Chaos to Order: Role of Toxin Producing Phytoplankton in Aquatic Systems[*]

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Abstract. Toxin producing phytoplankton (TPP) plays an important role in aquatic systems. To observe the role of TPP, we consider a three species food chain model consisting of TPP-zooplankton-fish population. The similar type of model considered by Upadhyay *et al.* [1] for terrestrial ecosystem and obtained chaotic dynamics in some region of parametric space. We modify their models by taking into account the toxin liberation process of TPP population and represented as aquatic systems. We consider Holling type I, type II and type III functional forms for this process. We observe that increasing the strength of toxic substance change the state from chaos to order. Our conclusion is that TPP has a stabilizing contribution in aquatic systems and may be used as a bio-control mechanism.

Keywords: toxin producing phytoplankton, chaos, limit cycle, functional response, aquatic system.

1 Introduction

The major concern in population and community ecology is to understand how a population of a given species influences the dynamics of population of other species, which are members of same interaction network [1]. Interaction networks

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in natural ecosystems can be visualized as consisting of simple units known as food-chains or food-webs that consists of a number of species linked by tropic interactions. Researcher have focused a great deal of their attention to analyzing the dynamical behavior of model food chain. Two species continuous time models of interacting species have been extensively studied in literature. These models exhibit only two basic patterns: approach to equilibrium (stable focus) or to a limit cycle. Three species continuous time models are reported to have more complicated patterns. These models form dissipative dynamical systems which can possess three distinct dynamical possibilities like stable focus, limit cycle and chaos in the phase space. The research of the last two decades demonstrates that very complex dynamics can arise in three or more species food chain models [2–4], while similar results are obtained for multi-species food web models [5–7]. May [8] reviewed the literature and concluded that the study of nonlinear systems are indispensable as far as understanding about nature is concerned. Since the seminal work [9, 10] of Sir Robert May deterministic chaos have been studied in models [11–13], in the laboratory [14, 15] and in the field [16–18]. Although it has been seen in the models quite a bit, yet there are very few examples from the laboratory as well as from the field. Therefore, it can be understood that no unambiguous evidence of chaos exists till date. The investigations by Upadhyay *et al.* [1, 19] into reason why chaos had been rarely observed in natural populations concluded that natural terrestrial ecosystems are not suitable candidates for the exploration of chaotic dynamics. This is paradoxial, since ecological systems have all the necessary characteristics (nonlinearity, high-dimensions, etc.) to be able to support chaotic dynamics. The existence of chaos in almost all the physical systems [20, 21] motivates one to critically study the same in natural population. Since almost all form of scientific enquiry have found application of ideas from nonlinear dynamics and chaos, there is a natural curiosity and urge to explore the possibility of aquatic systems evolves on strange chaotic attractor or not?

Recent studies on ecological systems [6, 13, 22] indicate that chaotic dynamics may play an important role in continuous time models. There are some evidences that the real time evolution of species involved in two or three food chains could be characterized by chaotic attractors as observed in many natural food chains. Now the more challenging issue is the observation that natural systems seems to have no difficulty switching from one state into the other, from

chaos to order and from order to chaos. In aquatic ecosystem, toxin producing phytoplankton may act as controlling factor for such dynamics. The role of toxin producing phytoplankton (TPP) for reduction of grazing pressure of zooplankton is well known [23]. Toxicity may be a strong mediator of zooplankton feeding rate as shown by field studies [24, 25] and laboratory studies [26]. Areas rich in some phytoplankton organisms, e.g. *Phacocyslis, Coscinodisem, Rhizosopenia* are un-accepted or avoided by zooplankton due to dense concentration of phytoplankton or the production of toxic substances released by phytoplankton. This phenomena are well explained by "Exclusion principle" [27, 28]. Chattopadhyay *et al.* [29] investigated the role of toxin producing phytoplankton for the termination of planktonic blooms.

In this paper, we modify first the model of Upadhyay *et al.* [1] by introducing an extra mortality term in specialist predator y and interpret the system for aquatic environment consisting of TPP-Zooplankton-fish food chain model. In their paper, Upadhyay *et al.* [1] have shown that chaos exists in very narrow parameter regimes and in region of 2D parameter space of measure zero and suggested for further investigation for its route cause. In this paper, using realistic regions of parameters, numerical qualitative analysis of the asymptotic behavior of the system is performed. The transition behaviour when some parameters of the system vary is studied. Chaotic dynamics is observed via sequences of period-doubling bifurcation of limit cycles. The period doubling phenomena leading to chaos is a well known feature of a range of nonlinear differential equations, often used in modeling biological population. This phenomena can suddenly break down and reverse, giving rise to period-halving bifurcation leading to stable limit cycles and again giving rise to stable focus. The results of the present study indicate that increasing the strength of toxic chemical release by TPP population reduce the propensity of chaotic dynamics and changing the state of chaos to limit cycle and finally settled down to stable focus or order.

