Dynamics of a Discrete Population Model for Extinction and Sustainability in Ancient Civilizations

Michael A. Radin, Ph.D.
Associate Professor of Mathematics
Rochester Institute of Technology
School of Mathematical Sciences
85 Lomb Memorial Drive
Rochester, New York 14623

E – mail: michael.radin@rit.edu

OUTLINE OF THE PRESENTATION:

- **THE BASENER – ROSS MODEL.**
- **THE INVASIVE SPECIES MODEL.**
- **THE REIMARK – SACKER BIFURCATION.**
- **THE NUMERICAL BIFURCATION ANALYSIS.**
- **GLOBAL ANALYSIS & BASIN OF ATTRACTION.**
- **THE JULIA SET.**

THE BASENER – ROSS MODEL:

- **Let *P* be a population** and let ***R* be the amount of resources**. In this model the carrying capacity is determined by the amount of resources. Those resources are themselves a biological population and are therefore governed by their own standard logistic differential equation. The Basener-Ross model is given by a system of two differential equations. One equation governs the growth rate of the population with the carrying capacity set as *R* and the second equation governs the growth rate of the resource, *R* (Basener & Ross, 2004).

- To derive the Basener-Ross equations, assume that the resources would equilibrate at their natural carrying capacity in the absence of people. So when the population is zero the equation for the resources should be the standard logistic equation with . As in the standard logistic model above we call ***c* the growth rate** and ***K* the carrying capacity** of the resources. The constant c has units of inverse time; it is the fraction by which the resource supply would increase per unit time were the resource supply far from the island's carrying capacity. The **carrying capacity *K*** has the same units as *R*, it is the maximum amount of resources that the island can support.

- The term *-hP* accounts for the harvesting of the resources. The **constant *h*, the per person harvesting constant**, has units of reciprocal time; it is on the order of the reciprocal of the average lifetime of members of the population. The population *P* has units of persons, as does *R*; one unit of the resources is the amount of resources required to support a member of the population through their lifetime. We assume that the resources are accessible so that the amount of harvesting is proportional only to the population. This is a reasonable assumption for people on a small island.

- At any given time the size of the population that our island can support depends on the amount of resources on the island. Given our choice of units, the island has the capacity to support *R* people. The evolution of the population is described by a **Logistic Equation** with the carrying capacity equal to *R*.

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{R}\right)$$
$$\frac{dR}{dt} = cR\left(1 - \frac{R}{K}\right) - hP$$

- The positive constant *a* has units of inverse time. The quantity *aP* is the net growth rate of the population in circumstances in which resources are abundant. Observe that when there are no resources ($R = 0$) the carrying capacity for the population is zero. This makes sense, but it causes mathematical trouble in the form of a singularity on the *P*-axis. The (*P/R*) term in the equation above places the Basener Ross model in the class of ratio-dependent models, a class that has recently received much attention in the population biology literature. (Turchin, 2003a,b)

- The main virtues of this model are that it incorporates a variable carrying capacity for the population and that it is based on a simple but sensible account of the interaction between a population and its resources. Moreover, the predictions of this model match archaeological data for the population of Easter Island; the predictions of standard models, such as the logistic model or the Lotka-Volterra model, do not.

THE INVASIVE SPECIES MODEL:

- Terry Hunt hypothesizes that Polynesian rats greatly curtailed the growth of the human population of Easter Island (Hunt, 2006, 2007). We assume that the trees are the primary foundation for the resources. For example, the people used the trees to make boats for fishing and the trees enabled a bird population to live on the island. Hence, we assume that the amount of resources available for the people is proportional to the number of trees, and the differential equation modeling the growth rate of the human population will be a logistic growth equation with the carrying capacity being the amount of trees. Our units on the trees are chosen such that one unit of trees is sufficient to sustain one person. In these units the carrying capacity is not just proportional to the amount of trees; it is simply equal to the amount of trees. We denote the growth rate of the human population in abundance of resource as a. This yields the following equation:

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{T}\right)$$

- The seeds of trees on the island provided the resource for the rat population. Thus the differential equation modeling the growth rate of the rat population, *R(t)*, is the standard logistic growth model with the amount of trees, *T(t)*, determining the carrying capacity. We measure *R* in units of the number of rats that are supported by one tree unit. We denote the growth rate of the rats when the trees are abundant as *c*.

$$\frac{dR}{dt} = cR\left(1 - \frac{R}{T}\right)$$

- The growth rate of the trees, in the absence of the harvesting by the human population, will be modeled by a modified logistic equation. The initial growth rate of the resource, $\frac{b}{1+fR}$, is equal to *b* in the absence of rats and decreases with an increasing rat population. The rats eat the tree seeds, reducing the overall growth rate of the trees. The carrying capacity, *M*, of the resources will be considered constant with respect to the rat population. As in the Basener-Ross model, we assume the humans harvest the resource at a rate *hP*. This harvesting rate assumes that the number of trees harvested is proportional to the number of people, a reasonable assumption on a small island where the people have easy access to the trees.

$$\frac{dT}{dt} = \frac{b}{1 + fR}T\left(1 - \frac{T}{M}\right) - hP$$

- In the absence of rats the invasive species model simplifies to the Basener-Ross model. Thus the full model is:

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{T}\right)$$

$$\frac{dR}{dt} = cR\left(1 - \frac{R}{T}\right)$$

$$\frac{dT}{dt} = \frac{b}{1+fR}T\left(1 - \frac{T}{M}\right) - hP$$

- We measure *P* in people. We will measure *T* in units of the amount of trees that would support 1 human. We measure *R* in the number of rats that would be supported by one tree unit.

- When *P = 1* there is one person; when *T = 1* there are 10 trees assuming that a person can be supported by 10 trees; when *R = 1* there are 1000 rats, assuming that each tree can support 100 rats. These numbers are presented only to illustrate the relationship between the units and the objects they measure. They are not the actual values. The model parameters are estimated in the next section.

THE PARAMETER ESTIMATION:

- We will provide estimations of the six parameter values *a, b, c, f, h* and *M*. It is impossible to determine the values with precision for an ancient civilization in an ecosystem that no longer exists. Consequently, for each parameter we determine a range of reasonable values using established biological research on similar ecosystems.

- The **growth rate of the population of people a** could reasonably range from 0.005 to 0.05 per year. The growth rate for a pre-industrialized civilization tends to be around 0.0045. (Cohen, 1995) However, in the presence of abundant food this rate can be significantly higher. For example, historically documented cases (Birdsell, 1957) place the growth rate of a human population on Pitcairn Island at 0.034.

- The **growth rate of the Polynesian rats c** could reasonably range from 5 to 25 per year. A litter size ranges from 1 to 10, with an average of 3.8. A female rat can have up to 13 litters in a year, with an average of 5.2. The time to maturity for a female rat is less than one year. (Williams 1973) The sex ratio is usually close to 1:1, but this changes to a male bias, it seems, in more dense, stable populations. Yearly production rate for females in similar islands are 17.2 (Hawaii); 9.8 (Ponape); 4.8 (Kure), 25.7 (Malaya) (Tamarin & Malecha, 1972).

- It is also worthwhile considering the **maximum number of rats** that could have been supported on the island. For comparison, the density of rats on Kure Atol, a North Western Hawaiian Island is 45 rats per acre, fluctuating from 30 per acre to 75 per acre. The area of Easter Island is 171 sq-km., or 42255 acres. Thus, it would be reasonable to observe 2,000,000 or more rats on the Easter Island.

- We assume that the **growth rate of the Rapa Nui Jubaea palm trees** could range between 0.01 per year to 1 per year or more, since each tree produces about 100 kg of nuts per year.

- **The Carrying Capacity**; It has been estimated that the amount of fertile land needed to supply food for one person is approximately 350 square meters (Cohen, 1995), varying to a great degree on the type of land and climate. The area of Easter Island is approximately 166,000,000 square meters. If all of it were fertile and if it were farmed efficiently there would be enough food for 475,000 people. Since only some of the land is farmable and optimal agricultural methods were not being implemented our approximation of a maximum sustainable population of 12,000 reasonable. We estimate that the carrying capacity of the Rapa Nui Jubaea palm trees in units of people is $M = 12{,}000$. We take this as the carrying capacity for the trees in the absence of people and rats.

- **Per Person Harvesting Rate h;** It is difficult, perhaps impossible, to get an accurate value for the rate at which the population used the trees. We take $h = 0.25$, meaning roughly that every 4 islanders cut down one tree each year.

- **The Parameter f**; The growth rate of the trees is a function of the rat population. The growth rate approaches zero as the rat population approaches infinity. The parameter f is a measure of the decrease in the growth rate of the trees as the number of rat units increases. The growth rate of the trees will be halved when $Rf = 1$. We estimate that this occurs when $R = 1{,}000$. Thus we estimate f to be approximately 10^{-3}.

- **Numerical Simulations**; Numerical solutions to the invasive species model with the parameter values taken from the ranges derived above are shown in Figure 1. The parameters used were **a = 0.03, b = 1, c = 10, M = 12,000, h = 0.25 and f ranges from 0.0004 to 0.001**. Observe that, if we assume all parameters other than f are held constant then the rate at which the rats eat nuts determines the long term success or collapse of the human population. The top three traces imply the plausibility of Hunt's hypothesis.

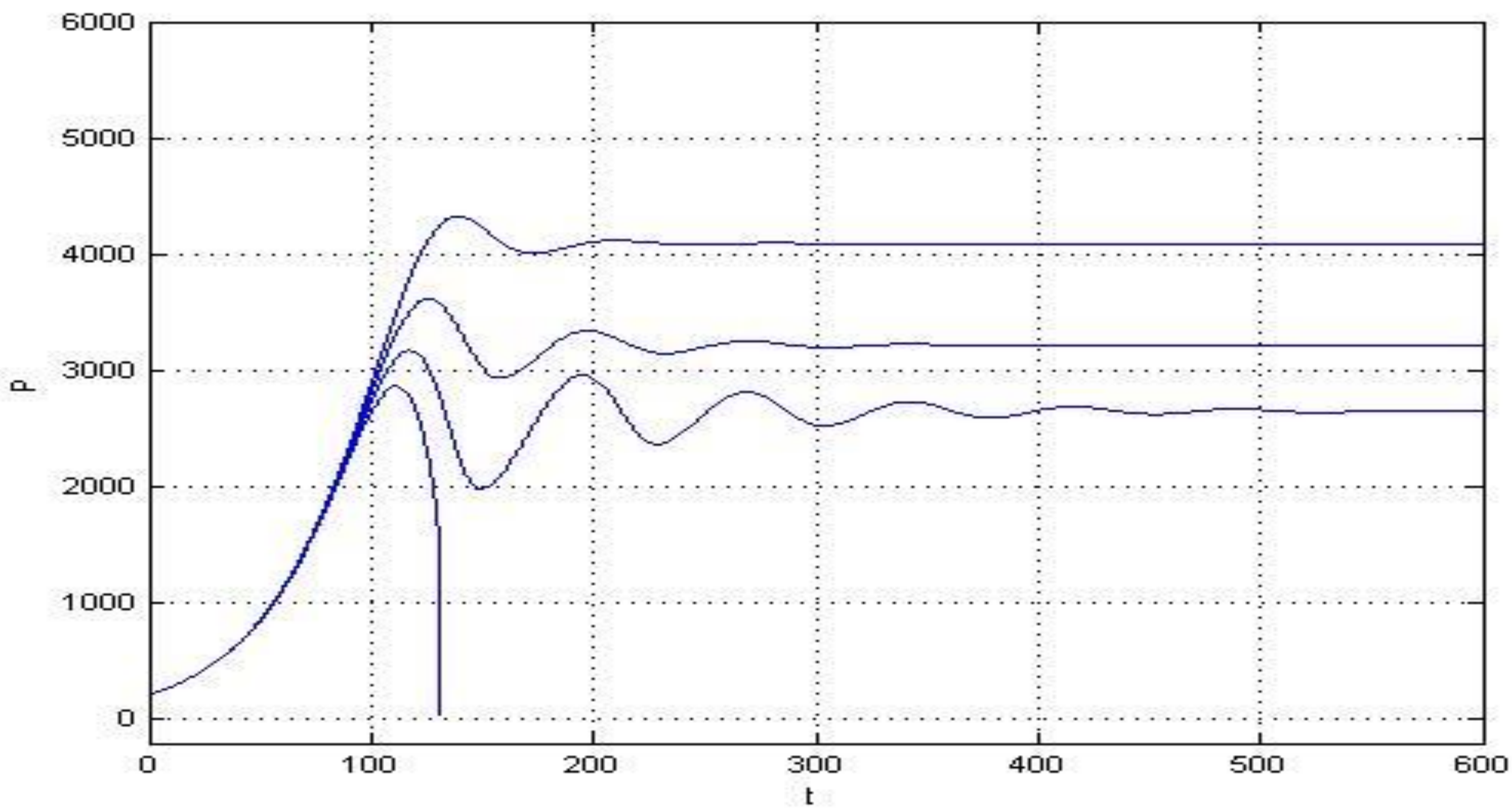


Figure 1: The human population is graphed for <u>*f* ranging from 0.0004 to 0.001</u>. It can be seen that for small values of *f* the population oscillates around the coexistence equilibrium and for larger values of the *f* parameter the human population is unstable and crashes. This illustrates that the stability of the coexistence equilibrium in the Invasive Species Model is sensitive to the parameter modeling the effect of the rats.

