Analysis of Plankton Populations

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Abstract

I use numerical and analytical techniques to study the dynamics of various models of plankton food webs with and without resource fluctuations. Plankton are ideal organisms because they are very small, fast-reproducing organisms so they can easily be used in laboratory experiments to verify any results. We can study simple food webs to develop a better understanding of more complex food webs. The three archetypical food webs are a single grazer with a resource (growth), multiple grazers with a common resource (competition), and one grazer and one predator with a base resource (predator-prey).

1 Background

Plankton are microbial organisms that live in aquatic environments. There are two types of plankton: phytoplankton and zooplankton. Phytoplankton are autotrophic organisms that use photosynthesis to generate their own food from sunlight, water, and various nutrients. Zooplankton are heterotrophic organisms that use phytoplankton as food sources themselves [2]. To understand the dynamics of the phytoplankton-zooplankton systems, one could use the analogy of self-sustaining plants and the animals that graze on them.

In 1961, Hutchinson presented the paradox of the plankton: ”The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials [1]”. Hutchinson hypothesized that different species of plankton can coexist if they exploited differences in other factors, such as efficiency of resource consumption under different levels of resources.

One can model phytoplankton as one of two archetypes: gleaners and opportunists. Gleaner plankton thrive on low food levels (such as dim light) whereas opportunist plankton thrive on high food levels (such as bright light). As a result, opportunists tend to grow faster than gleaners because resources are usually abundant in the beginning of growth periods when phytoplankton levels are low. After both species reach their growth potential, resources become limited, and the gleaner becomes the dominant species. Figure 1 illustrates this trait. While it is more realistic to look at the gleaner-opportunist trait as a continuum rather than rigid archetypes, the simplistic binary characterization that we employ can prove insightful. Nevertheless, Plankton are only opportunist or gleaners relative to other species of plankton [3]. It is also possible for one species of plankton to outperform another in all resource regimes if it has a higher maximum intake (the maximum amount of resource a species can consume) and lower half-saturation (the point at which the resource intake is at its half capacity).

In addition to helping control the amount of carbon dioxide in the environment, phytoplankton also form the base of many food chains in aquatic ecosystems [2]. Because phytoplankton are so integral to the overall health of its environment, it is important to study the changes in their population caused by different ecological conditions such as fluctuating resources and the introduction of other plankton species. In addition, plankton are ideal organisms to study because they are easy to conduct experiments with due to their high growth rate, short life span, and small size [2].

The rest of this paper is organized as follows. We first look at the competition model and find its equilibrium populations. Then we introduce resource fluctuations and observe what happens when the period of the resource is adjusted (Section 3). We move on to the unforced chain model consisting of one phytoplankton population and one zooplankton population. We begin by finding a way to calculate the bifurcation points, special parameter values that cause a qualitative change in the system's dynamical behavior if changed [4]. Then we find a way to approximate the time series of the system for parameter regimes close to the bifurcation point (Section 4). We conclude by discussing our work (Section 5).

2 The Model

Working on the assumption that the plankton populations are well-mixed in their environment with no population drifts, one can remove the system's spatial dependence (a term representing diffusion of plankton from high density areas to low density area), leaving only the temporal dependence. This allows us to model the time-dependent system using ordinary differential equations (ODE) rather than partial differential equations.

One can use the following system of ODEs to model a system of phytoplankton and zooplankton

$$\begin{aligned}\dot{P}_i &= c_{p_i} g_i(R) P_i - m_{p_i} P_i - h_j(P_i) Z_j,\\ \dot{Z}_j &= c_{z_j} h_j(P) Z_j - m_{z_j} Z_j \end{aligned} \tag{1}$$

Here, P_i, Z_j, and R denote phytoplankton population i, zooplankton population j, and the resource (sunlight, water, *etc.*) respectively. As P_i and Z_j are not necessarily integers, letting them represent discrete plankton organisms does not make sense. Rather, we view them as populations densities, which allow non-integer values. The nutrient yield from consumption and death rates of species i are c_i and m_i, respectively. The plankton's consumption functions, which indicate how much resource is processed for nutrition, are represented by $g_i(x)$ and $h_j(x)$ and modelled by the Monod function [2]

$$f_n(x) = \frac{v_n x}{x + k_n}, \tag{2}$$

where k_n and v_n denote the half saturation rate and the maximum intake of resource by species n, respectively. This functional response, which has a limit to the maximum intake, is called a type II response. The type I functional response, which does not consider a maximum limit on resource intake can be modelled by the simplified Monod function: $f(x) = vx/k$ [2]. The type II functional response is the more realistic model, but the difference in consumption between the two models is small in systems consisting of plankton with high maximum intake or low amounts of resources. In these situations, a type I response may be implemented to make the analysis tractable.