2 Three species model systems

Consider a situation where a prey population x is predated by individuals of population y. The population y, in tern serves as a favourite food for individuals of population z. This interaction is represented by the following system of a simple

prey – specialist predator – generalist predator interaction [7, 30]

$$\frac{dx}{dt} = a_1 x - b_1 x^2 - \frac{wxy}{x+D}, \tag{1a}$$

$$\frac{dy}{dt} = -a_2 y + \frac{w_1 xy}{x+D_1} - \frac{w_2 y^2 z}{y^2 + D_2^2} - \theta f(x)y, \tag{1b}$$

$$\frac{dz}{dt} = cz - \frac{w_3 z^2}{y}, \tag{1c}$$

where $a_1, a_2, b_1, w, w_1, w_2, w_3, D, D_1, D_2, D_3$ and c are positive constants. In this model, TPP population (prey) of size x serve as the only food for the specialist predator zooplankton population of size y. This zooplankton population, in turn, serves as a favorite food for the generalist vertebrate predator fish population of size z. The equations for rate of change of population size for prey and specialist predator have been written following the Volterra scheme i.e., predator population dies out exponentially in the absence of its prey. The interaction between this predator y and the generalist predator z is modeled by the Leslie-Gower scheme where the loss in a predator population is proportional to the reciprocal of per capita availability of its most favorite food. a_1 is the intrinsic growth rate of the prey population x, a_2 is the intrinsic death rate of the predator population y in the absence of the only food x, c measures the rate of self-reproduction of generalist predator z. The parameters w, w_1, w_2, w_3 are the maximum values which per capita growth rate can attain. b_1 measures the strength of intra-specific competition among the individuals of the prey species x. D and D_1 quantify the extent to which environment provides protection to the prey x and can be thought of as a refuge or a measure of the effectiveness of the prey in evading a predator's attack. D_2 is the value of y at which per capita removal rate of y becomes $w_2/2$. The coefficient $w/(x+D)$, of the third term on the right hand side of (1a) is obtained by considering the probable effect of the density of the prey's population on predators attack rate. If this coefficient is multiplied by x (the prey population at any instant of time), it gives the attack rate on the prey per predator. Denote $p(x) = wx/(x+D)$, when $x \to \infty, p(x) \to w$, which is the maximum that it can reach. The third term $\frac{w_2 y^2 z}{y^2 + D_2^2}$ on the right hand side of (1b) represents the per capita functional response of the vertebrate predator z and was first introduced by Takahashi (May [9]). The ecological role of per capita functional response was well described by May [9]. Some insect top-predators

very often switch to alternative prey in situations when their favorite food is in short supply. This fact can be accommodated by replacing y^2 with y in this term of equation (1b) as their functional response is of Holling type II. Here $f(x)$ represents the toxin liberation process of TPP population for which the mortality of zooplankton increases and a result the grazing pressure of zooplankton on TPP population decrease. The parameter θ is the rate of toxin release by TPP population. Since the generalist predators z (in (1c)) are assumed to be sexually reproducing species, their growth has two phases: a linear phase and a quadratic phase [30]. For almost all the predator densities the linear phase prevails. Since a single mathematical formulation can not be given to describe these two pases, we write separate model for them. In this case, the last equation (1c) is modified to

$$\frac{dz}{dt} = cz^2 - \frac{w_3 z^2}{y + D_3}. \tag{1d}$$

This third equation also says that in the absence of the middle predator ($y = 0$, but the Leslie-Gower formulation breaks down in such a case), the top predator goes extinct if $cD_3 < w_3$ and grows unboundedly if the inequality reverse, which is, of course, biologically not acceptable [31]. In conducive medium, aquatic organisms stimulate their growth by releasing allelopathic substances which have similar genetic make-up. Sparse populations rarely provide sufficient opportunities for social interaction necessary for reproduction. Equations (1a)–(1c) define the linear phase of the model. The non-linear phase is described by equations (1a), (1b) and (1d) which represent model 1B (as used in Upadhyay *et al.* [1]). The typical situation represented by the model is presented in Fig. 1.
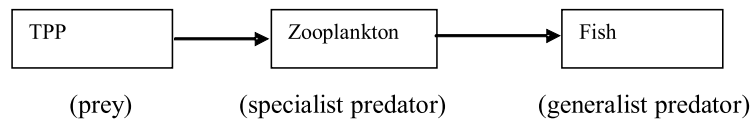

Fig. 1. Typical ecological situation presented by food-chain model 1B.

