Nutrients and toxin producing phytoplankton control algal blooms – A spatio-temporal study in a noisy environment

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Nutrients and toxin producing phytoplankton control algal blooms – a spatio-temporal study in a noisy environment

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A phytoplankton-zooplankton prey-predator model has been investigated for temporal, spatial and spatio-temporal dissipative pattern formation in a deterministic and noisy environment, respectively. The overall carrying capacity for the phytoplankton population depends on the nutrient level. The role of nutrient concentrations and toxin producing phytoplankton for controlling the algal blooms has been discussed. The local analysis yields a number of stationary and/or oscillatory regimes and their combinations. Correspondingly interesting is the spatio-temporal behaviour, modelled by stochastic reaction-diffusion equations. The present study also reveals the fact that the rate of toxin production by toxin producing phytoplankton (TPP) plays an important role for controlling oscillations in the plankton system. We also observe that different mortality functions of zooplankton due to TPP have significant influence in controlling oscillations, coexistence, survival or extinction of the zooplankton population. External noise can enhance the survival and spread of zooplankton that would go extinct in the deterministic system due to a high rate of toxin production.

1. Introduction

The dynamics of rapid (or massive) increase or decrease of plankton populations is an important subject in marine plankton ecology. Generally high nutrient levels and favourable conditions play a key role in rapid or massive growth of algae and low nutrient concentration as well as unfavourable conditions limit their growth. The water must contain high levels of inorganic nutrients (nitrogen and phosphorus) for the algae to feed on and also water temperature and salinity levels must be within a certain range to be conducive to planktonic growth. A frequent outcome of planktonic bloom formation is massive cell lysis and rapid disintegration of large planktonic populations. This is closely followed by an equally rapid increase in bacterial numbers, and in turn by a fast deoxygenation of water, which could be detrimental to aquatic plants and animals. These blooms also reduce the chance of growth for aquatic vegetation. Hence, studies regarding the pattern of blooms are necessary towards this serious ecological problem. In recent years, there has been considerable scientific attention towards harmful algal blooms (HABs) (Blaxter and Southward 1997; Chattopadhyay *et al* 2002b). In a broad sense planktonic blooms can be derived into two types, "spring blooms" and "red tides". Spring blooms occur seasonally for the changes in temperature or nutrient availability which are connected with seasonal changes. Red tides are localized outbreaks and may occur due to high water temperature (Truscott and Brindley 1994). The nature of blooms, in the sense of the rapid onset and disappearance of oscillations under supposedly favourable environmental condition is one of the main characteristics in plankton ecosystem. Phytoplankton species which cause fish poisoning (*Ciguatera*) and shellfish-vectored poisoning of humans are clearly harmful (Hallegraeff 1993). Harmful species can be characterized by three distinct models of negative impact such as 'toxic', noxious and nuisance used either

synonymously or to characterize their relative degree of impact. There are at least eight different modes and mechanisms by which harmful phytoplankton species can cause mortality, physiological impairment, or other negative *in situ* effects. These fall into two general types: non-chemical effects which lead to starvation or cause harmful mechanical and physical damage, and chemical effects attributable to physical-chemical reactions, phycotoxins, or other metabolites. Among the chemically harmful mechanisms, die-offs due to anoxia or hypoxia following blooms of large, relatively ungrazed species, such as *Ceratium*, are well known (Mahoney and Steimle 1979; Graneli *et al* 1989). Mortality can occur through direct ingestion (endotoxin) of the harmful species, upon exposure to secreted toxins (exotoxins), or from toxin vectoring through the food web, accompanied by conformational changes in the toxic principles and their potencies (Shimizu 1989; Yasumoto and Murata 1993). The impact may be on a directly targeted predator or lead to indiscriminate die-offs and physiological impairment during food-web vectoring. Despite convincing evidence that harmful phytoplankton species occur and bloom, knowledge of what defines a harmful species is qualitative. Such species are still being identified, and the modes and mechanisms of harmful effects, and ecophysiological divergence of harmful taxa from species considered to be non-harmful are still being described.

Blooms, as a phenomenon, collectively have properties other than biomass, numerical population density, and the potential of the bloom species to inflict harm. These features are also relevant to their definitions, occurrences and *in situ* trophodynamic consequences. The processes influencing species occurrences, whether harmful or not, may differ significantly from those regulating their blooms. And, at any given time or spatial location, as an inherent aspect of species succession, one or more species are in a state of bloom even though they may not achieve high biomass or high population density. The presence of toxic species does not necessarily lead to a deleterious impact; such effects require a threshold population density level, above which it becomes inimical. However, the basic distinction between harmful and non harmful blooms is not only warranted, it is an important first step toward classification of the various types of phytoplankton blooms which undoubtedly occur. The adverse effect of harmful algal blooms is clear, but the control of such problems is under investigation.

Mathematical modelling is a useful tool to explore the features of the interaction between nutrient, toxin producing phytoplankton and zooplankton, and predict relationships that may be looked for in experimental studies. Many models have already been built to simulate zooplankton-phytoplankton interactions. Most of them at least account for effects of nutrient recycling and temperatures (see Jørgensen 1983 for a review). More elaborate versions include several species and structured populations of zooplankton (Rose and Swartzman 1988). The complexity of such models prohibits a simple generic analysis of the effect on the system of predation on zooplankton. Recent studies reveal that some times bloom of certain harmful species leads to release of both toxins and allelopathic substances. Allelopathic substances are distinguished from phycotoxins in being secondary metabolites; both can co-occur within a given harmful species. Allelopathic substances tend to be directly targeted and may physiologically impair, stun, repel, induce avoidance reactions, and kill grazers. Examples of these diverse models of impact were given by Smayda (1992). Information on the recently discovered, remarkable ambush predatory behaviour of the harmful dinoflagellate, *Pfiesteria piscicida* was presented by Burkholder and Glasgow (1995). Toxin producing plankton (TPP) release toxic chemicals in the water and reduce the grazing pressure of zooplankton. As a result TPP may act as biological control for the termination of planktonic blooms (Chattopadhyay *et al* 2002a,b; Sarkar and Chattopadhyay 2003).

Recently, Chattopadhayay *et al* (2002a,b) tried to describe a suitable mechanism to explain the cyclic nature of bloom dynamics by using different forms of toxin liberation process, in a simple model of phytoplankton-zooplankton interaction. They also studied the effect of time delay to explain the bloom phenomenon. The results obtained from their theoretical and field observations suggest that toxic phytoplankton (TPP) may serve as a key factor in the termination of blooms. But, the major drawback of their observation is, they have only changed different forms of mortality functions for zooplankton due to TPP, in a single model, to explain the bloom phenomenon as well as control, respectively (with the same functional form by changing the parameter values of the toxin production rate). Whether TPP is really effective to control blooms in a naturally occurring situation? – is not clear from their study. It has been well established fact, that, differences in nutrient concentrations effect algal growth and play a significant role in bloom formation. Hence, it is very much needed to study the role of TPP for controlling plankton blooms in a realistic situation where nutrients help to form oscillations in plankton populations. In another study, Sarkar and Chattopadhyay (2003) observed the effect of environmental fluctuations and its possible control mechanism for occurrence of planktonic blooms. They introduced additive colour noise in a delay induced phytoplankton-zooplankton system and observed that TPP as well as artificial eutrophication control oscillatory successions of planktonic blooms. Since from the literature it is still a matter of controversy that which type of noise is more realistic to model ecological systems? A commonly expressed intuitive argument is

that temporally correlated environments (colour noise) lead to higher risk of population extinction than white noise environment (Lawton 1997). In the study of Sarkar and Chattopadhyay (2003) though TPP and external influence play significant role to reduce oscillations but the question whether this reduction lead to high risk of population extinction is not clear. In conservation biology, from management point of view, it is very much important to study the risk of population extinction. Moreover, all the above studies are based on temporal dynamics of phytoplankton-zooplankton interaction. A more natural consideration is to study the plankton dynamics under temporal, spatial and spatio-temporal aspects. In our paper, we have tried to explain all the above difficulties in a more realistic way.