THE EQUILIBRIA OF THE MODEL:

The model has four equilibrium points:

- $P = 0,\ T = M,\ R = 0$
- $P = 0,\ T = M,\ R = M$
- $P = T = \frac{(b-h)M}{b},\ R = 0$ **(Coexistence Equilibrium)**
- $P = T = R = \frac{(b-h)M}{b+fhM}$

• The linearized stability of the equilibrium points is described by the following **Jacobian Matrix**:

$$\begin{bmatrix} a - \dfrac{2aP}{T} & \dfrac{aP^2}{T^2} & 0 \\ -h & b\,\dfrac{M-2T}{(1+fR)M} & bfT\,\dfrac{-M+T}{M(1+fR)^2} \\ 0 & \dfrac{cR^2}{T^2} & c - \dfrac{2cR}{T} \end{bmatrix}$$

THE HOPF BIFURCATION AT THE COEXISTENCE EQUILIBRIUM:

- The linearized stability of the coexistence equilibrium is described by the following Jacobian Matrix:

$$J = \begin{bmatrix} -a & a & 0 \\ -h & -\dfrac{b - fhM - 2h}{1 + fR} & -hM(b-h)\dfrac{f}{b(1+fM)} \\ 0 & c & -c \end{bmatrix}$$

- The characteristic equation then is given by

$$\lambda^3 + A\lambda^2 + B\lambda + C = 0,$$

where $A = -tr(J), B = \Sigma M(J)$ and $C = -\det(J)$.

We know (Brooks, 2006) that for the eigenvalues λ_1, λ_2 and λ_3

$$\lambda_1 + \lambda_2 + \lambda_3 = -A$$
$$\lambda_1\lambda_2 + \lambda_1\lambda_3 + \lambda_2\lambda_3 = B$$
$$\lambda_1\lambda_2\lambda_3 = -C$$

- We will go through a Hopf bifurcation when two of the eigenvalues cross the imaginary axis. This will happen when $\lambda_2 = i\omega$ and $\lambda_3 = -i\omega$. Using the previous equations we obtain that in this case $\lambda_1 = -A, \omega^2 = B$ and $\lambda_1\omega^2 = -C$.

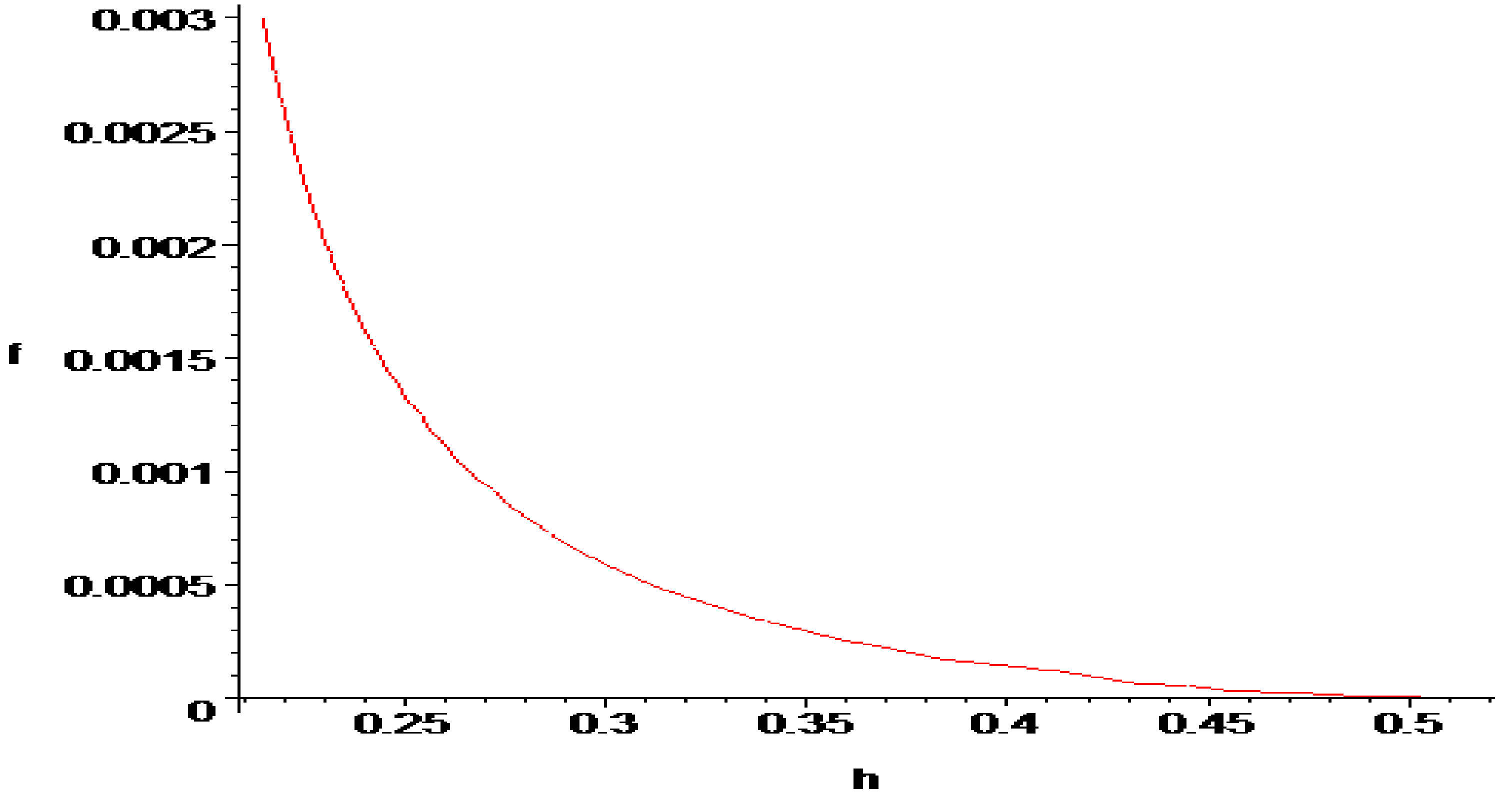


Figure 2: The equation ***AB = C*** is implicitly plotted in the parameters *h* and *f*. Below the curve the coexistence equilibrium is linearly stable. A **Hopf Bifurcation** occurs on the curve and above the curve the coexistence equilibrium is linearly unstable. Thus for any level of harvesting by the human population there exists a level of damage that the rats could cause that would crash the human population.

THE DISCRETE MODEL:

- By discretizing the Logistic Model by Turchin in 2003

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{R}\right)$$

$$\frac{dR}{dt} = cR\left(1 - \frac{R}{K}\right) - hP$$

we get the following system of difference equations:

$$P_{n+1} = P_n + aP_n\left(1 - \frac{P_n}{R_n}\right)$$

$$R_{n+1} = R_n + cR_n\left(1 - \frac{R_n}{K}\right) - hP_n$$

- The discrete population model was developed to investigate the population dynamics of Easter Island. The model does achieve its original goal as can be seen in the figure below by depicting the population predicted from the model together with data points estimated from archeology. (The archeology gives us not only a few data points, but also, more significantly, the length of time of the extended growth period and the collapse.) The parameters are a = 0.044, c = 0.001, h = 0.018, K = 70,000, and the initial conditions are P_0 = 50, R_0 = 70000. The value for K is easy to estimate from the size and fertility of Easter Island. The value for a is in the standard range for pre-industrial revolution civilizations. (See (Cohen, 1995)) The values for c and h are more difficult to estimate, but as given are reasonable for tree growth and harvesting rates.

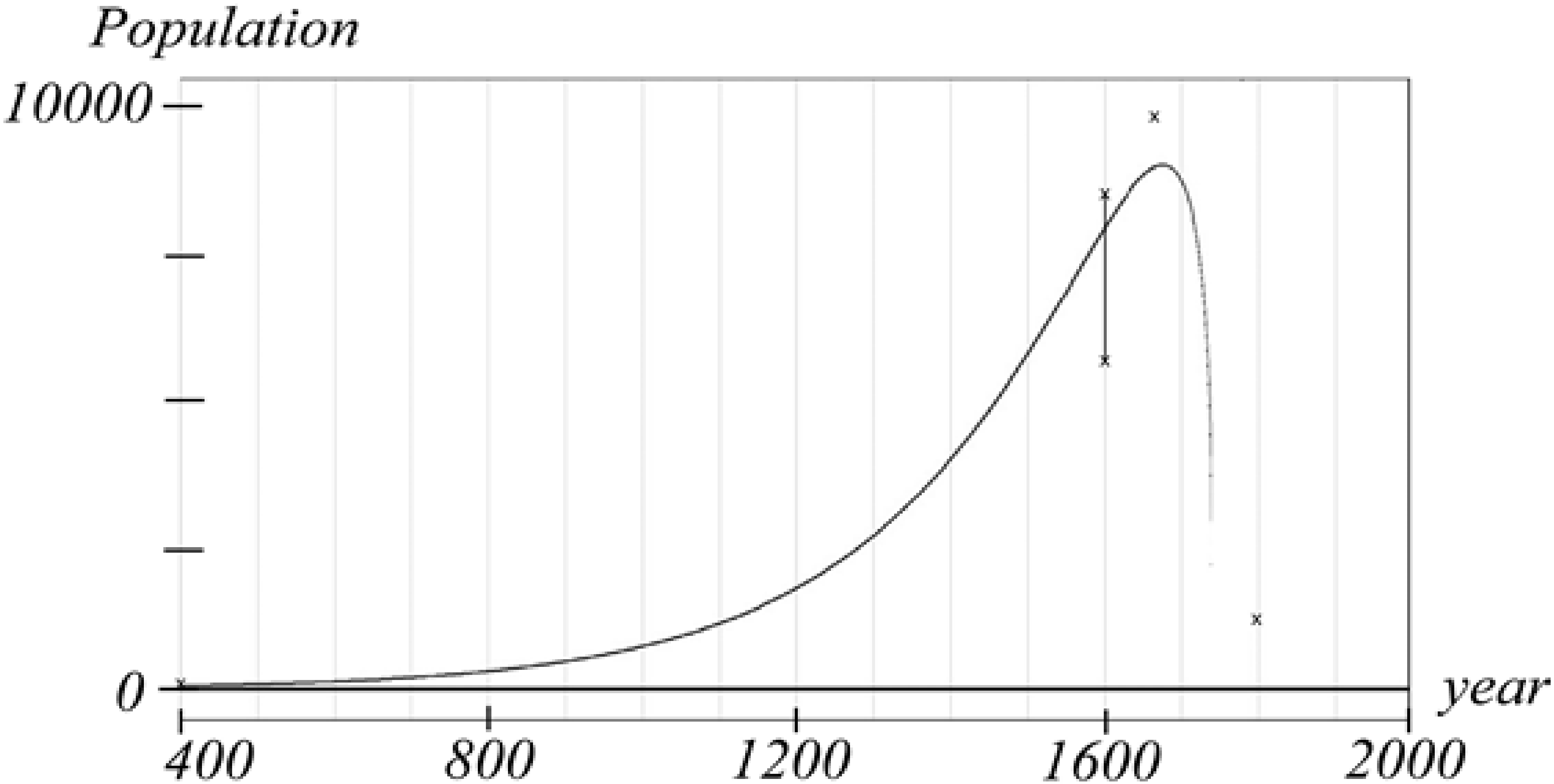


Fig. 3. The graph of population verses time using the discrete model applied to Easter Island. Each 'x' is a data point or data range approximated through archeological evidence. It is important to observe that not only does our model match the archeological data and qualitative description; it does so with realistic parameter values. For example, the 1-dimensional logistic model can experience a growth and collapse, but not with parameter values close to human growth rates. Moreover, the one dimensional logistic equation could not experience a growth on collapse matching the qualitative timescale provided by archeology for any parameter values.

