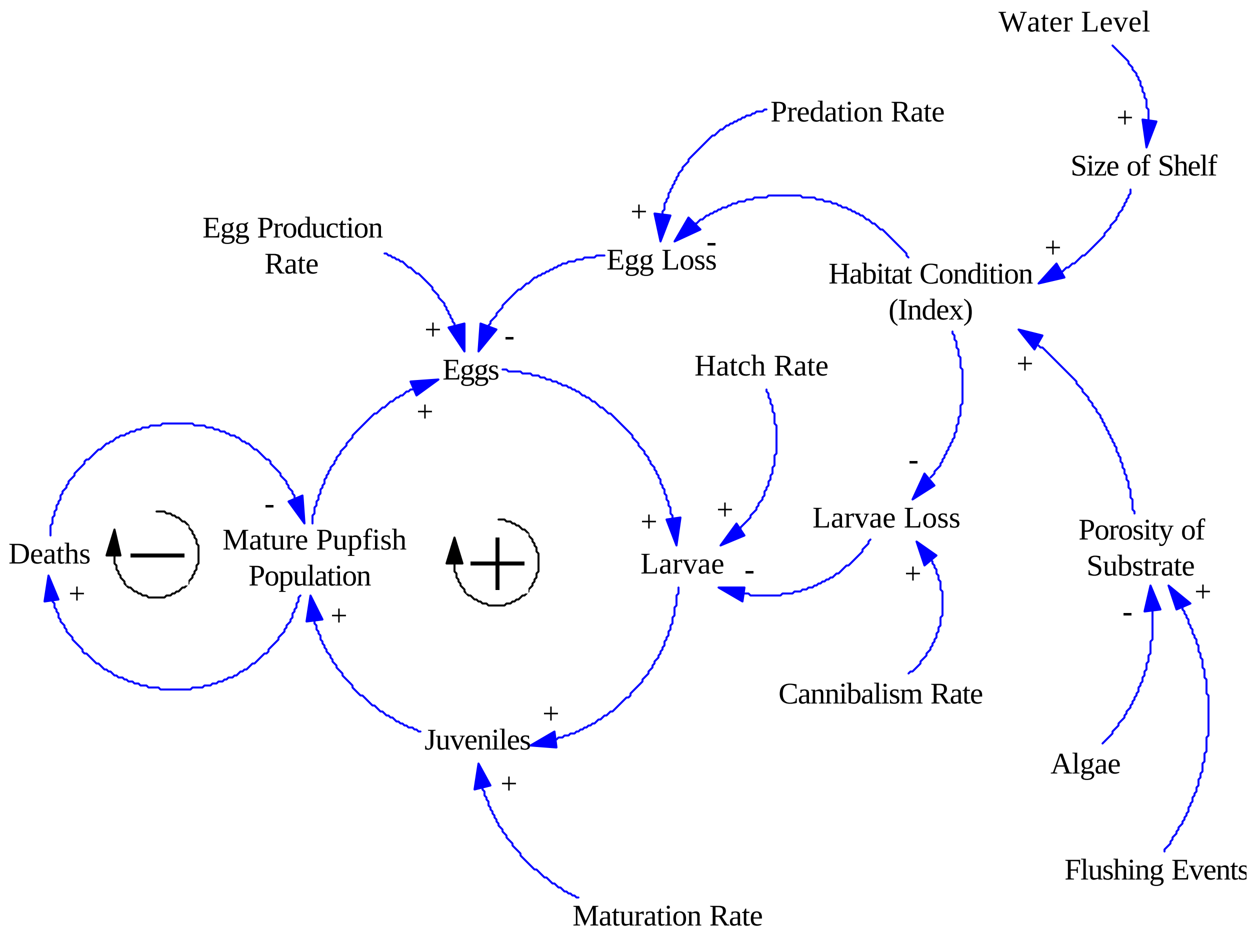
Figure 5.

MODEL OUTPUT



Graph for Pupfish

Figure 6.



Water Level
+
Predation Rate
Size of Shelf
+
Egg Production Rate
+
-
Egg Loss
Habitat Condition (Index)
+
+
-
Eggs
Hatch Rate
+
+
-
+
-
Larvae Loss
Porosity of Substrate
-
Deaths
Mature Pupfish Population
+
Larvae
-
+
+
+
-
+
+
Cannibalism Rate
+
Juveniles
Algae
+
Flushing Events
Maturation Rate

Figure 7.