The gleaner and opportunist archetypes only make sense in systems that have type II functional responses. In a system of two competing type I plankton, one species always outperforms the other because of the linear nature of the responses.

Note that in equation 1, neither the phytoplankton nor the zooplankton interact with each other. The plankton only interact with species of a different trophic level. Had there been interactions within one level, as would be the case with symbiosis, it would be necessary to incorporate coupling factors in the equations. For this project, we ignore such relationships.

The resource (which is sunlight for this project) is modelled by the following [3]

$$R = I_{in}e^{-a\sum_i P_i} \tag{3}$$

Here, a is the absorption of sunlight by the phytoplankton bodies. For systems with resource fluctuations, the function which represents the incoming light, I_{in}, might be taken to be a periodic step function with amplitude, $\bar{I}_{in}$ and period, T. The fraction of the period in which resource is present is denoted p. It is also possible to use a smoothly fluctuating function to model the incoming light [3]. If the resource does not fluctuate, however, it is constant function with $I_{in} \equiv \bar{I}_{in}$ for all time regimes. The system's dynamical behavior can change by adjusting the length of the period.

3 Phytoplankton Competition

In this section, we look at the system that consists of sunlight and two competing phytoplankton. The phytoplankton do not directly interact, but affect each other indirectly through consumption of resources. As this system contains no zooplankton, $Z_j \equiv 0$ for all j, which gives us the following system of equations from equation 1

$$\begin{aligned} \dot{P}_1 &= c_{p_1}g_1(R)P_1 - m_{p_1}P_1, \\ \dot{P}_2 &= c_{z_2}g_2(R)P_2 - m_{p_2}P_2, \\ R &= I_{in}e^{-a(P_1+P_2)} \end{aligned} \tag{4}$$

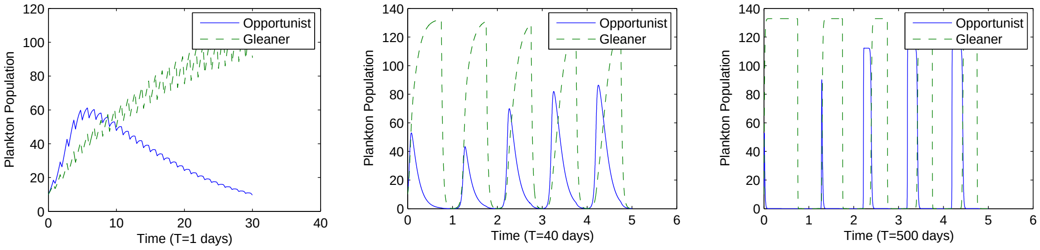
Without loss of generality, let P_1 be the opportunist and P_2 be the gleaner.

In the absence of resource fluctuation, this system has three equilibria

$$(0,0), \quad (0, \frac{1}{a}\ln(\frac{\bar{I}_{in}}{k_2}(\frac{v_2}{m_2}-1))), \quad (\frac{1}{a}\ln(\frac{\bar{I}_{in}}{k_1}(\frac{v_1}{m_1}-1)), 0)$$

The first is the trivial equilibrium where there are no phytoplankton. The other two are the cases where one species dies off and the system collapses into the growth model. As there are no non-trivial solutions for the equations above when the derivatives are set to 0, there can be no coexistence in a system without resource fluctuation. Which equilibrium point the system moves towards depends on both the initial conditions and the parameter values.