THE EQUILIBRIA OF THE MODEL:

The model has two equilibrium points:

- $P = 0$, $R = 1$
- $(P_e, R_e) = \left(1 - \frac{h}{c}, 1 - \frac{h}{c}\right)$

  - These two equilibrium points and the singularity at $(P,R) = (0,0)$ will each be analyzed for linear stability in turn.

  - First let us show that any neighborhood of the singularity $(P,R) = (0,0)$ is unstable for all positive parameters, a, c, and h by considering the $P = 0$ axis. One can see that the origin is not stable by noting that for any small R, $F_R(0,R) > R$. Thus, in the absence of a human population, the resource does not become extinct on its own except in the case of very large growth rates. In the absence of a human population the resource dynamic behaves as the logistic map.

  - The second equilibrium of the system, $(P,R)=(0,1)$, will also be shown to be linearly unstable. In order to demonstrate that instability. The Linearized Stability of equilibrium points is described by the following Jacobian Matrix **J**.

$$\mathrm{J} = \begin{bmatrix} a - 2a\dfrac{P}{R} + 1 & a\dfrac{P^2}{R^2} \\ -h & c - 2cR + 1 \end{bmatrix}$$

- Now we consider the stability of the equilibrium point $(P_e, R_e) = \left(1 - \frac{h}{c}, 1 - \frac{h}{c}\right)$. In order for this equilibrium to exist in the first quadrant we require $h < c$ The Jacobian **J** evaluated at the equilibrium is

$$J = \begin{bmatrix} 1 - a & a \\ -h & -c + 2h + 1 \end{bmatrix}$$

- At the equilibrium $(P,R) = (0,1)$, the Jacobian Matrix is:

$$J = \begin{bmatrix} a + 1 & 0 \\ -h & 1 - c \end{bmatrix}$$

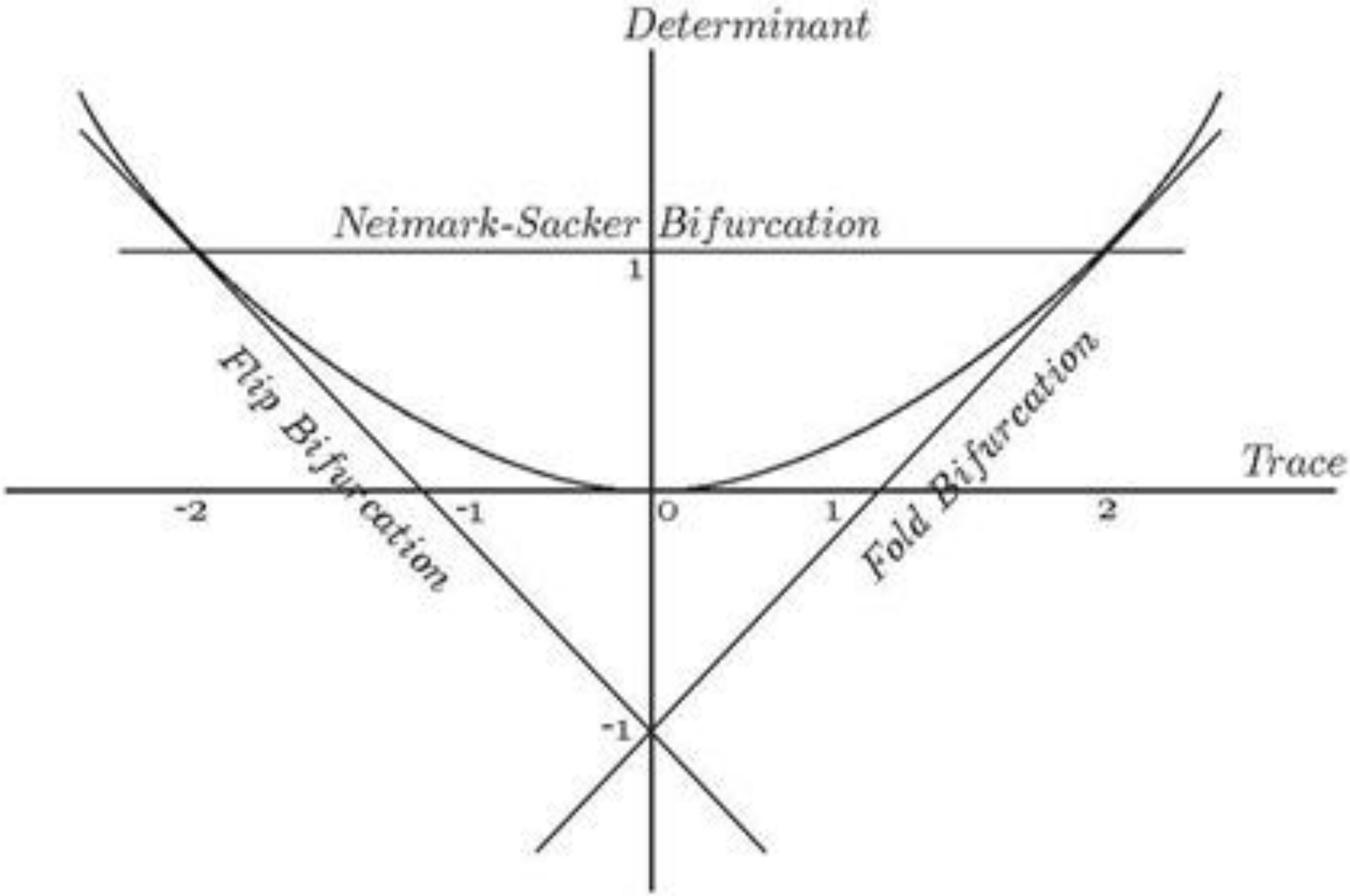
- The $a + 1$ eigenvalue of this lower triangular matrix is greater than 1 for any choice of $a > 0$ and thus this equilibrium is linearly unstable. The modeling interpretation is of course that when the settlers first arrive on the island their little colony has a chance to grow. Their arrival on the island can be seen as a perturbation from the equilibrium point $(P,R) = (0,1)$.

- Now we consider the stability of the equilibrium $(P_e, R_e) = \left(1 - \frac{h}{c}, 1 - \frac{h}{c}\right)$. In order for this equilibrium to exist in the first quadrant we require $h < c$ The Jacobian Matrix **J** evaluated at the equilibrium (P_e, R_e) is:

$$J = \begin{bmatrix} 1-a & a \\ -h & -c+2h+1 \end{bmatrix}$$

- The stability triangle in the trace-determinant plane is bounded by the inequalities:

$$\det(J) < 1$$
$$tr(J) - 1 < \det(J)$$
$$-tr(J) - 1 < \det(J).$$



Determinant
Neimark-Sacker Bifurcation
Flip Bifurcation
Fold Bifurcation
Trace
1
-1
-2
-1
0
1
2

- The stability triangle will now be used to analyze the stability of the equilibrium . The $tr(\mathbf{J})=2 - a - c + 2h$ and the $det(\mathbf{J})=h(2 - a) + (1 - a)(1 - c)$ are generated from the Jacobian evaluated at that equilibrium. The upper side of the stability triangle, which corresponds to a Neimark-Sacker bifurcation, is given by the inequality

$$h(2-a)+(1-a)(1-c)<1.$$

- The right side of the stability triangle, which corresponds to a fold bifurcation (also called a period doubling bifurcation), is given by

$$2-a-c+2h-1<h(2-a)+(1-a)(1-c).$$

- The left side of the stability triangle, which corresponds to a flip bifurcation, is given by

$$-(2-a-c+2h)-1\ <\ h(2-a)+(1-a)(1-c).$$

- These three equations simplify to

$$h(2-a)+(1-a)(1-c)\ <1,\ \mathit{N.{-}S.\ Bifurcation}$$
$$h<c,\quad \mathit{Fold\ Bifurcation}$$
$$(2-a)(c-h-2)<2h,\ \mathit{Flip\ Bifurcation}$$

- Because the population in a given region has the most control over the harvesting parameter *h*, the two remaining inequalities will be combined to produce a stability condition on *h*. The resulting stability zone, assuming $a < 1$, is

$$\frac{(a-2)(c-2)}{a-4} < h < \frac{1-(1-a)(1-c)}{2-a}.$$

- Of the three parameters, *a* is known with the most confidence. Anthropological studies estimate *a* 0.0045. (See (Basener & Ross, 2004)) Observe that for this *a* value Eq.(6) rounded to 2 significant figures becomes

$$0 < c - 2h < 2.$$

- For $a = 0.0045$ the intersection between the lines and occurs at the biologically irrelevant value of $c \approx 1773$.

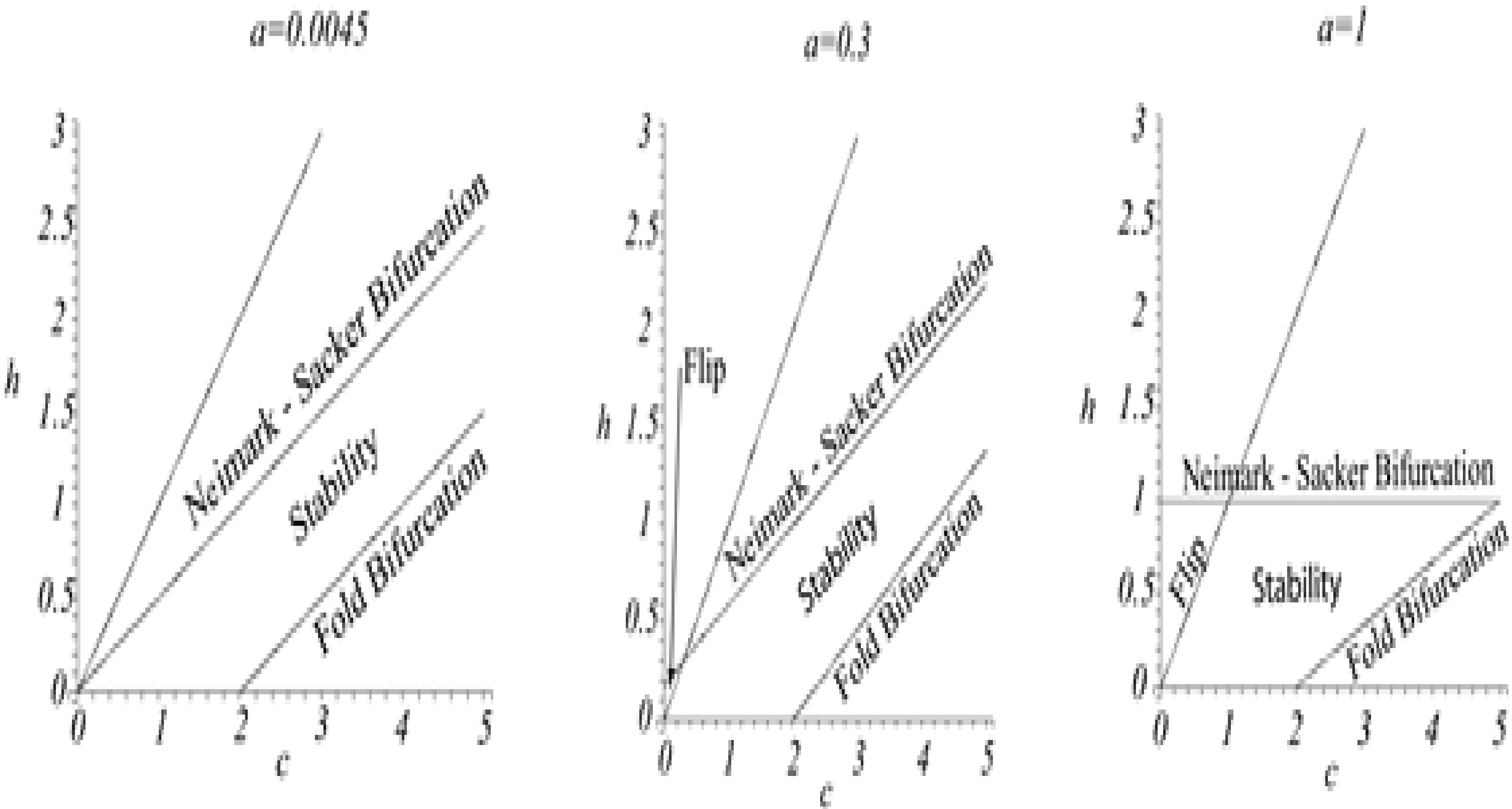


Fig. 4. The stability region for a = 0.0045, a = 0.3, and a = 1.