In this paper, a simple model of the zooplankton-phytoplankton interaction is used to analyse the potential effects of different nutrient concentrations. The role of TPP for controlling the bloom is studied when nutrients lead to oscillatory behaviour of the system. Furthermore, the impact of multiplicative noise (Allen 2003; Anishenko *et al* 2003) is investigated. The role of environmental noise for survival of plankton populations is discussed. It is observed that choice of density dependent multiplicative noise in the form of spatio-temporal Gaussian process minimize the extinction risk of plankton population and this type of modelling approach is useful to apply in conservation biology problems. Our theoretical as well as numerical studies support the field observations available from literatures. Our main objective is to study the influence of nutrients, TPP and external noise on the spatio-temporal pattern formation of interacting plankton populations and to give possible ranges of thresholds to control oscillations (or blooms) as well as to save the population from extinction risk.

2. The mathematical model

The basic marine food chain nutrients → phytoplankton → zooplankton is modelled here. In this paper, an extremely simple model of phytoplankton-zooplankton interaction is used to analyse the potential effects of toxicity and external noise. The approach is in the classical tradition of minimal modelling. By lumping many different phenomena into a few dimensions, a simple model is produced. Such models are especially suitable to examine the generic behaviour of the system (for example, Rosenzweig 1971 discussed the expected response of some minimal phytoplankton-zooplankton models to eutrophication). For simplicity we do not consider the dynamics of the nutrient concentrations and we emphasize on the fact that the growth of phytoplankton depends on the nutrient variability. In the case of bio-manipulation, nutrient

is a manipulated variable, which acts as an external control parameter, and we are in the response of the first and second trophic level. We further assume that phytoplankton population releases a toxic substance which reduces the growth of zooplankton. This model is an extended form of the existing systems (Pascual 1993; Malchow *et al* 2000) where the potential effects of TPP on zooplankton mortality and the influence of external noise has not been considered. Moreover, this model resembles with the model of Chattopadhyay *et al* (2002b) despite the fact that phytoplankton growth is been considered to be dependent on the nutrient concentrations and the whole dynamics has been studied in spatio-temporal aspect. The corresponding simple prey-predator model of the interaction and motion of toxin producing phytoplankton P and zooplankton Z at time τ and position $r = \{x_1, x_2, x_3\}$ reads

$$\frac{\partial P}{\partial t} = \boldsymbol{b}\,\frac{N}{H_N + N}\,P - \boldsymbol{d}_P\,P^l - \boldsymbol{g}\,\frac{P^p}{H_1^p + P^p}\,Z + D_P\,\Delta P, \quad (1)$$

$$\frac{\partial Z}{\partial t} = e_Z \boldsymbol{g}\,\frac{P^p}{H_1^p + P^p}\,Z - \boldsymbol{d}_Z\,Z^q - \boldsymbol{q}f(P)Z + D_Z\,\Delta Z. \quad (2)$$

Here $\boldsymbol{b}$ is the maximum growth rate of phytoplankton, $\boldsymbol{g}$ is the grazing rate of zooplankton on phytoplankton, e_Z is the biomass conversion efficiency and $\boldsymbol{d}_i$; $i = P, Z$; are mortalities of phytoplankton and zooplankton respectively. H_N and H_1 are the half-saturation constants of functional responses and nutrient limitation. Time τ and length $x_i \in [0, L_i]$; $i = 1, 2, 3$; are measured in days [*d*] and meters [*m*] respectively. N, P, Z, H_N and H_1 are usually measured in mg of dry weight per litre [*mg·dw/l*]; e_Z; is dimensionless parameter; the dimension of $\boldsymbol{b}$ and $\boldsymbol{g}$ is [d^{-1}], $\boldsymbol{d}_i$; $i = P, Z$; are measured in [$(mg·dw/l)^{1-l}\,d^{-1}$] and [$(mg·dw/l)^{1-q}\,d^{-1}$] respectively. The diffusion coefficients D_P and D_Z are measured in [$m^2\,d^{-1}$]. Δ is the Laplace operator. The exponent p describe different types of functional response of zooplankton, whereas $q = 1, 2$ stand for simple density-dependent mortality of zooplankton. Keeping in mind the additional factor that the release of toxic substance by toxin producing phytoplankton species reduces the growth of zooplankton, we introduce an additional mortality factor ($\boldsymbol{q}f(P)Z$, $f(P) = P^m/(H_2^m + P^m)$) for zooplankton, where $\boldsymbol{q}$ is the rate of toxin production and the dimension is [d^{-1}]. As the fractional changes in the TPP population per unit time effectively illustrates the impact of predation on the population at any particular time, it is interesting to examine the specific predation rate for the system as the outbreak advances. Keeping the above mentioned properties in mind, different types of functional forms have been assumed for the zooplankton mortality and formulation of the model e.g. Holling type II [$f(P) = P/(H_2 + P)$] and Holling type III [$f(P) = P^2/(H_2^2 + P^2)$] where H_2 is the half-saturation constants of func-

tional response measured in mg of dry weight per litre [$mg \cdot dw/l$] (Holling 1959).

The model will be further simplified now. We choose the standard logistic form with $l = 2$ and a Monod type of nutrient limitation. In the absence of zooplankton, algal growth will saturate at a carrying capacity of $P = [N/(N + H_N)] * b/d_P$. Growth limitations by different nutrients and light are not treated separately. Instead it is assumed that overall carrying capacity which is a function of the nutrient level of the system. The effect of planktivorous fish (third trophic level) is neglected because of the same reason for bio-manipulation and idea of minimal modelling. Also, the focus of this paper is on the influence of nutrient concentration and rate of toxin production by TPP on the minimal model of phytoplankton-zooplankton interaction. But, all the external influences (including the effect of planktivorous fish) which change over time, are lumped through adding a white noise process to the model justifying the need of modification of the deterministic system to a stochastic system.

As an alternative to the deterministic model, we therefore assume that the interaction process is not smooth, subject to a variety of internal and external influences, which change over time. We have chosen to model the variations in the phytoplankton-zooplankton growth rates by adding a spatio-temporal white noise process. This is justified by two considerations:

(i) It is believed that growth of phytoplankton and zooplankton is influenced by large number of factors, each with small individual effects on the others (for example, pH, salinity, temperature, etc.). A natural way to model this is by some kind of Wiener process or Gaussian white noise process. Gaussian white noise is a good approximation of many real world situations and generates mathematically tractable models.