Upon introduction of resource fluctuation, the system exhibits more interesting dynamics. As shown figure 1, two types of behavior can occur. For resource fluctuations of very small periods (figure 1a), the overall behavior of the system does not change. The system moves towards equilibrium, and one of the phytoplankton species dies off. For resource fluctuations of sufficiently large periods (figures 1bc), however, coexistence of both phytoplankton species becomes possible. In addition, the system exhibits a stable limit cycle, a periodic curve which contains a damping term that causes all nearby time series to converge to the curve. In the long period case, we can treat the plankton populations as periodic multi-step functions. This method allows us to analytically determine many qualities about the system [3]. Whether or not coexistence is possible depends on parameter values. We focus only on situations in which there is coexistence. Observe that, in the intervals in which there is light, the growth patterns of the plankton behave as expected. The opportunist is the first species to dominate as there is a large amount of resource at the beginning of the period. Then after some time, the phytoplankton population becomes sufficiently high and resources become scarce causing dominance to shift to the gleaner.



(a) **(b)** **(c)**

Figure 1: Plankton times series under resource fluctuation. One unit of time represents one period. In (a), the period is 1 day. In (b), the period is 40 days. In (c), the period is 500 days. Note in (a), the opportunist dies off whereas in (b) both species coexist.

One can approximate the time at which this change occurs by looking at the intake of resources by the plankton.

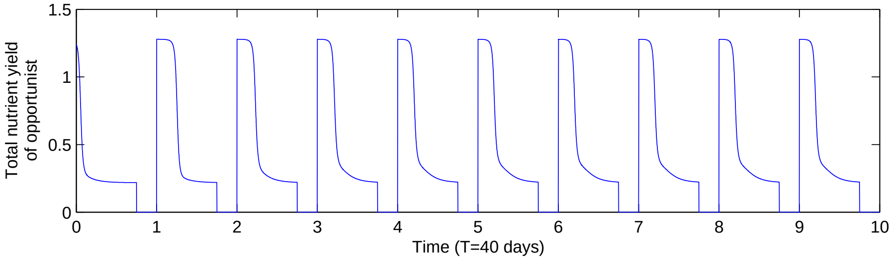


Figure 2: The total nutrient yield ($f(R)$) of the opportunist under intermediate resource fluctuation (T=40 days)

From figure 1b, one sees that the population levels vary greatly throughout the period. However, from figure 2, one sees that the nutrient yield of the opportunist stays rather even. Thus, we can approximate the nutrient yield as a multi-step function. This allows us to use a method employed by Klausmeier [3] to analytically find certain biologically interesting times. However, notice the jumps in populations for the long term period (figure 1c) is more sudden than the transition in the medium term period (figure 1b). As the method utilized by Klausmeier treats these transitions as instantaneous, applying the method to medium term fluctuation systems is expected to give less accurate results when compared to the results of the long term fluctuation systems. Nevertheless, we can still use this method to extract some information about the qualitative behavior of the system.

Because the opportunist is dominant at the beginning of the period, (that is, in the time interval $[0, t_0]$), we approximate the functional response as if the system were composed of only the opportunist, giving

$$P_1 + P_2 = P_1 = \frac{1}{a}\ln(\frac{\bar{I}_{in}}{k_1}(\frac{v_1}{m_1} - 1)) = a_1$$

After the dominance changes, we approximate the functional response as if the system were composed of only the gleaner for the interval $(t_0, pT]$, giving

$$P_1 + P_2 = P_2 = \frac{1}{a}\ln(\frac{\bar{I}_{in}}{k_2}(\frac{v_2}{m_2} - 1)) = a_2$$

During the interval (pT, T), $I_{in} \equiv 0$. All this depends on our initial assumption of treating the plankton populations as discrete multi-step function. As the per capita growth $(\dot{P}_i/P_i)$ of each plankton over a cycle averages to 0, we have the following equation

$$\int_0^{t_0} f_1(\bar{I}_{in}e^{a_1}) - m_{p_1}dt + \int_{t_0}^{pT} f_1(\bar{I}_{in}e^{a_2}) - m_{p_1}dt + \int_{pT}^{T} -m_{p_1}dt = 0 \tag{5}$$

Solving for t_0 yields

$$t_0 = \frac{T(pf_1(\bar{I}_{in}e^{a_2}) - m_{p_1})}{f_1(\bar{I}_{in}e^{a_1}) - f_1(\bar{I}_{in}e^{a_2})} \tag{6}$$

Notice that t_0 varies proportionally with T. Thus, if one normalizes the period by substituting a new time parameter, $\tau = t/T$, τ_0, the corresponding value of t_0 for τ, is independent of T. This shows that, if we normalize the time scale to the period of the resource fluctuation, systems of different resource fluctuation periods qualitatively behave the same. This is illustrated in figure 3.