The Neimark-Sacker Bifurcation:

- Now let's turn our attention to the Neimark-Sacker bifurcation of the stability triangle. This corresponds to the boundary with $h(2-a)+(1-a)(1-c)=1$. We focus on the value of *h* because, as before, we assume that the population has the most control over the harvesting rate. If we fix the values of *a* and *c* and slowly change the value of *h* then we can see that we will leave the stability triangle on this boundary when

$$h=\frac{a+c-ac}{2-a}.$$

We also need that $-2<tr(J)<2$ at this *h* value

$$-2<2-a-c+2h<2.$$

- This gives us the following inequalities:

$$\frac{a+c}{2}-2<\frac{a+c-ac}{2-a}<\frac{a+c}{2}.$$

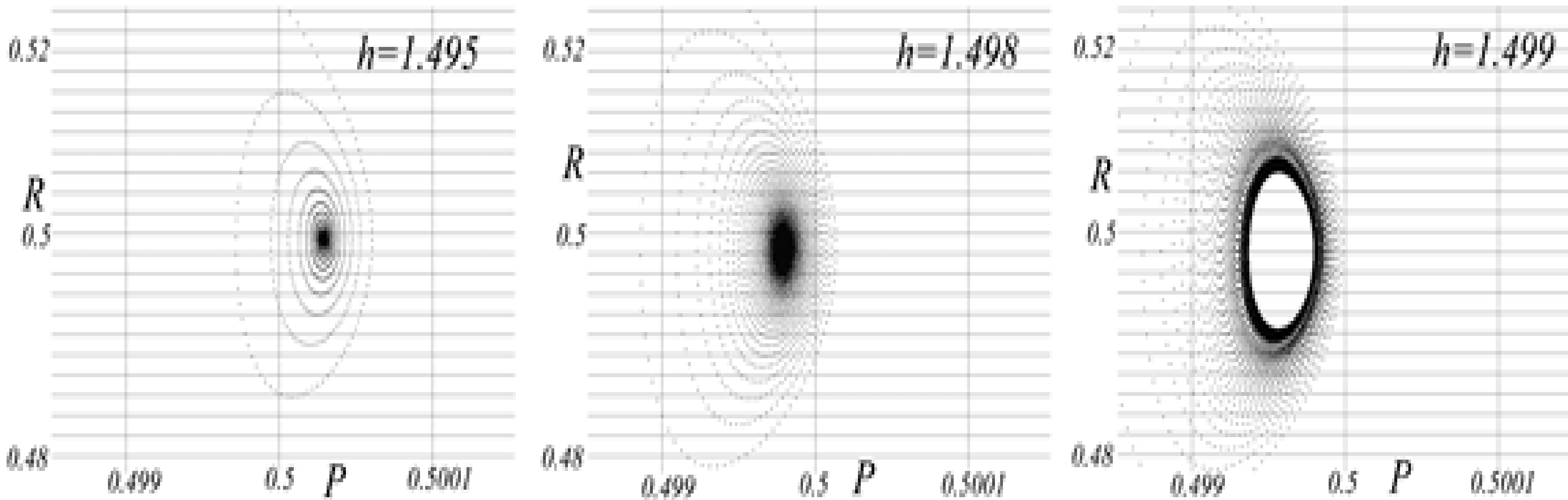


Fig. 5. Three phase planes are shown with *a* = 0.0045, *c* = 3 and *h*-values near the Neimark-Sacker bifurcation.

Numerical Bifurcation Analysis:

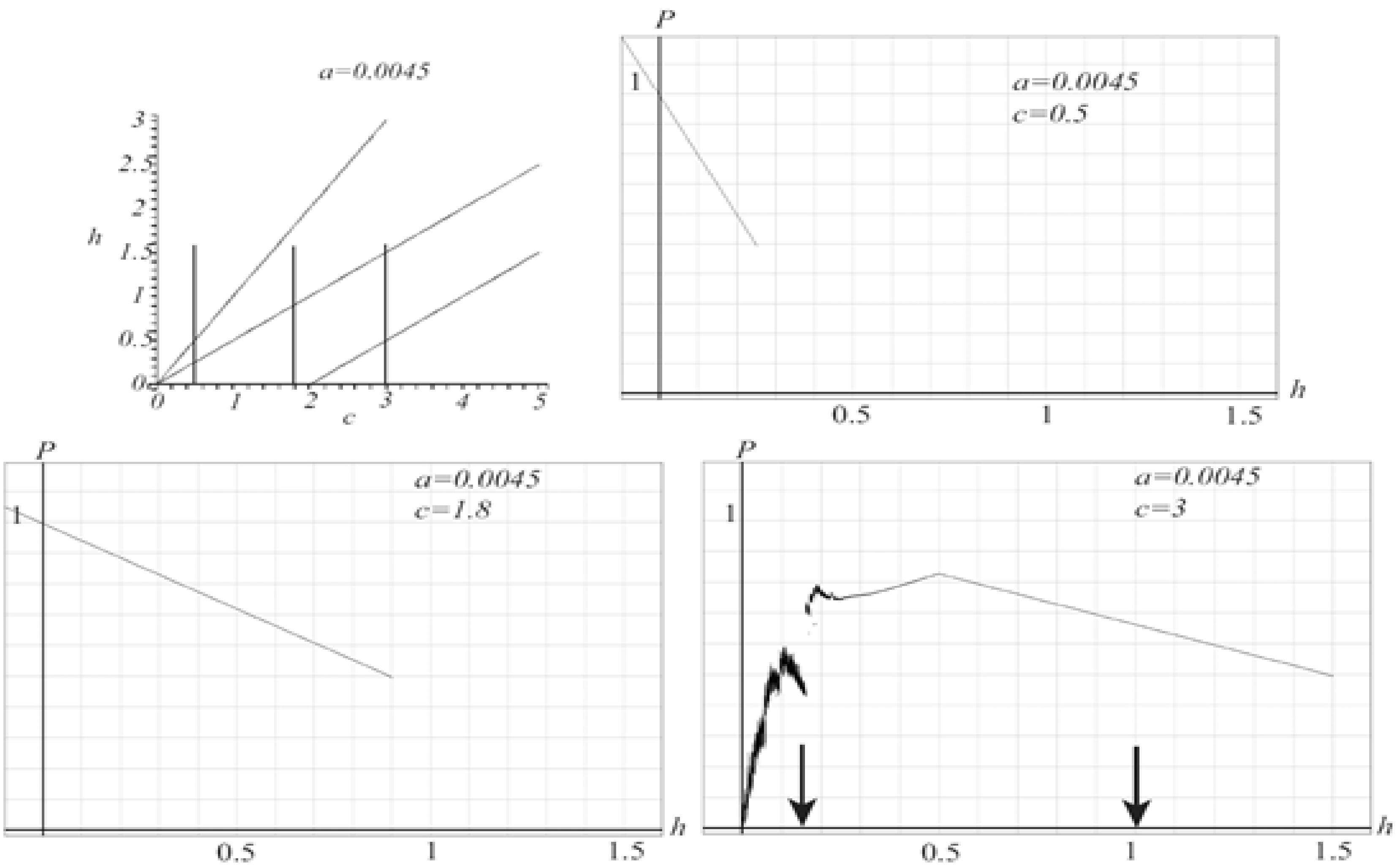


Fig. 6. The first plot is the stability region in the *c*,*h*-parameter plane for *a* = 0.0045 with lines indicating the parameter values for the bifurcation diagrams. Bifurcation diagrams are shown for *a* = 0.0045 with *c* = 0.5, *c* = 1.8, and *c* = 3.

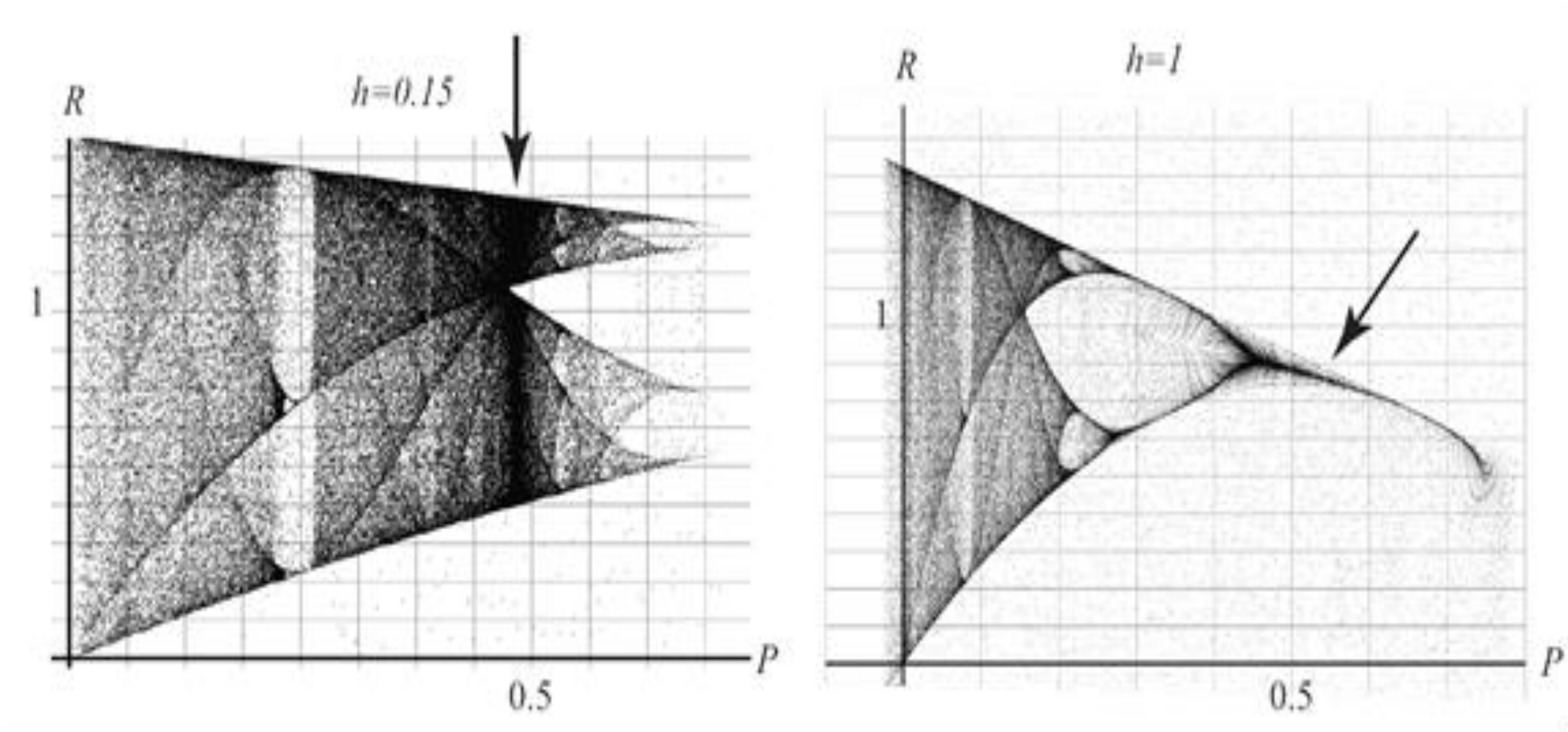


Fig. 5. The first 1000 iterates of 5000 initial conditions for a = 0.0045, c = 3 and h = 0.15 and h = 1. These parameter values are indicated by the arrows in the bifurcation diagram in Fig. 6. In the case with h = 0.15 the attractor is a chaotic region indicated by the arrow. In the case with h = 1 the attractor is an equilibrium point, also indicated by an arrow. In each case, the set resembling a bifurcation diagram for the logistic equation forms a ``stable set'' for the attractor.