(ii) The erratic variations (caused by nutrient variations, changes in light due to depths, differences in temperature, etc.) are very likely occurring with a faster time scale than the growths of species. These will then be seen as 'noise' on the slower time scale. White noise process explains this situation very well and can be used as external stochasticity to the system.

In this paper, we have not considered all the events individually occurring due to environmental fluctuations but coupled with white noise process, which is a very general technique to describe a noise induced system. This process of adding a density dependent noise (multiplicative noise is more realistic than additive noise) to a model (continuously drifting), in order to account for its irregular oscillations with time, gives rise to rich class of models, namely stochastic differential equations models driven by Brownian motion. Further, it has been shown from field observations that phytoplankton-zooplankton

population spectrum is significantly rougher (whiter, specifically zooplankton can have much whiter spectrum) under the effect of coastal heterogeneity on the variability of *in situ* salinity, oxygen, temperature, optical transmissivity, fluorescence, etc. (Lovejoy *et al* 2001). These justify our consideration of white noise process to modify our deterministic model to a stochastic model of phytoplankton-zooplankton system. So, equations (1–2) now read

$$\frac{\partial P}{\partial t} = b \frac{N}{H_N + N} P - d_P P^2 - g \frac{P^p}{H_1^p + P^p} Z +$$
$$D_p \Delta P + a_1 [\mathbf{P}(\vec{r},t)] \cdot \mathbf{x}_1(\vec{r},t), \tag{3}$$

$$\frac{\partial Z}{\partial t} = e_z g \frac{P^p}{H_1^p + P^p} Z - d_z Z^q - q \frac{P^m}{H_2^m + P^m} Z +$$
$$D_z \Delta Z + a_2 [\mathbf{Z}(\vec{r},t)] \cdot \mathbf{x}_2(\vec{r},t), \tag{4}$$

where $\xi_i(\vec{r},t); i = 1, 2$ is a spatio-temporal Gaussian white noise, i.e. a random Gaussian field with zero mean and delta correlation, defined below as

$$\langle \mathbf{x}_i(\vec{r},t) \rangle = 0, \langle \mathbf{x}_i(\vec{r}_1,t_1) \mathbf{x}_i(\vec{r}_2,t_2) \rangle =$$
$$d(\vec{r}_1 - r_2) d(t_1 - t_2), i = 1,2 \tag{5}$$

and $\alpha_1 [\mathbf{P}(\vec{r},t)], \alpha_2 [\mathbf{Z}(\vec{r},t)],$ are the density dependent noise intensities. The axiom of parentness in population dynamics requires this density dependence, i.e. multiplicative noise.

Now, dimensionless quantities of densities, time and space are introduced:

$$n = \frac{N}{H_N}, X_1 = \frac{P}{H_1}, X_2 = \frac{Z}{e_z H_1},$$
$$t = e_z g t, \{x, y, z\} = \frac{S}{L} \{x_1, x_2, x_3\}, \tag{6}$$

where L is the characteristic length in all 3 space dimensions, S is an integer scale factor.

The usual technique of model analysis is to reduce the number parameters of the system. The advantage of dimensionalizing the equations reduces the number of parameters by coupling them together into dimensionless groups. This reduction always simplifies the analysis (Lin and Segel 1988). One finds the dimensionless form of our equations as

$$\frac{\partial X_1}{\partial t} = r \frac{n}{1+n} X_1 - s X_1^2 - \frac{X_1^p}{1+X_1^p} X_2 +$$
$$d_1 \Delta X_1 + w_1 [\mathbf{X}_1(\vec{r},t)] \cdot \mathbf{x}_1(\vec{r},t), \tag{7}$$

$$\frac{\partial X_2}{\partial t} = \frac{X_1^p}{1+X_1^p} X_2 - m_2^q X_2^q - \frac{g^m X_1^m}{1+h^m X_1^m} X_2 +$$
$$d_2 \Delta X_2 + w_2 [\mathbf{X}_2(\vec{r},t)] \cdot \mathbf{x}_2(\vec{r},t), \tag{8}$$

with

$$r = \frac{b}{e_z g}, \; s = \frac{d_p H_1}{e_z g}, \; m_2 = e_z H_1 \{\frac{d_z}{e_z^2 g H_1}\}^{\frac{1}{q}},$$

$$h = \frac{H_1}{H_2}, \; g = h(\frac{q}{e_z g})^{\frac{1}{m}},$$

(9)

and

$$w_1 = \frac{a_1}{e_z g}, \; w_2 = \frac{a_2}{e_z g}, \; d_1 = \frac{S^2}{L^2 e_z g} D_P, \; d_2 = \frac{S^2}{L^2 e_z g} D_z. \quad (10)$$

Throughout this paper, it is chosen

$$w_1[\mathbf{X}_1(\vec{r},t)] = w X_1(\vec{r},t), \; w_2[\mathbf{X}_2(\vec{r},t)] =$$
$$w X_2(\vec{r},t); \; w = \text{const.}$$
(11)

2.1 *Parameter set*

We will now concentrate on model equations with $p = 1$, $q = 1$. Our assumptions depict that grazing rate of zooplankton is dependent on the phytoplankton concentration according to a functional response type II (Holling 1959) i.e. following simple Monod kinetics. Only horizontal processes will be further on considered. The characteristic horizontal length units are fixed at $L_1 = L_2 = L$. Moreover, we consider that the diffusion coefficients d_1, d_2 describe eddy diffusion. Therefore, they must be equal for both species, i.e. $d_1 = d_2 = d$.

We have considered the parameter values within a realistic range. Nutrient level and consequently the parameter H_N are expressed in relative units. The maximal algal growth rate is realistic in eutrophic situation. The parameters determining the zooplankton grazing rate, assimilation efficiency, mortality are taken near the median of the literature ranges of parameters reported by Rose and Swartzman (1988) for medium sized Daphnia. The dimensions and other values of the parameters are chosen from literature (Scheffer 1991; Pascual 1993; Malchow *et al* 2000) which are well established for a long time to explain the phytoplankton-zooplankton dynamics in various contexts. The parameter determining the mortality of zooplankton due to toxic phytoplankton is set more or less arbitrarily. Effects of different shapes of the functional response will be discussed and they also change significantly depending on the types of phytoplankton species. We have only used the dimensionless forms of the above parameter sets according to our scaling method and tried to explain the dynamics of our model. The following set of parameters are taken after scaling differently:

$r = 1 \cdot 0, \; s = 0 \cdot 2, \; m_2 = 0 \cdot 6, \; h = 2 \cdot 0,$

$S = 100, \; x_1 \; ^{\mathbf{a}} \; [0, S], \; x_2 \; ^{\mathbf{a}} \; [0, S], \; x_3 \equiv 0, \; d = 0 \cdot 05.$

The local properties, i.e. the emergences and stability of stationary states, can be analysed by means of numerical analysis with different nutrient concentration (n) and rate of toxin production (g). Moreover, we will discuss the effect of different types of functional forms for zooplankton mortality due to toxin liberation by varying the exponent m.