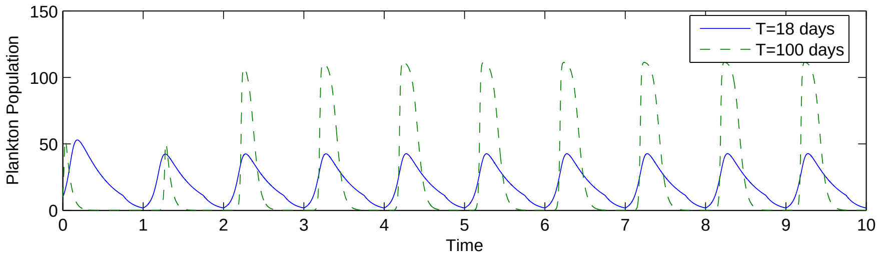


Figure 3: Comparison of the opportunist time series of two different resource fluctuation periods. The time scale has been normalized so that one unit of time is equal to one period. Notice that, in this normalized time scale, the peaks of both population time series occurs at the same time

4 Phytoplankton-Zooplankton Food Chain

In this section, we look at the system that is composed of non-fluctuating sunlight, one species of phytoplankton, and one species of zooplankton that feeds on the phytoplankton.

$$\begin{aligned}
\dot{P} &= A(P,Z) = c_p g(R)P - m_p P,\\
\dot{Z} &= B(P,Z) = c_z h(P)Z - m_z Z,\\
R &= I_{in}e^{-aP}
\end{aligned} \tag{7}$$

Without resource fluctuations, this system has three equilibrium points. One is the trivial equilibrium where both species die out. Another occurs when the system collapses into the phytoplankton growth model as the zooplankton die out. The last and most interesting equilibrium is when there is coexistence of zooplankton and phytoplankton. By setting $\dot{Z}$ equal to 0, one finds that the nontrivial equilibrium population for phytoplankton is $\hat{P} = \frac{-k_z m_z}{v_z + m_z}$. The equilibrium populations are

$$(0,0), \quad (\hat{P},0), \quad (\hat{P}, \frac{\hat{P}+k_p}{v_p}(m_p - \frac{v_p I_{in} e^{a\hat{P}}}{I_{in}e^{a\hat{P}} + k_p}))$$

Any of the equilibrium points can be attracting or repelling because their stability depends on parameter values. Should the third equilibrium population be unstable, however, the system will exhibit a stable limit cycle. These two possibilities are illustrated in figure 4ab.

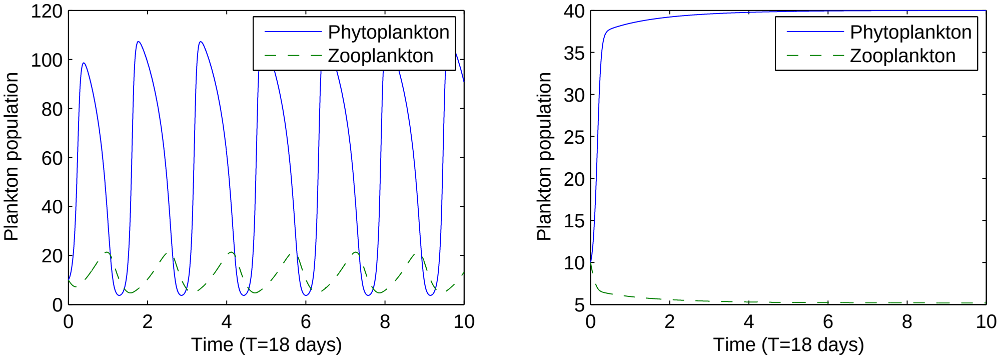
To determine whether the equilibrium point is unstable, one looks at the eigenvalues [4], λ of the Jacobian:

$$\begin{pmatrix} \frac{\partial A}{\partial P} & \frac{\partial A}{\partial Z} \\ \frac{\partial B}{\partial P} & \frac{\partial B}{\partial Z} \end{pmatrix}$$

If the real components of both eigenvalues are negative, then the equilibrium population is stable, and, as time increases, the system moves arbitrarily close to the equilibrium population. If the real component of either eigenvalues is positive, however, then the equilibrium population is unstable, and system moves asymptotically away from the equilibrium population. For this case, the real components of both eigenvalues are positive, and the system eventually settles into a limit cycle.