Consider now the case when the predator z is a invertebrate predator [32]. Then (1b) is modified as

$$\frac{dy}{dt} = -a_2 y + \frac{w_1 y x}{x + D_1} - \frac{w_2 y z}{x + D_3} - \theta f(x) y. \tag{2}$$

Equations (1a), (2) and (1d) represent model 1A (as used in Upadhyay *et al.* [1]).The real world example for this model is presented in Fig. 2.
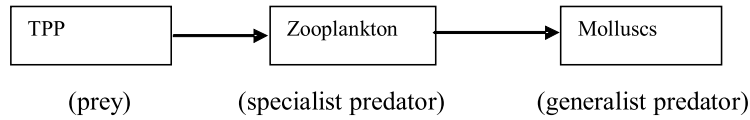

Fig. 2. Typical ecological situation presented by food-chain model 1A.

To characterize interface between phytoplankton and zooplankton population in the presence of toxic chemical, Holling type I, II, III functional responses are considered to study the behaviour of the system.

Explanation (origin of the model). Let us explain that the first two equations of both the phases (linear and nonlinear) are standard. These are Classical Rosen-zweig-MacArthur predator-prey type used to interpret the dynamical behavior of certain predator-prey communities. The third term of the second equation in both the phases is due to middle predator y being a vertebrate. The equation (1d) is absolutely not standard one.

For discussing the stability, bifurcation or chaotic behavior, many authors [3,4] consider the third equation as

$$\frac{dz}{dt} = \Big(- d_1 + \frac{d_2 y}{d_3 + y} \Big) z,$$

that is a system in which x is the number of logistic-type prey, y is the number of Holling-type II specialist predator and z the number of Holling type II generalist predator. An interesting formulation of this equation for discussing the predator dynamics was given by Leslie [33] and reported in the book by Pielou [34]. This equation was taken as

$$\frac{dz}{dt} = cz\Big(1 - \frac{z}{my}\Big),$$

where c and m are parameters. In this formulation, the growth of the predator population is taken as

$$\frac{dz}{dt} = cz\Big(1 - \frac{z}{K}\Big),$$

of logistic type, where the measures of the environmental carrying capacity K is assumed to be proportional to the prey abundance that is, $K = my$. Thus, the logistic equation becomes

$$\frac{dz}{dt} = cz\left(1 - \frac{z}{m_1 + my}\right),$$

the additional constant m_1 normalizes the residual reduction in the predator population z because of severe scarcity of the favourite food. Simplifying, we obtain

$$\frac{dz}{dt} = cz - \frac{c}{m}\left[\frac{z^2}{\frac{m_1}{m} + y}\right] = cz - \frac{w_3 z^2}{y + D_3},$$

where $D_3 = \frac{m_1}{m}$ and $w_3 = c/m$.

Let us now assume that a generalist predator z predates on predator y. Even though the generalist predators have their favourite preys, they switch over to other preys when these are in short supply. Taking this into account and using Holling's type III functional response, the growth rate equation for the predator z can be written as

$$\frac{dz}{dt} = cz - \frac{w_3 z^2}{y}.$$

Most of the generalist predators are sexually reproducing. In sexually reproducing populations a behavioral phenomenon known as sexual selection [35] is common. Since sexual selection depends on the success of certain individuals over others of the same sex and involves behavioral traits such as choosiness and species recognition, it is natural to expect that the growth of a sexually reproducing population will be proportional to the number densities of two sexes. It is known from population genetics that evolution attempts to maintain the ratio of the number densities of two sexes to unity. In order to accommodate these facts, above equation is modified to

$$\frac{dz}{dt} = cz^2 - \frac{w_3 z^2}{y + D_3},$$

where w_3 measures the limitation on growth of the generalist predator by its dependence on its most favorite prey y.

We chose to study the non-linear phase as the linear phase does not support the chaotic behavior at all. The sexually reproducing populations are covered by

this phase when they are under Allee effect. We have also done the extensive simulation experiment with the linear phase of the model systems (1a)–(1c). It was observed that the system only supports stable focus and limit cycle (i.e., order) not chaos.