3. The deterministic local dynamics

At first, the local dynamics is studied, i.e. we look for stationary and oscillatory solutions of system (7–8) for $d = 0$ and without external noise ($w = 0$). It is apparent that $\{(X_1, X_2)/X_1 = 0\}$ and $\{(X_1, X_2)/X_2 = 0\}$ are invariant subspaces, so that no orbit starting in $R = \{(X_1, X_2)/X_1 > 0 \text{ and } X_2 > 0\}$ can ever cross the border, i.e. there will always be a positive biomass.

The analytical investigation of the system without toxin production ($g = 0$) yields the following stationary solutions:

(0) Trivial solution $X_1^{0S} = X_2^{0S} = 0$, always unstable.
(1) Extinction of zooplankton: $X_1^{1S} = (n/(1 + n))*r/s$, $X_2^{1S} = 0$, stable or unstable depending on $n <$ or $> n_c$ respectively, where $n_c = sm_2/[r - m_2(r + s)]$.
(2) Coexistence of phytoplankton and zooplankton: $X_1^{2S} = m_2/(1 - m_2)$, $X_2^{2S} = [1/(1 - m_2)]*[(n/(1 + n))*r - (sm_2/(1 - m_2))]$, stable or unstable depending on $n <$ or $> n_c$ respectively, where $n_c = s(1 + m_2)/[(r - s) - m_2(r + s)]$.

It is interesting to note that depending on the nutrient concentration (n), the point (X_1^{2S}, X_2^{2S}) may be either a node or a focus, stable or unstable. Moreover, if it loses its stability, a stable limit cycle is generated and can be related to planktonic blooming. For low values of nutrient concentration, we observe coexistence and the following relaxation to the non-oscillatory stable situation. This can be related to control of planktonic blooming through low nutrient concentration.

We observed that for different ranges of n there exist different stationary solutions for $g = 0$. For $n = 0 \cdot 4$, zooplankton goes extinct and the phytoplankton population remain stable with low density (solutions 1). For $n = 0 \cdot 8$, the zooplankton population survives and we observe that the system becomes non-oscillatory stable (solutions 2). Further increase in n, i.e. $n = 2 \cdot 0$ results in damping of the oscillations and for $n = 8 \cdot 0$ stable limit cycle is observed (solutions 2) which can be related to planktonic blooming. The solution diagrams (figure 1) display the dependence of the steady-state solutions on the nutrient concentrations. In the stable parameter range with strong external noise ($w = 0 \cdot 20$), we also observe recurrent outbreaks related to planktonic blooming. In the oscillatory parameter range with strong external noise, we observe

qualitatively the same outcome as the deterministic computations (figures not included). However, one should have in mind that the latter must only hold for the average of a sufficient number of runs. In a noisy environment, there are only certain probabilities for the survival or extinction of the populations. It is worth noted that the dynamic patterns generated from the model reveal the occurrence of oscillations in the densities of zooplankton and algae under certain nutrient concentrations. This is caused by the change of the stable point-equilibrium into a limit cycle resulting in predator-prey oscillations. Alternatively, numerical analysis can be used to reveal the dependence of stability on nutrient concentrations. The lowering of nutrient concentration has the stabilising effect on the oscillating plankton community and can be used as control parameter for planktonic blooming.

Now, we observe the effect of TPP for controlling the oscillations in plankton population. For this, we first consider Holling type II functional response ($m = 1$) for zooplankton mortality due to TPP. We fix $n = 8\cdot0$, as we observed limit cycle oscillations for $g = 0$ presented in figure 1d. Now for $g = 0\cdot1$ we observe damping of oscillations. Further increase in g i.e. $g = 0\cdot3$ yields nonoscillatory steady states with coexistence of both the populations. Next, if we increase g more ($g = 0\cdot5$) then zoo-

plankton goes to extinction followed by a non-oscillatory stable phytoplankton population. It is interesting to see that introduction of strong external noise ($w = 0\cdot25$) helps to survive the zooplankton population. A corresponding example is presented in figure 2.

Control of oscillations (blooms) in planktonic community can also be well documented if we consider the functional responses as Holling type III ($m = 2$) for zooplankton mortality due to TPP. We observe in this case that increase of rate of toxin production (g) yields loss of oscillations but non-oscillatory stable coexistence of both phytoplankton and zooplankton. Further increase in g leads to extinction of zooplankton. It is interesting to note that external noise enhances survival of zooplankton. Corresponding example is presented in figure 3.

3.1 *Biological relevance*

How do temporal correlations in environmental variability influence the risk of population extinction – is an important question in conservation biology, which calls both for analysis of empirical data sets, and for theoretical studies on model populations (Lawton 1997). Environmental noise is usually incorporated into models to esti-
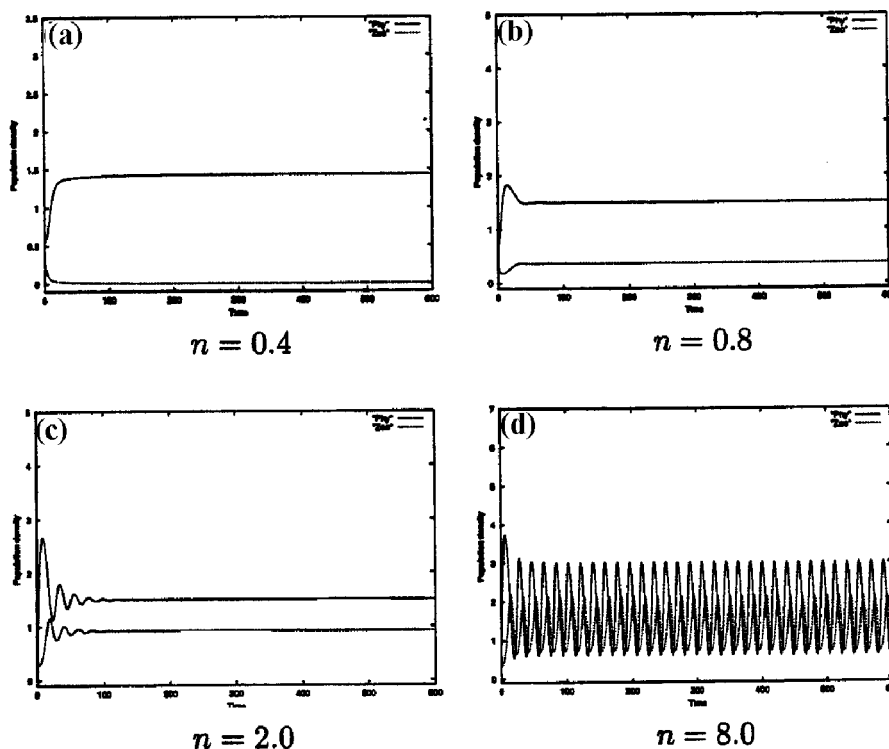

Figure 1. Local dynamics with (**a**) extinction of zooplankton, (**b**) survival of zooplankton, stable node, (**c**) coexistence of phytoplankton and zooplankton, damped oscillations, stable focus and (**d**) stable oscillations (limit cycle) with $g = 0$.

mate extinction risk or to assess management decision. A commonly expressed intuitive argument is that temporally correlated environments lead to higher risk of population extinction than white noise environments (Lawton 1997). Some literatures give strong support to the lower risk of population extinction when modelled by white noise environments (Foley 1994; Petchey *et al* 1997). Extinction because of demographic stochasticity is unlikely simply because population size do not stay low long enough – usually an extinction because uninhabitable environment occurs first. Thus, for populations, the extinction risk is really characteristic of the environment, not population dynamics (Heino *et al* 2000). Moreover, environmental stochasticity in the population dynamics always gives the chance to survive since it considers the probability. In our case, we have shown that external noise plays a significant role for survival of zooplankton population. This observation is in good agreement with the field studies conducted by Fransz *et al* (1984) and Holligan and Harbour (1977), where the abundances and survival of zooplankton as well as phytoplankton population varies with temperature and other environmental factors.