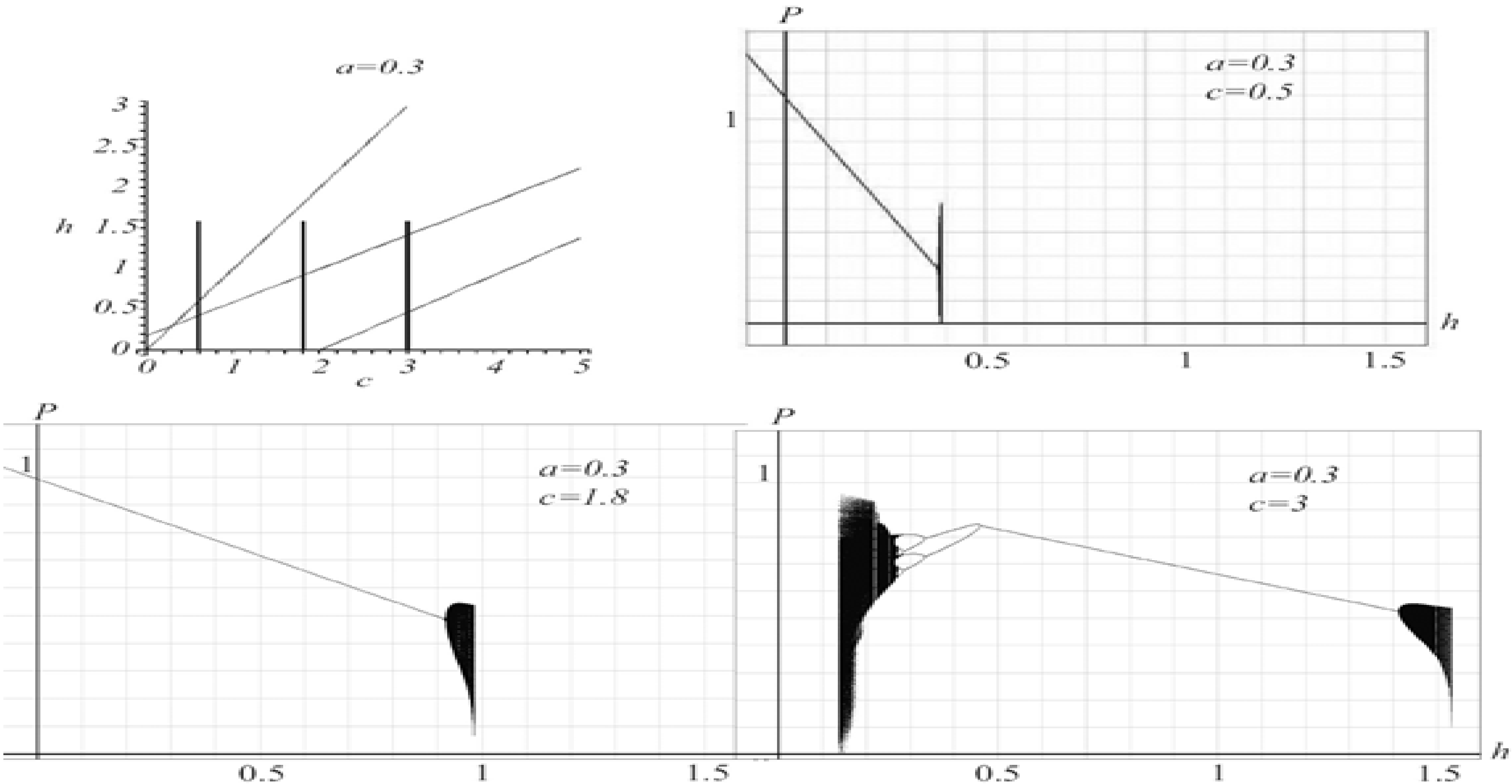
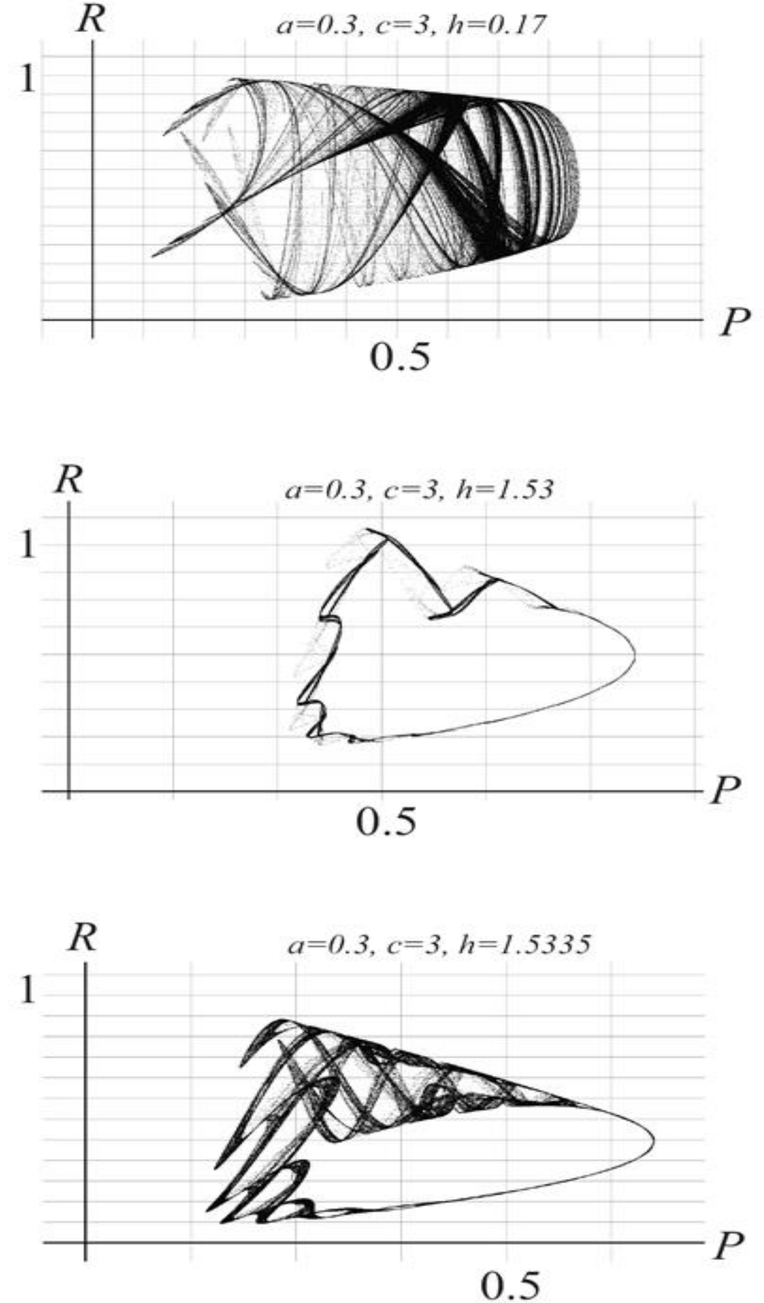
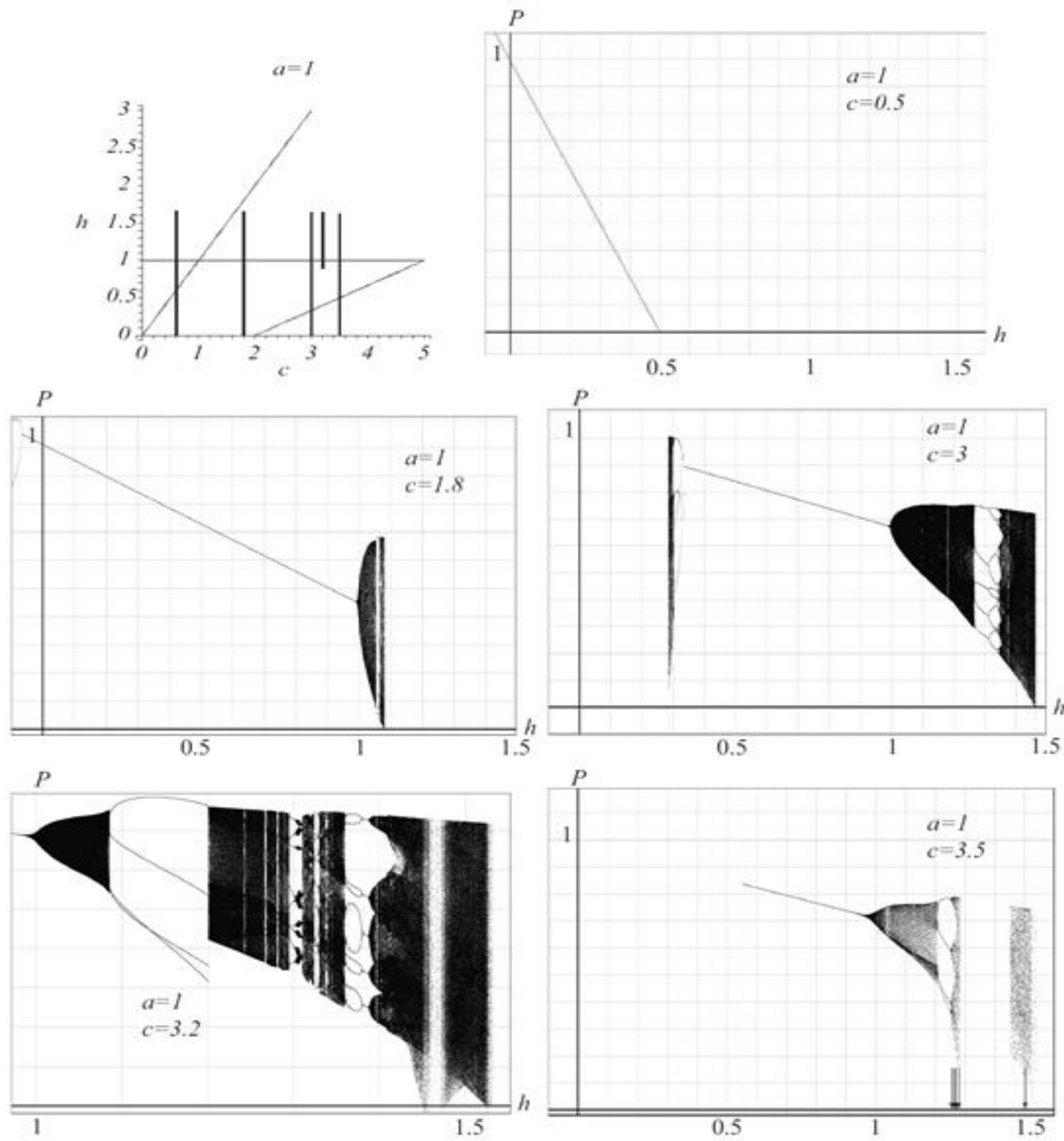