From this method, one can find the system's bifurcation points. One first sets the parameter of interest to be an indeterminate and computes the eigenvalue of the Jacobian. Thus, as $\dot{P} = P\zeta(P,Z)$ and $\dot{Z} = Z\eta(P,Z)$, the Jacobian is

$$\begin{pmatrix} \zeta(P,Z) + P\zeta_P(P,Z) & P\zeta_Z(P,Z) \\ Z\eta_P(P,Z) & \eta(P,Z) + Z\eta_Z(P,Z) \end{pmatrix}$$



(a) **(b)**

Figure 4: Plankton times series under resource fluctuation. In (a), $a = 0.04$. In (b), $a = 0.1$. In (a), one sees a limit cycle. In (b), one sees that both populations asymptotically approach equilibrium.

This matrix has eigenvalues

$$\frac{1}{2}(\zeta + \eta + 2\zeta_P P \pm \sqrt{\zeta^2 - 2\zeta\eta + \eta^2 + 4\zeta_P\zeta_Z PZ}) \tag{8}$$

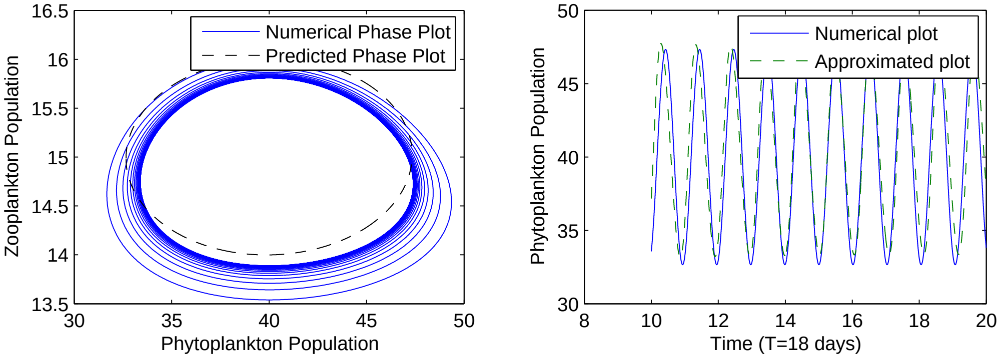
Then one can simply set the real components of both eigenvalues to 0 (making sure that one does not get a double root) and solve for the indeterminate to find the bifurcation point.

A system's *normal form* is the simplest form the system takes under linear transformations. By finding it, we can approximate the chain model for parameter values close to the bifurcation point. To find the normal form, one first transforms the matrix of the linear terms into an antisymmetric matrix. Then one applies another transformation that turns the variables into complex variables. This gives us two equations, one of which is the complex conjugate of the other. Thus, we need only look at one. From this, we apply one final transformation that turns the complex equation into a system of polar equations. The normal form is derived in the appendix. The process transforms equation 7 to the following equation:

$$\begin{aligned} \dot{r} &= \alpha r + a r^3 + ..., \\ \dot{\theta} &= \omega + b r^2 + ... \end{aligned} \tag{9}$$

Here α and ω are coefficients that appear after all the transformations are applied.

By solving $\dot{r} = 0$, one can find the limit cycles of the normal form. Of course, one still has to apply the reverse transformations on the limit cycle predicted by equation 9 to obtain the proper limit cycle predicted by the normal form. An example of the approximation yielded by this method is shown in figures 4ab.



(a) **(b)**

Figure 5: A comparison of (a) the numerical phase plot vs. the phase plot predicted by finding the normal form and (b) the corresponding time series. Here, $a = \hat{a} - 0.0005$. Notice there is a phase drift in the time series.

5 Discussion

Certain plankton population models can be simplified (whether it's by approximations or transformations) while still retaining many of the same qualitative features. This allows us to study the simplified versions of the systems to extract information about the original systems.

For the competition model, the analytical methods reveal that, even for medium term fluctuations, one can predict biologically interesting times by using rough approximations. For this project, we found the time at which the plankton populations change dominance. We accomplished this by extending Klausmeier's method to medium term fluctuations by making the assumption that, even though the plankton populations were smoothly changing, we could still view them as multi-step functions. This method also showed that systems of different fluctuation periods can still behave the same, qualitatively. Thus, when the time scale is normalized, the times at which biologically interesting events occur are independent of the period.