The analytical as well as numerical investigation of the local behaviour of the system (7–8) has given us a rough idea about the control of oscillations (blooms) in algal biomass through nutrient concentration and TPP.

4. The deterministic and stochastic spatial dynamics

In this section, we consider the spatio-temporal dynamics of the plankton model (7–8), i.e. zooplankton, grazing on toxin producing phytoplankton, under the influence of nutrient concentration, environmental noise and diffusing in horizontally two-dimensional space. The diffusion terms have been integrated using the semi-implicit Peaceman-Rachford alternating direction scheme, cf. Thomas (1995). For the interactions and the Stratonovich integral of the noise terms, the explicit Euler-Maruyama scheme has been applied (Kloeden and Platen 1999; Higham 2001).

The following series of figures summarizes the results of the spatio-temporal simulations for different nutrient concentrations and rate of toxin productions from § 3, but now including diffusion and noise. Periodic boundary conditions have been chosen for all simulations. The grey scale changes from high population densities in black colour to vanishing densities in white.
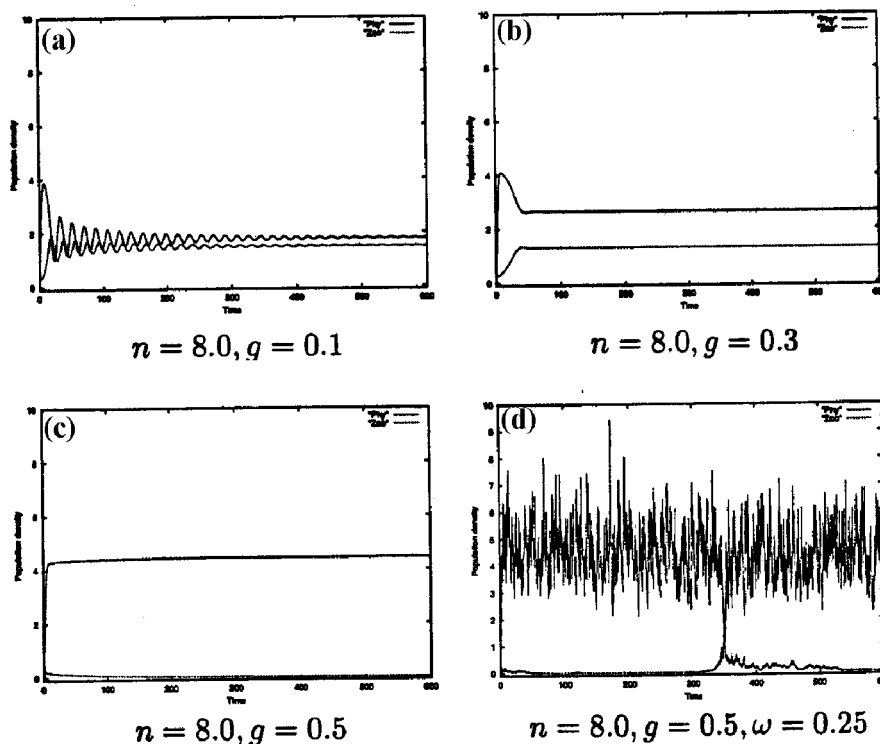

$$n = 8.0, g = 0.1$$

$$n = 8.0, g = 0.3$$

$$n = 8.0, g = 0.5$$

$$n = 8.0, g = 0.5, \omega = 0.25$$

Figure 2. Local dynamics with Holling type II functional response for zooplankton mortality due to TPP (**a**) damping of oscillations, stable focus, (**b**) non-oscillatory stable coexistence, stable node, (**c**) extinction of zooplankton, non-oscillatory stable phytoplankton and (**d**) survival of zooplankton in noisy environment with ***w*** = 0·25.

The initial conditions are localized patches in empty space, and they are the same for deterministic and stochastic simulations. They can be seen in the left column of all following figures. For all the figures 4 and 5, there are central patches of both species with phytoplankton ahead of zooplankton and this special initial configuration leads at first to the propagation of concentric waves for the deterministic case. For each of different nutrient concentration and rate of toxin production, the first row shows the dynamics of the phytoplankton and the second row the zooplankton respectively.

In figure 4, one can see the final spatial dynamics of both species for different nutrient concentrations. For low nutrient concentration (figure 4a), zooplankton goes extinct and phytoplankton propagates with diffusive fonts. Further increase in nutrient concentrations yields coexistence of both species and a uniform spread of both with a leading diffusive front ahead (figure 4b,c). Finally with higher nutrient concentration the localized initial patches generate concentric waves with localized oscillations (figure 4d). The noise only blurs these unrealistic patterns (figure 4e). The effect of nutrient concentration is readily seen.

In figure 5, one can see the final spatial dynamics of both species with Holling type II functional responses for

zooplankton mortality due to TPP. We consider the situation with high nutrient concentration and it is expected to have concentric waves with localized oscillations. But increase in rate of toxin production yields the dynamic stabilization of the locally unstable focus in space (see, figure 5a) and a long plateau is formed with a leading diffusive front ahead, cf. Petrovskii and Malchow (2000) and Malchow and Petrovskii (2002). Further, increase in rate of toxin production yields uniform spread of both populations with leading diffusive fronts (see, figure 5b,c). With high rate of toxin production zooplankton population goes extinction. Moreover, zooplankton is somehow trapped in the center (see, figure 5d). The noise enhances the 'escape', spread and survival of the zooplankton (see, figure 5e). The situation can also be well documented in the case of Holling type III functional response (figures not included). The role of TPP is readily seen.