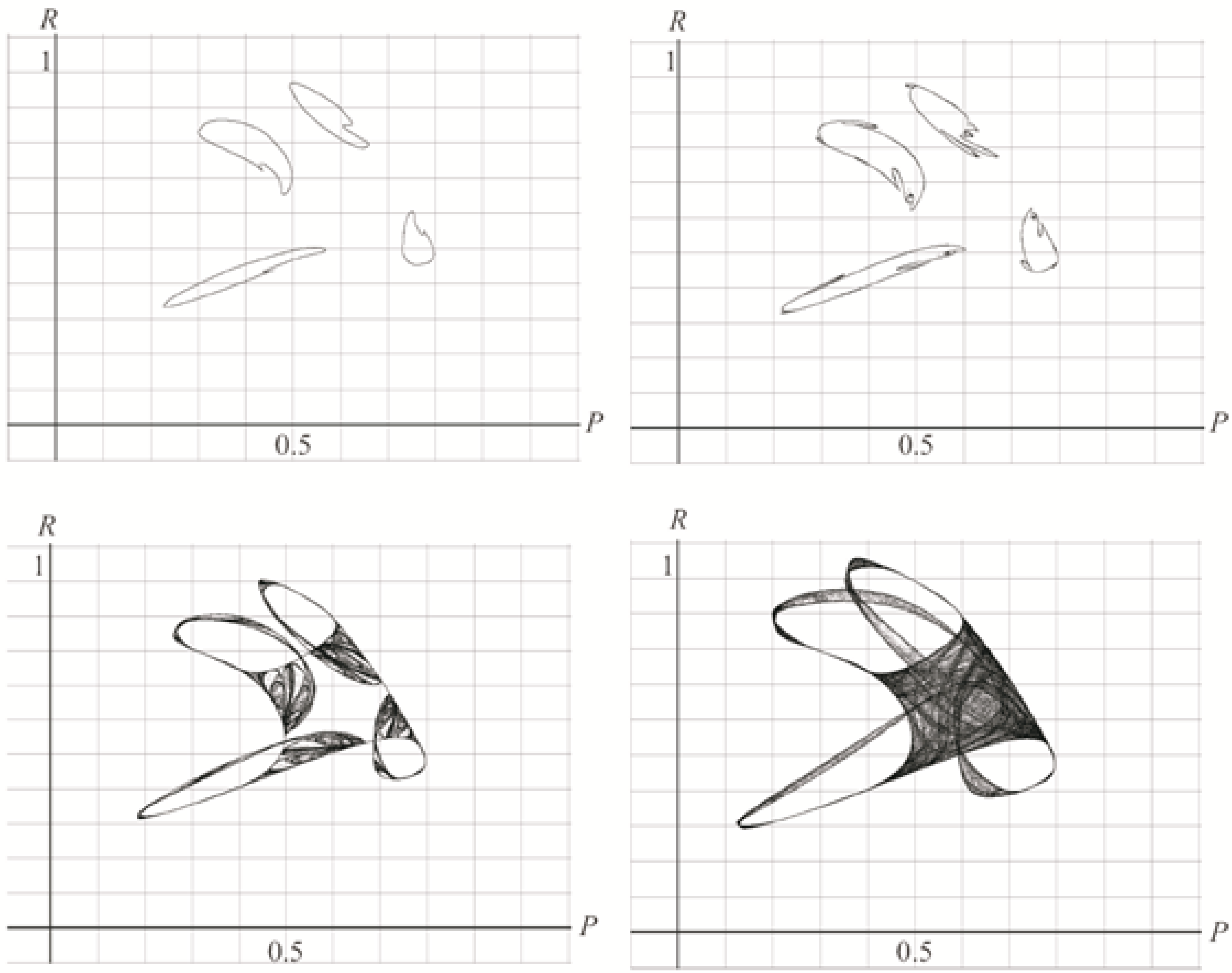
Fig. 6. The first plot is the stability region in the *c*,*h*-parameter plane for *a* = 0.3 with lines indicating the parameter values for the bifurcation diagrams. Bifurcation diagrams are shown for *a* = 0.3 with *c* = 0.5, *c* = 1.8, and *c* = 3. Observe the nontrivial attractors that occur just outside the stability region.



R
a=0.3, c=3, h=0.17
1
P
0.5
R
a=0.3, c=3, h=1.53
1
P
0.5
R
a=0.3, c=3, h=1.5335
1
P
0.5



a=1
h
c
a=1
c=0.5
P
h
a=1
c=1.8
P
h
a=1
c=3
P
h
a=1
c=3.2
P
h
a=1
c=3.5
P
h


R
1
P
0.5
R
1
P
0.5
R
1
P
0.5
R
1
P
0.5

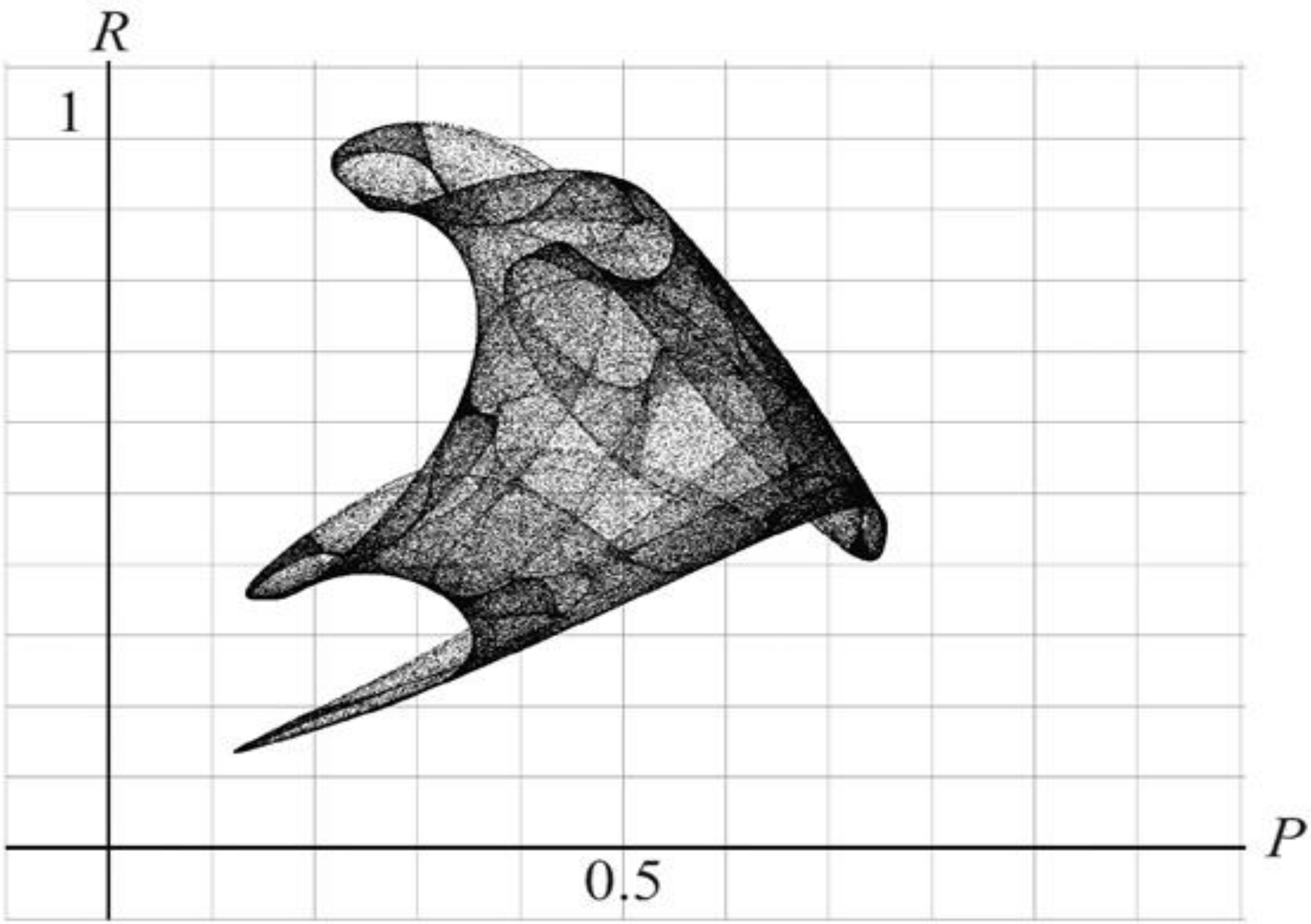


Fig. 7. The attractor for the system with a = 1, c = 3.5, and h = 1.5.

Global Analysis and Basins of Attraction:

- We focus on the basin of attraction of the attractor, which constitutes the set of initial conditions that do not lead to extinction. (The attractor may be a stable equilibrium point orbit may be a more complicated set. The basin of attraction is often also called the Julia set.) The basin of attraction is not the entire first quadrant. As is common for discrete systems, the basin of attraction is fractal in nature, and hence is difficult to determine precisely. In this section we provide some qualitative analysis of its size and shape for various parameter values. Let