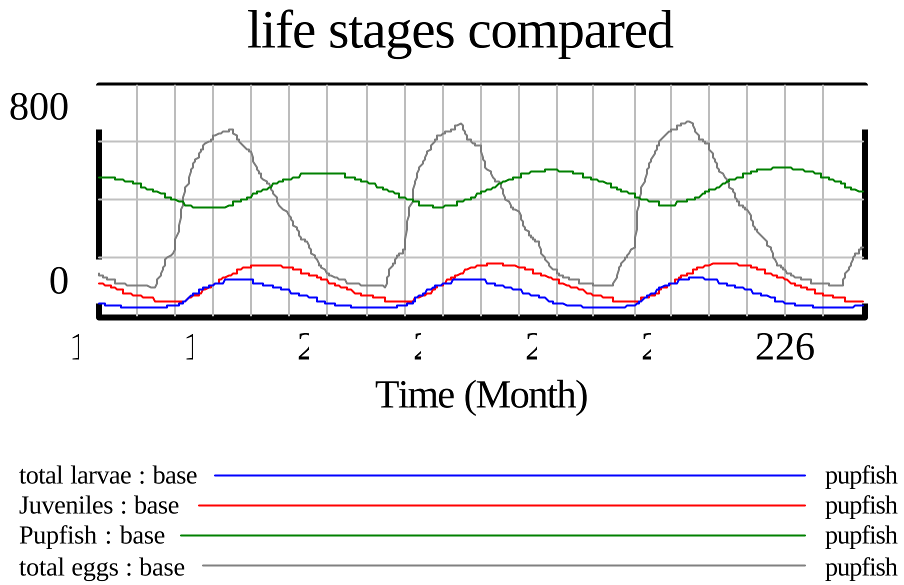

life stages compared
800
0
1
1
2
2
2
2
226
Time (Month)
total larvae : base pupfish
Juveniles : base pupfish
Pupfish : base pupfish
total eggs : base pupfish

Figure 8.

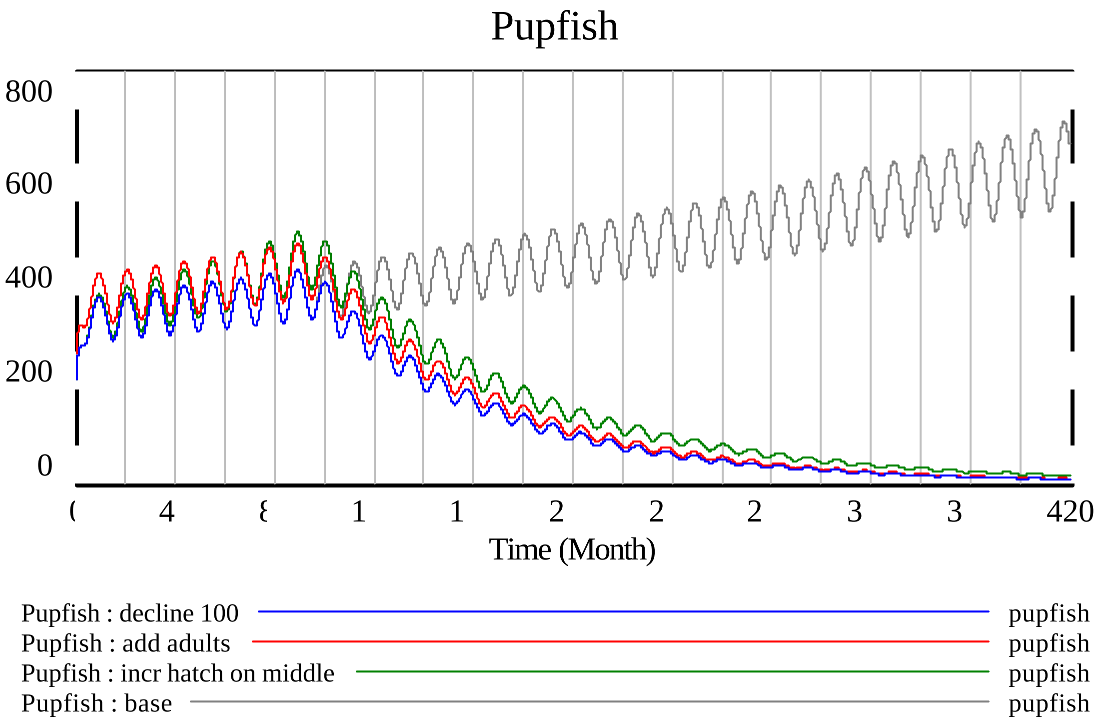


Figure 9.

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