4.1 *Biological relevance*

The effects of temperature (in different seasons), rainfalls, salinity, different hydrodynamic characteristics and inflow of human wastes (in the form of artificial
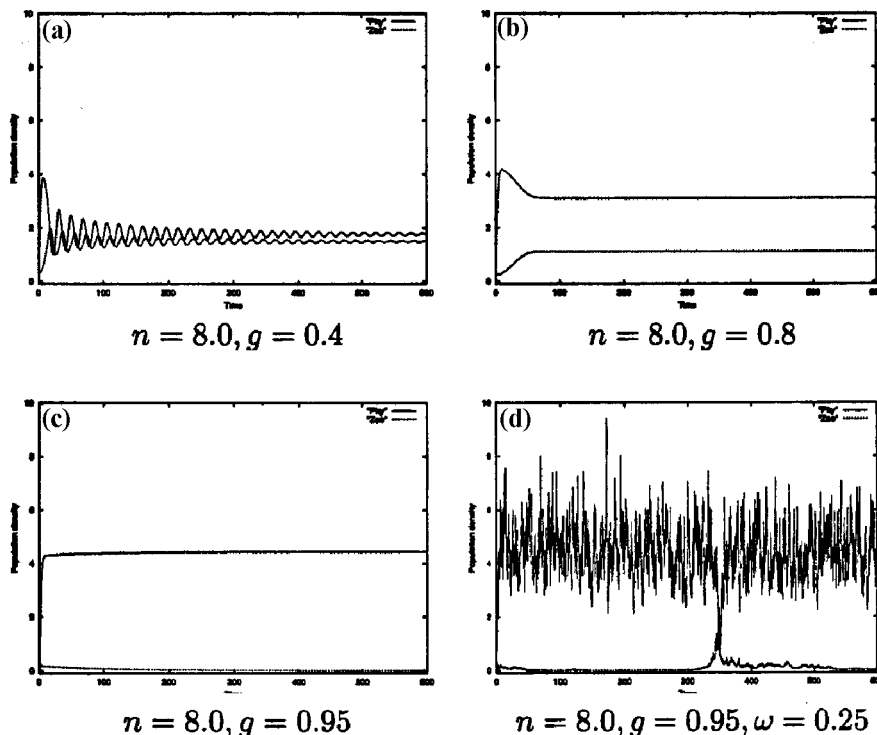

$$n = 8.0, g = 0.4$$

$$n = 8.0, g = 0.8$$

$$n = 8.0, g = 0.95$$

$$n = 8.0, g = 0.95, \omega = 0.25$$

Figure 3. Local dynamics with Holling type III functional response for zooplankton mortality due to TPP (**a**) damping of oscillations, stable focus, (**b**) non-oscillatory stable coexistence, stable node, (**c**) extinction of zooplankton, non-oscillatory stable phytoplankton and (**d**) survival of zooplankton in noisy environment with $w = 0.25$.

(**a**) $n = 0.4$

(**b**) $n = 0.8$

(**c**) $n = 2.0$

(**d**) $n = 8.0$

(**e**) $n = 8.0$, $\boldsymbol{w} = 0.20$

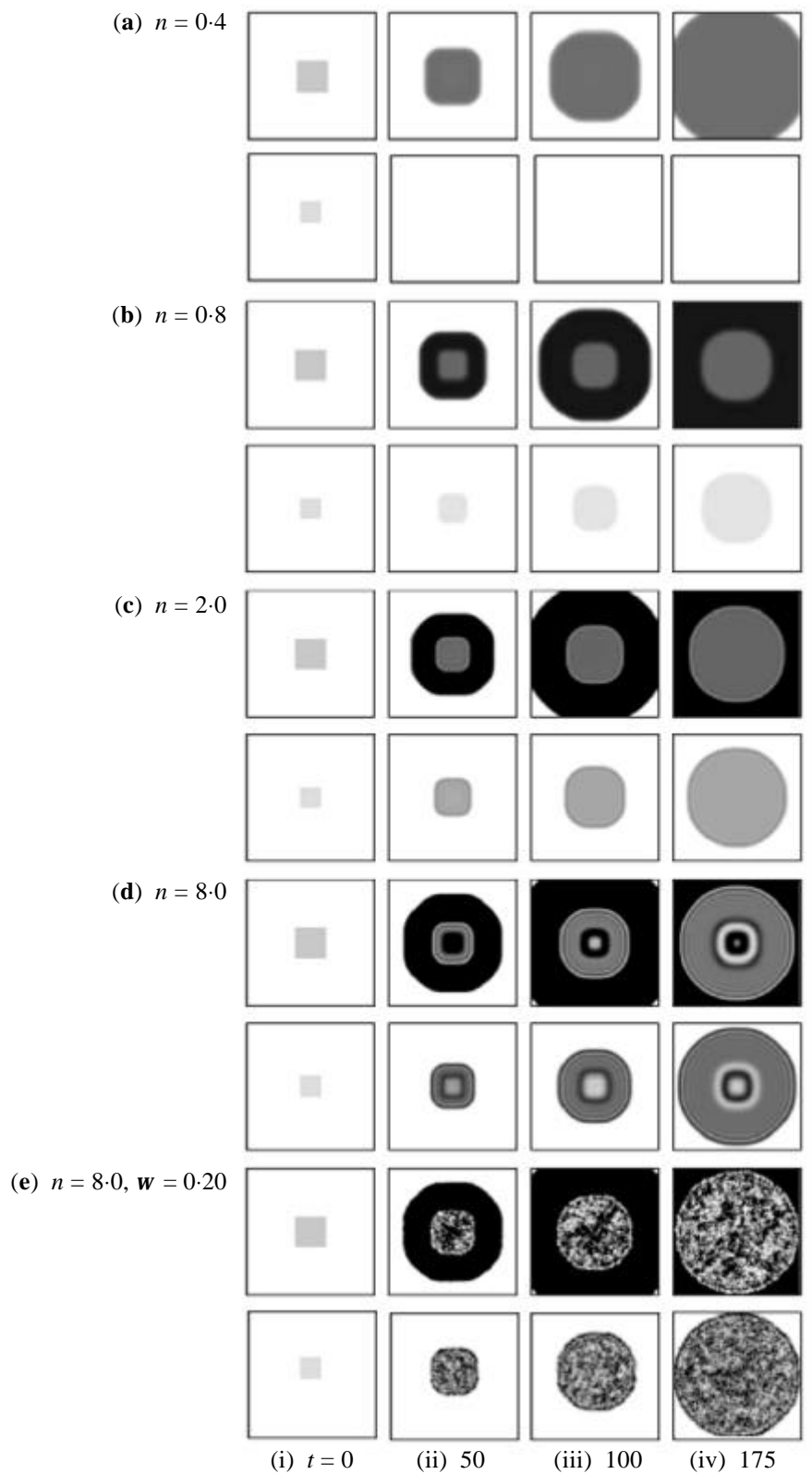(i) $t = 0$ (ii) 50   (iii) 100   (iv) 175

Figure 4. Spatial dynamics with different nutrient concentrations for phytoplankton (first row) and zooplankton (second row), respectively, with equal initial conditions (left column) and $g = 0$. Noise induced spatial patterns can also been observed.