$$Z_P = \{(P,R) | F_P(P,R) = 0\}$$

denote the zero set of F_P and let

$$Z_R = \{(P,R) | F_R(P,R) = 0\}$$

denote the zero set of F_R. Observe that Z_P is the pair of lines

$$Z_P = \{P = 0\} \cup \left\{P = R\left(1 + \frac{1}{a}\right)\right\}$$

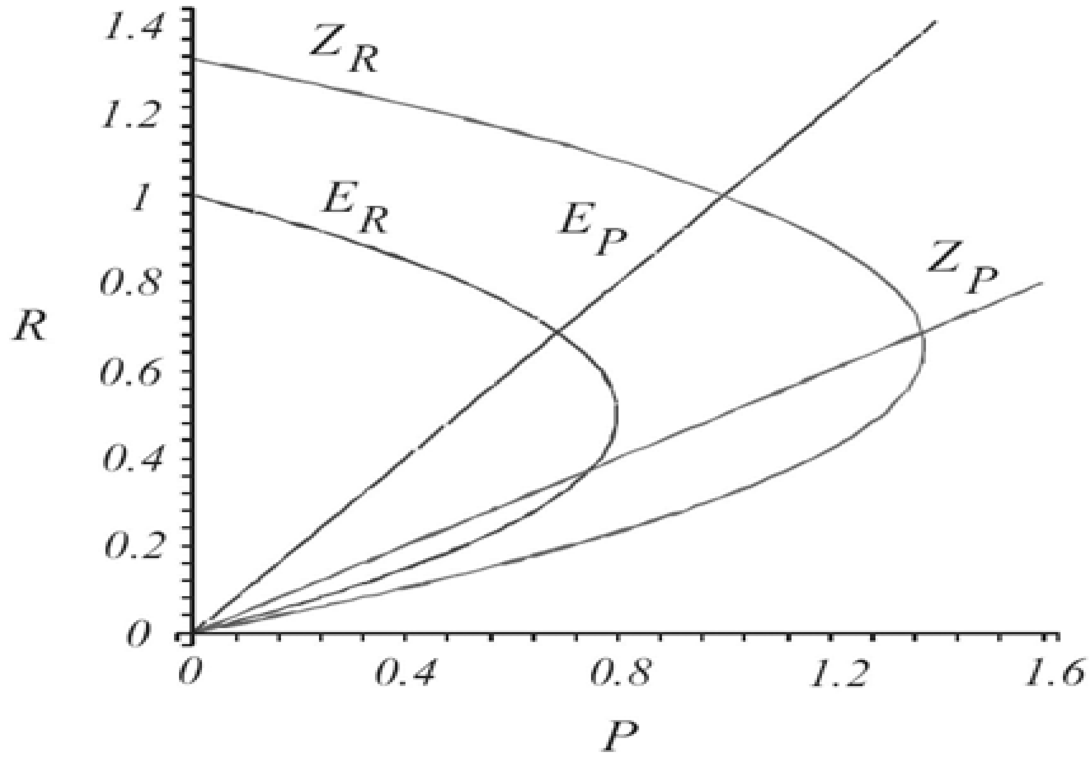
and Z_R is the parabola

$$Z_R = \left\{P = \frac{c}{h} R\left(1 + \frac{1}{c} - R\right)\right\}.$$

- So F maps Z_R to the P-axis and Z_P to the R-axis. Also useful are the sets

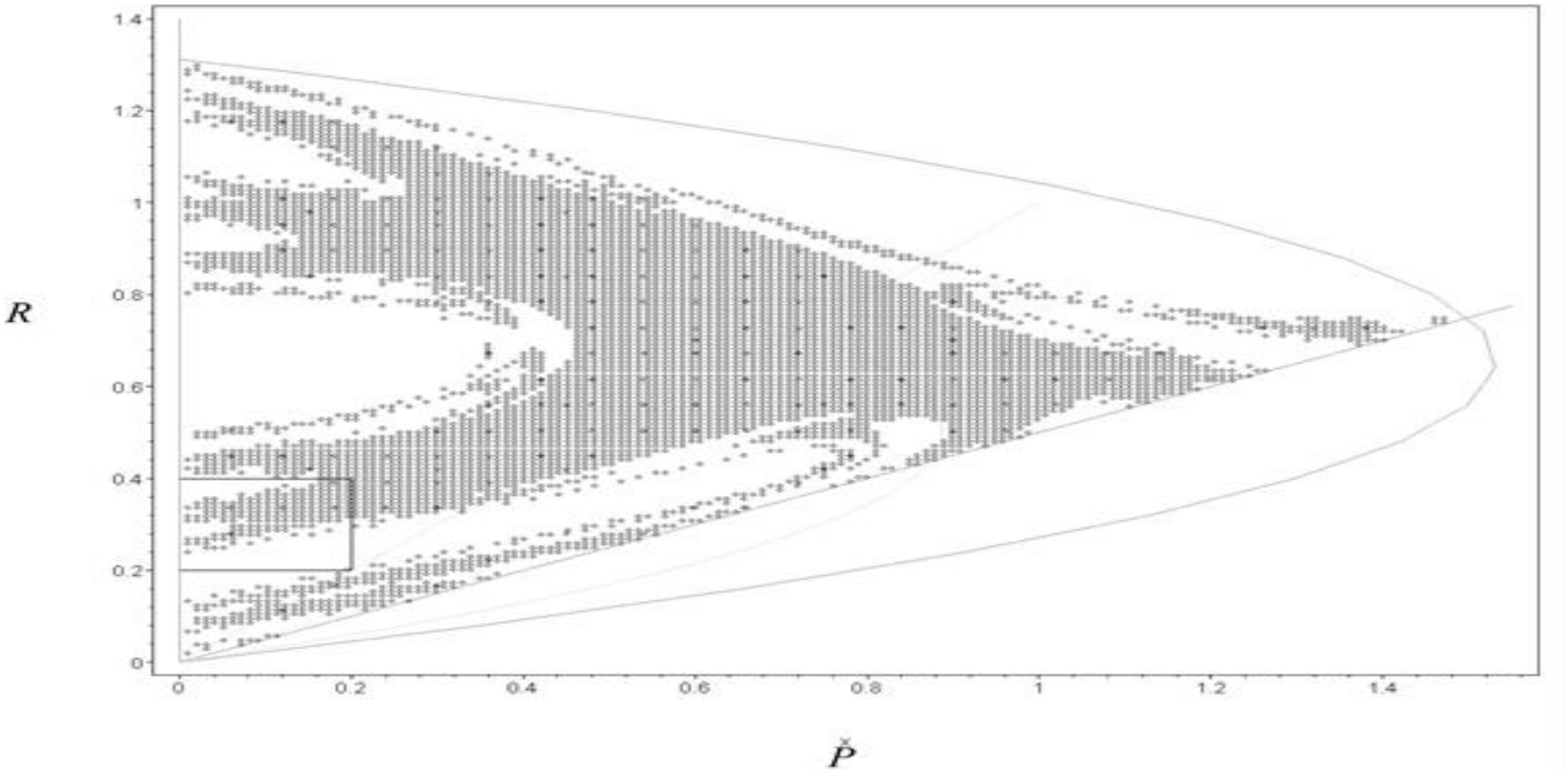
$$E_P = \{(P,R): F_P(P,R) = P\} = \{P = 0\} \cup \{P = R\}$$
$$E_R = \{(P,R): F_R(P,R) = R\} = \left\{P = \frac{c}{h}R(1-R)\right\}.$$

The points of intersection of with are the equilibrium points. These sets are shown below:



The Julia Set:

- The goal of this section is to determine the topology of the Julia set for *F*. The Julia set is defined to be the set of initial conditions whose positive orbits remain in the first quadrant and are bounded. It serves as the basin of attraction for all attractors in the first quadrant. Figure below shows the Julia set together with the sets Z_P, Z_R, E_P, and E_R for *a* = 1, *c* = 3.2, and *h* = 0.9.



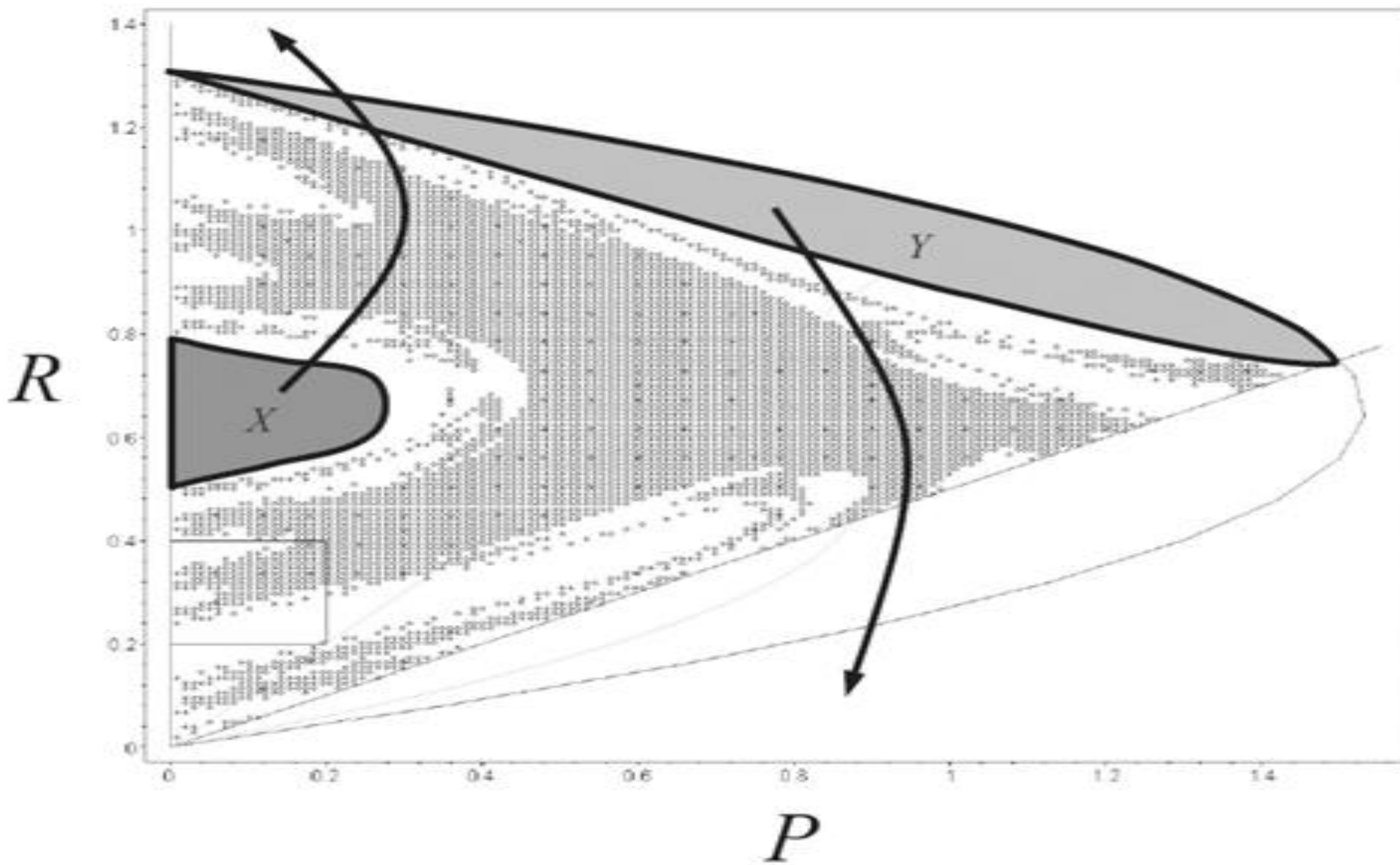


Fig. 8. The Julia set for a = 1, c = 3.2, and h = 0.9.

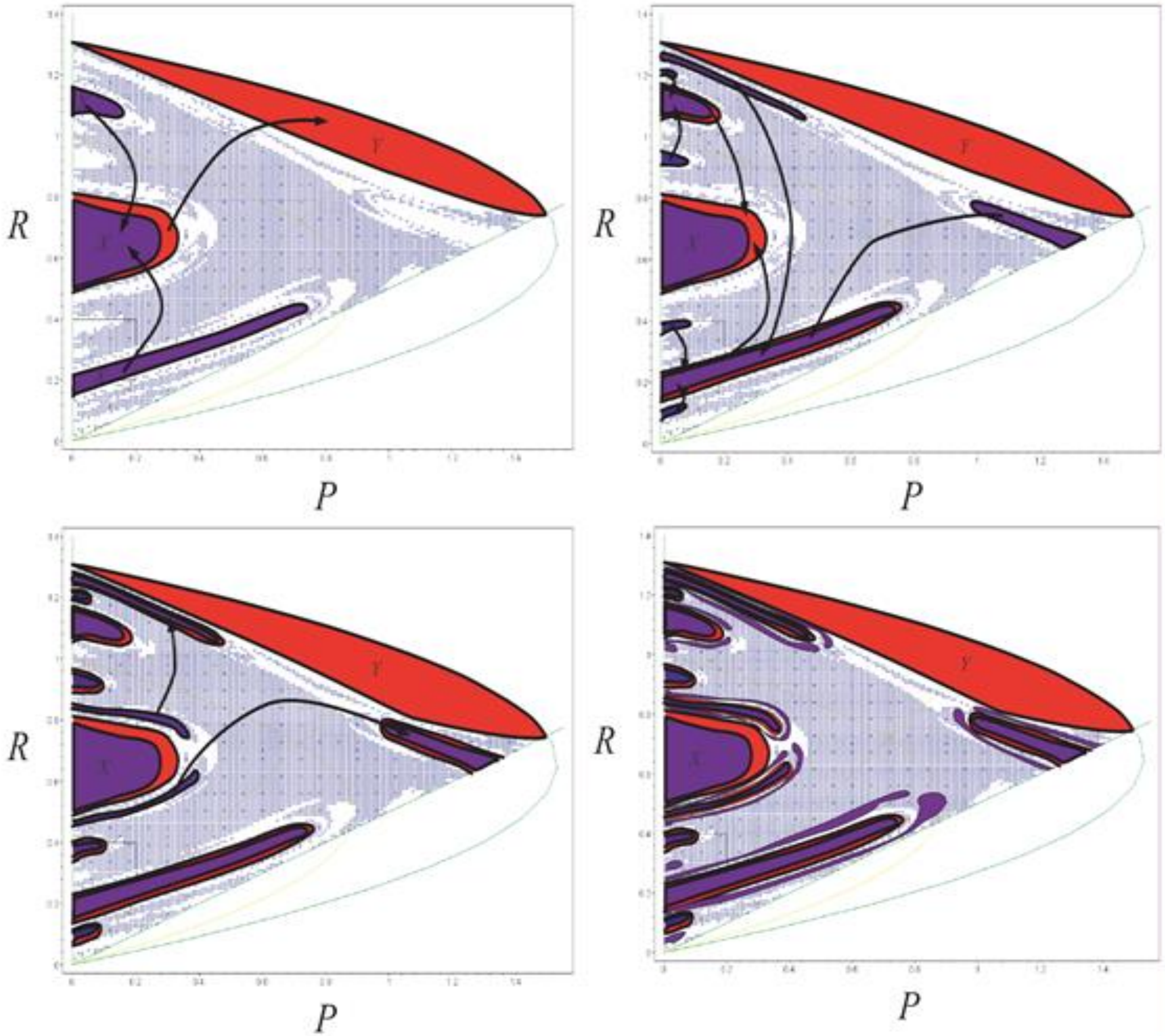


Fig. 9. The Julia set for $a = 1$, $c = 3.2$, and $h = 0.9$ showing the escape sets.