3   Results and conclusion

Upadhyay *et al.* [1] considered four model systems modeling different but very common ecological situations and obtained the chaotic solutions (SCA) in narrow parameter regimes as well as in regions of natural measure zero only for first model systems. The other model systems hardly display chaos. Our primary interest is to observe the role of toxin producing phytoplankton in such ecosystems. The role of TPP for controlling blooms or for decreasing grazing pressure is now well known, but the functional forms for releasing toxic substances are not known (Chattopadhyay *et al.* [29]). For this reason, we shall considered Holling type I, type II, and type III functional forms to describe the liberation of toxin production process.

Model 1A and model 1B are integrated using fourth-order Runge-Kutta method considering the parameter values of Upadhyay *et al.* [1, 19] except for θ. We observed stablity, limit cycle and chaotic dynamics of the system by changing the intrinsic growth rate coefficient a_1 of the TPP population. Our approach is first to fixed θ and then observe the exchange of states (stability-limit cycle-period doubling – chaos) in the model systems for different value of $a_1 \in [0.5, 3]$. We observe that, if $f(x)$ is Holling type II functional response, then for $\theta = 0.05$ and $a_1 \in [0.5, 1.5]$, the model system 1A settles down to a steady state solution, depicting a stable focus. Limit cycle oscillations of the system occur at $a_1 \in [2.4, 3.0]$. The period-doubling oscillations of the system occur at $a_1 \in [2.1, 2.3]$ and at $a_1 = 1.95$. Chaotic dynamics of the system occurs only at $a_1 = 2.0$. The similar behavior is observed for other form of the functional response functions and for model system 1B. Now, by changing the value of w_2 , the per capita reduction rate, from 0.55 to 1.45, Upadhyay *et al.* [1] obtained SCA (strange chaotic attractor) for both the model systems. Now, we shall observe how these dynamics are changing for different values of θ and also for different functional forms. In real life situations, it has been observed that increasing the strength of

toxic substances has a stabilizing effect. Here, we like to see whether this is true or not in our considered model systems?

From Table 1, it is observed that for both the models, the increase of value of toxic substances released by TPP has a stabilizing effect. This observation is true for different form of toxic substance liberation process (i.e., $f(x)$) as well as both the model systems. Now, we are demonstrating only the effect of θ for model 1A and with Holling type II functional response. The effect of θ for this model 1A and for model 1B are presented in Table 1. It is observed that, for $\theta \in [0.001, 0.0075], [0.0085, 0.015], [0.09, 0.1]$ and at $\theta = 0.2$, we obtain chaotic behavior (SCA) (see Fig. 3). By increasing the value of toxic substances in the range $\theta \in [0.02, 0.085], [0.25, 0.4]$ and for $\theta = 0.008, 0.15$, we obtain the oscillatory behavior (different order limit cycles P3, P4, P5, P6 and P7 are obtained) (see Fig. 4). For $\theta \in [0.45, 0.75]$, we obtain stable focus (SF) or order (see Fig. 5). The different dynamics of the system is studied through three-dimensional phase plot. As the fractional changes of TPP population have a great impact on the ecosystem functioning, and also the nature of toxic liberation process is still unknown, different possible combinations of these functional forms have been considered to search the order of the food chain model. We observe that the rate of toxic substance released by TPP is to be high for type I functional form than those of type II and type III functional form (see Table 1). These observations indicate us that to maintain the order of an ecosystem functioning, type II or type III functional form for toxin liberation process is more appropriate.
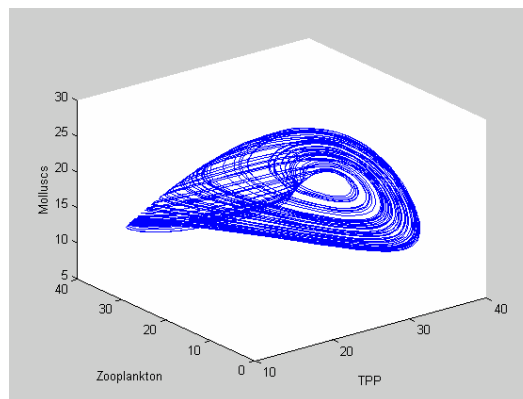