(a) $n = 8.0, g = 0.05$

(b) $n = 8.0, g = 0.1$

(c) $n = 8.0, g = 0.3$

(d) $n = 8.0, g = 0.5$

(e) $n = 8.0, g = 0.5, \boldsymbol{w} = 0.25$

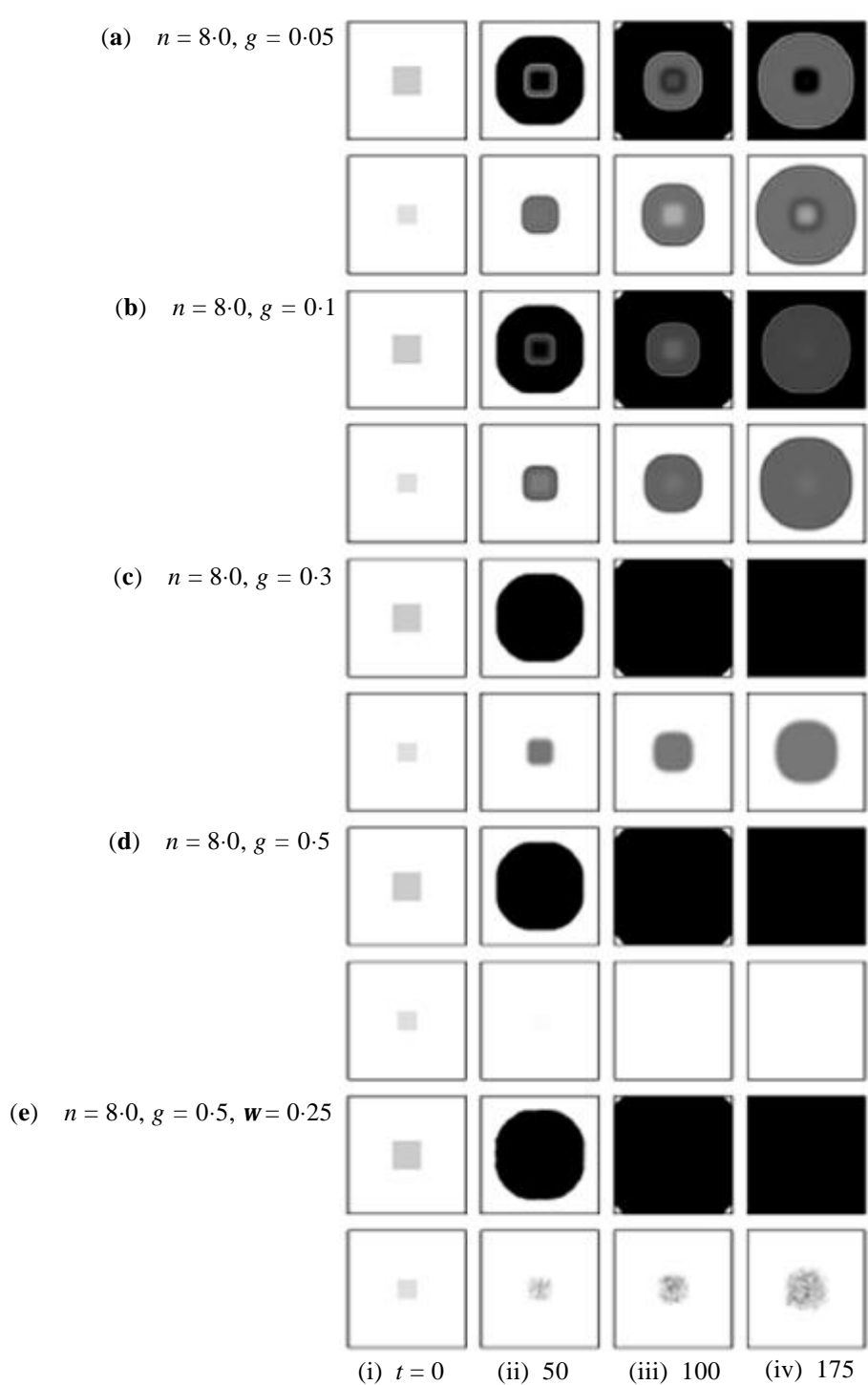(i) $t = 0$ (ii) 50   (iii) 100   (iv) 175

Figure 5. Spatial dynamics with Holling type II functional response for zooplankton mortality due to TPP, phytoplankton (first row) and zooplankton (second row), respectively, with equal initial conditions (left column). Phenomenon of dynamic stabilization of a locally unstable equilibrium (first and second row). Extinction of zooplankton with higher rate of toxin production (fourth row). With $\boldsymbol{w} = 0.25$ noise intensity noise-enhanced survival and spread of zooplankton (sixth row).

eutrophication or external fluctuations) on the spatio-temporal patterns of phytoplankton-zooplankton population have been well discussed by Badylak and Phlips (2004) in Indian River Lagoon, Florida, USA. They observed that changes in environmental variability, nutrient concentrations play an important role in the spread and survival of planktons. Some studies indicate that plankton community structure is frequently not a consequence of a single controlling factor, but a combination of factors that change over time (Smayda 1980; Karentz and Smayda 1984; Bledsoe and Phlips 2000). The outcome from our model analysis that external noise enhances survival, spread of the zooplankton population as well as high abundance or bloom of phytoplankton population supports the above experimental findings.

5. Conclusions

Building basic models based on a knowledge of ecological process allows us to explore the underlying mechanisms at work in a system. Finding out the reasons for occurrence of planktonic blooms is necessary but knowledge of the mechanisms for controlling the blooms are much more important and research into this direction needs urgent priority. The effect of environmental variability on the extinction and/or survival of the plankton populations is another field of study in conservation biology that can not be ignored. Understanding the effects of nutrients, environmental fluctuations and role of TPP on the plankton system is very much challenging as well as important area of research.

In this paper, we have investigated a simple phytoplankton-zooplankton model for temporal, spatial and spatio-temporal dissipative pattern formation in a deterministic and noisy environment, respectively. We have observed the role of nutrient concentrations and toxin producing phytoplankton for controlling the algal blooms. For the sake of simplicity, we have followed the classical tradition of minimal modelling and considered nutrient (manipulated variable) as an external control parameter. This approach of minimal modelling is very effective and well established to describe the dynamics of plankton system. We have observed that for different ranges of nutrient concentrations, the system becomes locally stable as well as oscillates around the equilibria related to planktonic blooming. Moreover, changes in the nutrient concentration lead to non-oscillatory stable situation and control of blooms through low nutrient concentration is clear. The present study also reveals the fact that the rate of TPP plays an important role for controlling oscillations in plankton system. The phenomenon of dynamic stabilization of a locally unstable equilibrium can also be observed for certain rate of toxin production. Different mortality functions of zooplankton due to TPP, control

oscillations, coexistence, survival or extinction of zooplankton. Previous studies (Chattopadhyay *et al* 2002a,b) in this direction do not consider the effect of nutrients leading to oscillatory dynamics (or plankton blooming) and simultaneous control by TPP towards dynamically stabilized situation around the steady states in spatio-temporal aspect. We have tried to explain this phenomenon in a more realistic way by considering the spatio-temporal patterns of the phytoplankton-zooplankton system in a noisy environment.

As an alternative to our deterministic model, we have observed the variety of internal and external influences, which change over time. This has been studied by adding a density dependent spatio-temporal Gaussian white noise which is a very natural consideration to observe those environmental factors (e.g. pH, salinity, temperature etc.) coupled together in a single process and have small individual effects on the others. In our paper, we have observed that fluctuating environment enhances the survival and the spatial spread of plankton populations. This phenomenon is in good agreement with the field observations conducted by several researchers (see, subsections 3·1 and 4·1 for details). Moreover, our study helps to address the important question in conservation biology that environmental variability indeed plays a significant role for survival of plankton populations. However, noise has not only supported the spatio-temporal coexistence of phytoplankton and zooplankton but it has been necessary to blur distinct artificial population structures, which is more realistic in ecological point of view. External noise has induced localized outbreaks or bloom phenomenon in the parameter range of stability. Our theoretical studies revealed the ranges of noise intensity that may be helpful to explain, when and how the plankton population can survive under high rate of toxin production by TPP.