FUTURE GOALS & PROBLEMS:

- **MIGRATION BETWEEN THE ISLANDS:**
- **Joint work with Bernie Brooks, Tamas Wiandt, Carl Lipo & Terry Hunt.**
- **MODELING SURVIVAL & EXTINCTION:**
- **Joint work with Harold Hastings & Tamas Wiandt.**
- **DUAL HARVESTER MODEL:**
- **Joint work with Bernie Brooks & Tamas Wiandt.**
- **DUAL POPULATION MODEL:**
- **Joint work with Bernie Brooks, Tamas Wiandt & David Weigs.**

DUAL HARVESTER MODEL

- $P_{1,n+1} = P_{1,n} + aP_{1,n}\left(1 - \frac{h_1 P_{1,n} + h_2 P_{2,n}}{h_1 R_n}\right)$
- $P_{2,n+1} = P_{2,n} + aP_{2,n}\left(1 - \frac{h_1 P_{1,n} + h_2 P_{2,n}}{h_2 R_n}\right)$
- $R_{n+1} = R_n + cR_n\left(1 - \frac{R_n}{K}\right) - h_1 P_{1,n} - h_2 P_{2,n}.$

This system has an equilibrium at

- $(P_1, P_2, R) = (0,0,K)$

which corresponds to an environment devoid of humans. The system also has equilibria at

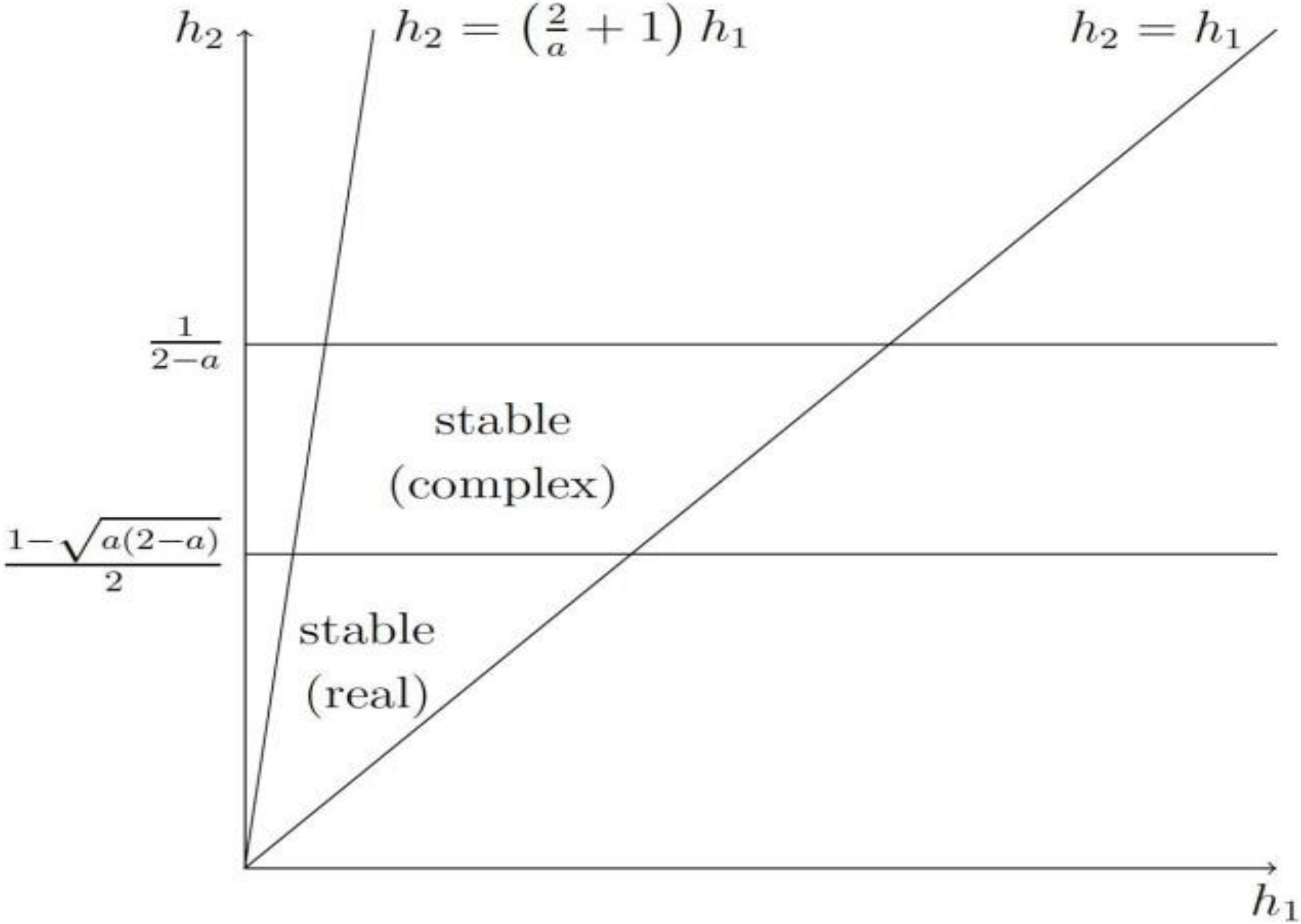
- $\left(\frac{K}{c}(c-h_1), 0, \frac{K}{c}(c-h_1)\right)$, and
- $\left(0, \frac{K}{c}(c-h_2), \frac{K}{c}(c-h_2)\right)$,

which corresponds to the elimination of one of the competing species. In order for either of these two equilibria to exist we require $c > h_2 > h_1$. Since $h_2 \neq h_1$, there is no interior equilibrium where all three variables are positive. Because all three variables model non-negative quantities, if an orbit maps outside the first octant we interpret the quantities that mapped to negative values as being mapped to extinction. Thus

- $\left(P_{1,34}, P_{2,34}, R_{34}\right) = (-0.2, 200, 300)$

would be interpreted as population 1 becoming extinct during the 33rd year. This would reduce the system to two equations for years 34 on.

LINEARIZED STABILITY DIAGRAM:



JACOBIAN MATRIX:

The Jacobian Matrix evaluated at the equilibrium $\left(0, \frac{K}{c}(c-h_2), \frac{K}{c}(c-h_2)\right)$ is:

$$J = \begin{bmatrix} 1+a-a\dfrac{h_2}{h_1} & 0 & 0 \\ -a\dfrac{h_1}{h_2} & 1-a & a \\ -h_1 & -h_2 & 2h_2 \end{bmatrix}$$

which has determinant

$$\det(J) = h_2\left(1+a-a\frac{h_2}{h_1}\right)(2-a),$$

and trace

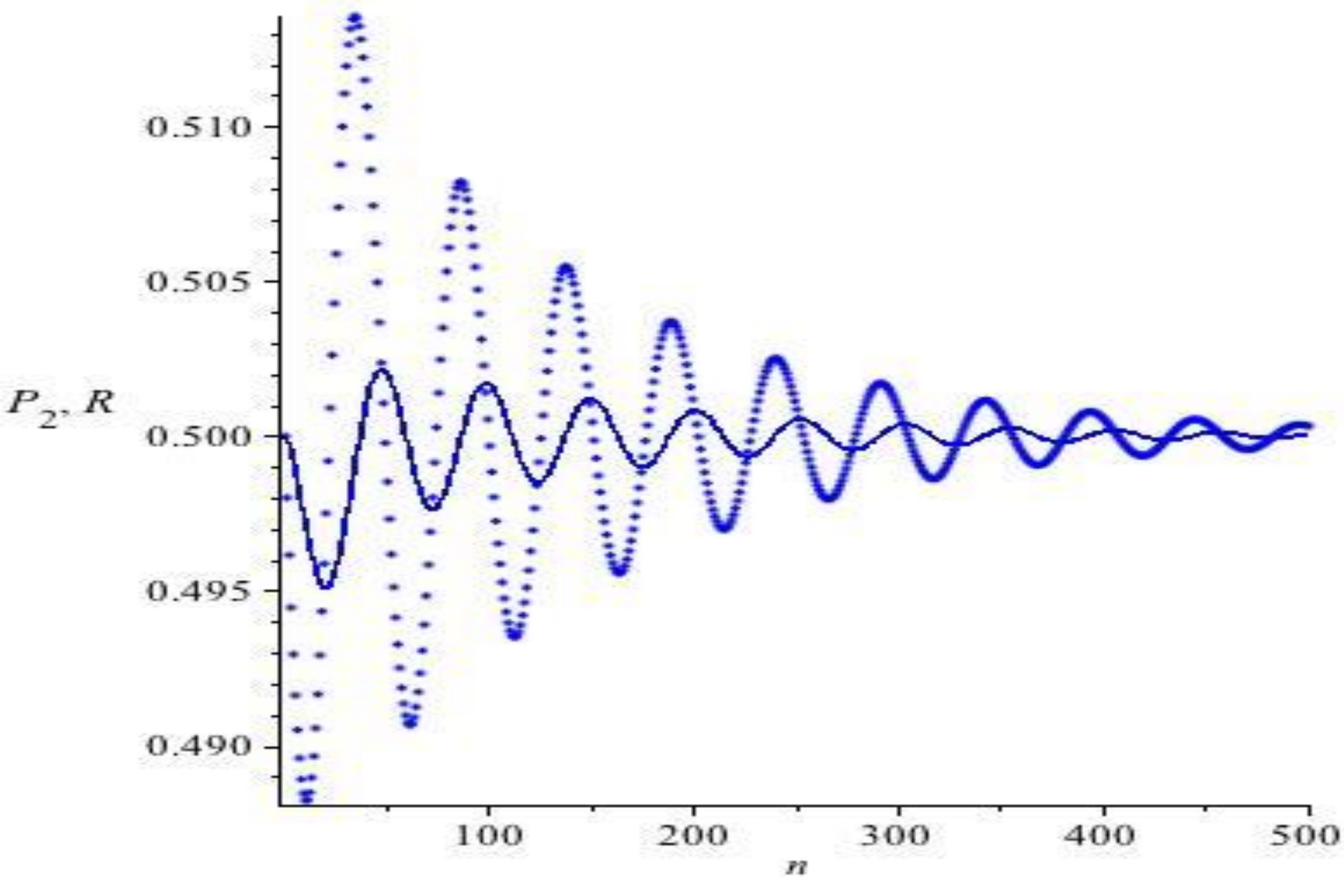
$$tr(J) = 2 + 2h_2 - a\frac{h_2}{h_1},$$

and sum of principal minors

$$SoM(J) = 4h_2 + 1 + \left(h_2 - \frac{h_2 + 2h_2^2}{h_1}\right)a + \left(\frac{h_2}{h_1} - 1\right)a^2.$$

GRAPHICS:

An orbit of the system with harvest parameters in the stable (complex) region of the stability triangle will produce a plot as shown in the figure below when perturbed from equilibrium $\left(0, \frac{K}{c}(c-h_2), \frac{K}{c}(c-h_2)\right)$ by a small group of low harvesters joining the system; we let $h_1 = 0.01$ and $h_2 = 0.05$.



REFERENCES:

- Basener, W., Brooks, B.P., Radin, M.A., & Wiandt, T., (2008) Dynamics of a Discrete Population Model for Extinction and Sustainability in Ancient Civilizations, *Nonlinear Dynamics, Psychology and Life Sciences*. 12, #1. 29-53.

- Basener, W., & Ross, D. (2004) Booming and crashing populations and Easter Island, *SIAM J. Appl. Math*. 65, #2, 684-701.

- Birdsell, J.B., (1957). Some population problems involving. Pleistocene man. *Cold Spring Harbor Symposium on. Quantitative Biology*. 22, 47-70.

- Brooks, B.P. (2006) The Coefficients of the Characteristic Polynomial in terms of the Eigenvalues and the Elements of an n×n Matrix, *Applied Mathematics Letters*, 19(6), 511-515.

- Cohen, J., (1995) *How Many People Can the Earth Support*. W. W. Norton and Company.

- Diamond, J., (2005), *Collapse, How Societies Choose to Fail or Succeed*. Viking.
- Hunt, T. (2007) Rethinking Easter Island's ecological catastrophe. *Journal of Archaeological Science*, 34, 485-502.
- Hunt, T. (2006) Rethinking the Fall of Easter Island: New evidence points to an alternative explanation for a civilization's collapse. *American Scientist*, 94,412-419.
- Kingsland, S. E. (1995) *Modeling Nature: Episodes in the History of Population Ecology*. University of Chicago Press
- Roughgarden, J., (1979). *Theory of Population Genetics and Evolutionary Biology*. MacMillan, New York.
- Tamarin, R. H. & Malecha S. R.. (1972) Reproductive parameters in Rattus rattus and Rattus exulans of Hawaii, 1968 to 1970. *Journal of Mammalogy* 53,513-528.
- Turchin, P., (2003a) *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton, Princeton.
- Turchin, P. (2003b) *Historical Dynamics: Why States Rise and Fall*. Princeton University Press.