Fig. 3. Phase plane diagram for model system 1A depicting chaotic attractor for $\theta = 0.2$ (other parameters are same as given in Table 1).
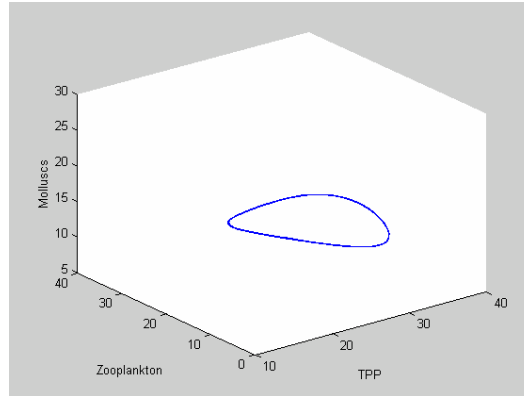
Fig. 4. Phase plane diagram for model system 1A depicting limit cycle attractor for $\theta = 0.35$ (other parameters are same as given in Table 1).
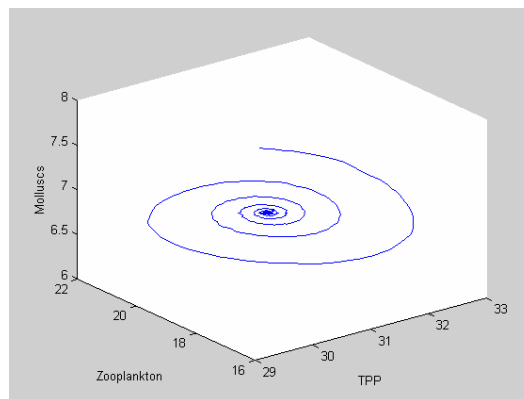

Fig. 5. Phase plane diagram for model system 1A depicting stable focus for $\theta = 0.5$ (other parameters are same as given in Table 1).

The above findings indicating that the strength of toxic substances released by TPP reduce the prevalence of chaos. The conclusion of such an observation is that toxic substances released by TPP population may act as bio-control by changing the state of chaos to order. As aquatic systems are very much complex, so it is not easy to conclude that order in aquatic systems is obvious. The role of TPP population in aquatic systems is still in a stage of infancy. The development of this topic needs special attention from experimental as well mathematical ecologists. We believe that our results may give some insight in this direction.

Table 1. Simulation experiments of model system (1) given in Upadhyay *et al.* [1]. The values of the common parameters used in the model are: $a_1 = 2.0$, $b_1 = 0.05$, $w = 1.0$, $D = 10$, $a_2 = 1.0$, $w_1 = 2.0$, $D_1 = 10$, $D_2 = 10$, $c = 0.0257$, $w_3 = 1.0$ and $D_3 = 20$. P3 – limit cycle of period 3, P4 – limit cycle of period 4, P5 – Limit cycle of period 5, P6 – limit cycle of period 6, P7 – limit cycle of period 7, SF – Stable focus, LC – Limit cycle, SCA – strange chaotic attractor

Results of Upadhyay *et al.* [1]	Results of the proposed model for Holling type I: $f(x) = x$		Results of the proposed model for Holling type II: $f(x) = x/(x + D_4)$		Results of the proposed model for Holling type III: $f(x) = x^2/(x^2 + D_4^2)$	
	θ		θ		θ	
Model 1A ($\theta = 0$): $w_2 = 0.55$, SCA	0.001–0.003	SCA	0.001–0.0075	SCA	0.001–0.0065	SCA
	0.004	P5	0.008	P5	0.007	P5
	0.005	P3	0.0085–0.015	SCA	0.0075–0.015	SCA
	0.006	P4	0.02	P3	0.02	P3
	0.0065–0.009	SCA	0.025	P5	0.025	P6
	0.0095	P6	0.03	P6	0.03–0.035	P8
	0.01	P5	0.035–0.04	Long order	0.04	P6
	0.015	SF	0.045	P6	0.045–0.06	P3
			0.05	P5	0.065	P5
			0.055–0.07	P3	0.07	P3
			0.075	P7	0.075–0.15	SCA
			0.08–0.085	P3	0.2	P2
			0.09–0.1	SCA	0.25–0.35	LC
			0.15	P2	0.4–0.6	SF
			0.2	SCA		
			0.25	P2		
			0.3–0.4	LC		
			0.45–0.75	SF		
Model 1B ($\theta = 0$): $w_2 = 1.45$, SCA	0.001–0.003	SCA	0.001–0.0075	SCA	0.001–0.0062	SCA
	0.004	LC	0.08	P7	0.063	P7
	0.0045–0.009	P2	0.085	P4	0.065–0.07	P4
	0.01	P3	0.09–0.1	P2	0.075–0.1	P2
	0.015	SF	0.15–0.359	LC	0.11–0.32	LC
			0.4–0.75	SF	0.33–0.64	SF

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