Finally, we may conclude that our simple modelling approach, simulation results and outcomes of the theoretical studies support different field observations and this could shed some light on the role of TPP as well as nutrient concentration in a phytoplankton-zooplankton system along with their spatio-temporal dynamics in a natural noisy environment.

References

Allen L 2003 *An introduction to stochastic processes with applications to biology* (Upper Saddle River, NJ: Pearson Education)

Anishenko V, Astakov V, Neiman A, Vadivasova T and Schimansky-Geier L 2003 *Nonlinear dynamics of chaotic and stochastic systems. Tutorial and modern developments* (Springer Series in Synergetics, Berlin: Springer)

Badylak S and Phlips E 2004 Spatial and temporal patterns of phytoplankton composition in a subtropical coastal lagoon, the Indian river lagoon, Florida, USA; *J. Plankton Res.* **26** 1229–1247

Blaxter J and Southward A 1997 *Advances in marine biology* (London: Academic Press)

Bledsoe E and Phlips E 2000 Relationships between phytoplankton standing crop and physical, chemical and biological gradients in the Suwanne river and Plume region, USA; *Estuaries* **23** 458–473

Burkholder J and Glasgow H Jr 1995 Interactions of a toxic estuarine dinoflagellate with microbial predators and prey; *Arch. Protistenkd* **145** 177–188

Chattopadhyay J, Sarkar R and Abdllaoui A E 2002a A delay differential equation model on harmful algal blooms in the presence of toxic substances; *IMA J. Math. Appl. Med. Biol.* **19** 137–161

Chattopadhyay J, Sarkar R and Mandal S 2002b Toxin-producing plankton may act as a biological control for planktonic blooms – field study and mathematical modelling; *J. Theor. Biol.* **215** 333–344

Foley P 1994 Predicting extinction times from environmental stochasticity and carrying capacity; *Conserv. Biol.* **8** 124–137

Fransz H, Miguel J and Gonzales S 1984 Mesozooplankton composition, biomass and vertical disribution and copepod production in the stratified central north sea; *Netherlands J. Sea Res.* **18** 82–96

Graneli E *et al* 1989 From anoxia to fish poisoning: The last ten years of phytoplankton blooms in swedish marine waters: in *Novel phytoplankton blooms* (eds) E Cosper *et al* (Springer) pp 407–427

Hallegraeff G 1993 A review of harmful algae blooms and the apparent global increase; *Phycologia* **32** 79–99

Heino M, Ripa J and Kaitala V 2000 Extinction risk under coloured environmental noise; *Ecography* **23** 177–184

Higham D 2001 An algorithmic introduction to numerical simulation of stochastic differential equations; *SIAM Rev.* **43** 525–546

Holligan P and Harbour D 1977 The vertical distribution and succession of phytoplankton in the western english channel in 1975 and 1976; *J. Mar. Biol. Assoc.* **57** 1075–1093

Holling C 1959 Some characteristics of simple types of predation and parasitism; *Can. Entomol.* **91** 385–398

Jørgensen S 1983 Modeling the ecological processes: in *Mathematical modeling of water quality: Streams, lakes and reservoirs* (ed.) G Orlob (New York: Wiley Interscience) pp 116–149

Karentz D and Smayda T 1984 Temperature and seasonal occurrence patters of 30 dominant phytoplankton species in narragansett bay over 22 year period (1959–1980); *Mar. Ecol. Prog. Ser.* **18** 277–293

Kloeden P and Platen E 1999 *Numerical solution of stochastic differential equations*, vol. 23 *Applications of mathematics* (Berlin: Springer)

Lawton J 1997 The science and non-science of conservation biology; *Oikos* **79** 3–5

Lin C and Segel L 1988 *Mathematics applied to deterministic problems in the natural sciences* (Philadelphilia: SIAM)

Lovejoy S, Currie W, Tessier Y, Claereboudt M, Bourget E, Roff J and Schertzer D 2001 Universal multifractals and ocean patchiness: phytoplankton, physical fields and coastal heterogeinity; *J. Plank. Res.* **23** 117–141

Mahoney J and Steimle F 1979 A mass mortality of marine animals associated with a bloom of *Ceratium tripos* in New York bright: in *Proceedings of the Second International Conference of the Toxic Dinoflagellate Blooms* (Elsevier) pp 225–230

Malchow H and Petrovskii S 2002 Dynamical stabilization of an unstable equilibrium in chemical and biological systems; *Math. Comput. Model.* **36** 307–319

Malchow H, Radtke B, Kallache M, Medvinsky A, Tikhonov D and Petrovskii S 2000 Spatio-temporal pattern formation in coupled models of plankton dynamics and fish school motion; *Nonlinear Analysis: Real World Applications* **1** 53–67

Pascual M 1993 Diffusion-induced chaos in a spatial predator-prey system; *Proc. R. Soc. London B* **251** 1–7

Petchey O, Gonzalez A and Wilson H 1997 Effects on population persistence: the interaction between environmental noise, colour, intraspecific competition and space; *Proc. R. Soc. London B* **264** 1841–1847

Petrovskii S and Malchow H 2000 Critical phenomena in plankton communities: KISS model revisited; *Nonlinear Analysis: Real World Applications* **1** 37–51

Rose K and Swartzman G 1988 Stepwise iterative calibration of a multi-species phytoplankton-zooplankton simulation model using laboratory data; *Ecol. Model.* **42** 1–32

Rosenzweig M 1971 Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time; *Science* **171** 385–387

Sarkar R and Chattopadhyay J 2003 Occurence of planktonic blooms under environmental fluctuations and its possible control mechanism – mathematical models and experimental observations; *J. Theor. Biol.* **224** 501–516

Scheffer M 1991 Fish and nutrients interplay determines algal biomass: a minimal model; *Oikos* **62** 271–282

Shimizu Y 1989 Toxicology and pharmacology of red tides: an overview: in *Proceedings of the First international Symposium on Red Tides* (Elsevier) pp 17–22

Smayda T 1980 Phytoplankton species succession: in *The physiological ecology of phytoplankton* (ed.) I Morris (Berkley, California: University of California Press) pp 493–570

Smayda T 1992 Global epidemic of noxious phytoplankton blooms and food chain consequences in large ecosystems: in *Food chains, models and management of large marine ecosystem* (eds.) K Sherman *et al* (Boulder, Co: Westview Press) pp 257–307

Thomas J 1995 *Numerical partial differential equations: Finite difference methods* vol. 22 *Texts in applied mathematics* (New York: Springer)

Truscott J and Brindley J 1994 Ocean plankton populations as excitable media; *Bull. Math. Biol.* **56** 981–998

Yasumoto T and Murata M 1993 Marine toxins; *Chem. Rev.* **93** 1897–1909