We found the bifurcation points of the system with respect to a chosen parameter. Using normal forms, one can approximate the phase plot of the system around the equilibrium point. From this, one can also approximate the behavior of the system near the coexistence equilibrium. However, if one goes too far away from the bifurcation point, the approximation breaks down.

Notice that none of the conditions used restricted our analysis exclusively to plankton. Thus, as long as our assumptions (well-mixing, no intra-trophic relations, *etc.*) are applicable to an organism of interest, our analytical techniques may be used to study its food web.

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A Appendix

To find a bifurcation's normal form, one first shifts the system so that the equilibrium point is at the origin and the bifurcation point occurs when the parameter of interest, μ, has a value of 0 [5]. This can be achieve by making the substitutions: $x = P - \hat{P}, y = Z - \hat{Z}$, and $\epsilon = \mu - \hat{\mu}$, where the bifurcation of equilibrium $(\hat{P}, \hat{Z})$ occurs at parameter value, $\hat{\mu}$.

Then one tries to reduce the number of variables in the systems. This can be accomplished by introducing complex variables. One first has to apply the linear transformation, $(x_1, y_1)^T = S_1 S_2^{-1}(x, y)^T$, where S_1 is the eigenvector matrix of the linearized system and S_2 is the eigenvector matrix of the antisymmetric matrix:

$$\begin{pmatrix} \mathrm{Re}(\lambda) & -\mathrm{Im}(\lambda) \\ \mathrm{Im}(\lambda) & \mathrm{Re}(\lambda) \end{pmatrix}$$

This turns the system into the form:

$$\begin{pmatrix} \dot{x_1} \\ \dot{y_1} \end{pmatrix} = \begin{pmatrix} \mathrm{Re}(\lambda) & -\mathrm{Im}(\lambda) \\ \mathrm{Im}(\lambda) & \mathrm{Re}(\lambda) \end{pmatrix} \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} + \begin{pmatrix} f_1(x_1, y_1; \epsilon) \\ f_2(x_1, y_1; \epsilon) \end{pmatrix} \tag{10}$$

Here, f_1 and f_2 are the higher order, nonlinear components of the equations. One then transforms to the complex variables, setting $(z, \bar{z}) = (x_1 + iy_1, x_1 - iy_1)$ to obtain:

$$\begin{pmatrix} \dot{z} \\ \dot{\bar{z}} \end{pmatrix} = |\lambda| \begin{pmatrix} e^{2\pi i\theta} & 0 \\ 0 & e^{-2\pi i\theta} \end{pmatrix} \begin{pmatrix} z \\ \bar{z} \end{pmatrix} + \begin{pmatrix} g_1(z, \bar{z}; \epsilon) \\ g_2(z, \bar{z}; \epsilon) \end{pmatrix} \tag{11}$$

One can verify that g_1 and g_2 are complex conjugate functions. Thus, as the above system contains two complex conjugate equations, we only needs to look at one, giving us the equation: $\dot{z} = |\lambda| e^{2\pi i\theta} z + g_1(z, \bar{z}; \epsilon)$. As discussed in Wiggins [5], when expanding g_1 out to four terms, only the $z^2\bar{z}$ cannot be eliminated for ϵ sufficiently small. This gives us the equation:

$$\dot{z} = |\lambda| e^{2\pi i\theta} z + cz^2\bar{z} + O(5) \tag{12}$$

where $O(5)$ denotes all terms with combined exponent greater than or equal to 5. Expressing the coefficients as complex numbers gives $|\lambda| e^{2\pi i\theta} = \alpha + i\omega$ and $c = a + ib$. By grouping like terms, one gets the following system:

$$\begin{aligned} \dot{x} &= \alpha x - \omega y + (ax - by)(x^2 + y^2) + O(5), \\ \dot{y} &= \omega x + \alpha y + (bx + ay)(x^2 + y^2) + O(5) \end{aligned} \tag{13}$$

Equation 13, in polar coordinates, can be expressed as

$$\begin{aligned} \dot{r} &= \alpha r + a r^3 + ..., \\ \dot{\theta} &= \omega + b r^2 + ... \end{aligned} \tag{14}$$

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