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Asymptotic and transient analysis of stochastic core ecosystem models *

Thomas C. Gard

Abstract

General results on ultimate boundedness and exit probability estimates for stochastic differential equations are applied to investigate asymptotic and transient properties of models of plankton-fish dynamics in uncertain environments

1 Introduction

Opposing general points of view on whether or not populations ultimately survive are succinctly expressed recently by Halley and Iwasa ([10]) and Jansen and Sigmund ([12]). Is extinction certain if random variability is taken into account? Or if parameters are restricted to realistic ranges and the mitigating effects of population communities are explicitly considered, will persistence occur possibly after some initial risk period? Answers to such questions for real systems are more than pedagogical niceties. They can, for example, lead to proposed strategies for maintaining large scale bio-physico-chemical systems such as the highly utilized natural systems constituting watershed ecosystems. Central to dynamical models for watershed ecosystems are what might be called core lake ecosystem models, such as plankton-fish models which describe the dynamics of a limiting nutrient P, and algae A, zooplankton Z, and small fish F populations

$$\begin{aligned} \frac{dP}{dt} &= \delta(P_I(t) - P) + g_P(t, P, A, Z, F) \\ \frac{dA}{dt} &= g_A(t, P, A, Z) - \delta A \\ \frac{dZ}{dt} &= g_Z(t, A, Z, F) - \delta Z \\ \frac{dF}{dt} &= g_F(t, Z, F) + F_I(t) \end{aligned} \tag{1}$$

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recently discussed in the literature.(See, for example Doveri et. al. [3] where specific functional forms for the interaction portions g_P, g_A, g_Z, and g_F of the net growth rates are given.) In (1) P_I denotes the nutrient input rate, and F_I the small fish recruitment rate from large fish. Simplified submodels of (1) have been discussed; the PA submodel is a resource-consumer model with similar dynamics to the simple chemostat model ([18]), the PAZ submodel has been discussed by Ruan ([16],[17]) and others, and the AZF model is a three-species food chain. The relative novelty of (1) is the explicit inclusion of small fish dynamics - the timing and size of large annual recruitment peaks simultaneously effecting and being determined by PAZ levels. Temperature and other seasonality time variations of parameters together with cyclic nonlinearities in the model can lead to chaotic regimes ([15]). All models of real biological systems account for uncertainty in parameters and structure in one way or another. There is always a variability ansatz, although in many cases such assumptions are implicit. An explicit approach on the other hand is to formulate models with well-defined stochastic features in order to account for random variability. The class of stochastic differential equation models for interacting populations is such a class which can take into account environmental randomness: the SDE model analogous to (1) has the general form

$$\begin{aligned} dP &= [\delta(P_I - P) + g_P]dt + \sigma_P\, dW_P \\ dA &= [g_A - \delta A]dt + \sigma_A\, dW_A \\ dZ &= [g_Z - \delta Z]dt + \sigma_Z\, dW_Z \\ dF &= [g_F + F_I]dt + \sigma_F\, dW_F\,, \end{aligned} \tag{2}$$

where W_P, W_A, W_Z, and W_F are standard Brownian motions and σ_P, σ_A, σ_Z, and σ_F denote the corresponding intensities of the noise fluctuations; the σ's may be functions of the state variables and time. A specific example of (2), motivated by a stochastic model of two competitors in a chemostat suggested by Stephanopoulos, Aris, and Fredrickson [19], is given by

$$\begin{aligned} dP &= [\delta_0(P_I - P) + g_P]dt + \delta_1(P_I - P)\, dW \\ dA &= [g_A - \delta_0 A]dt + \delta_1 A\, dW \\ dZ &= [g_Z - \delta_0 Z]dt + \delta_1 Z\, dW \\ dF &= [g_F + F_I]\, dt\,. \end{aligned} \tag{3}$$

System (3) arises when the dilution or washout rate δ is viewed as the sum of an average value δ_0 plus a random noise fluctuation with intensity δ_1 about the average:

$$\delta = \delta_0 + \delta_1 N\,. \tag{4}$$

In (4) N represents standard white noise - in a generalized sense

$$N = \frac{dW}{dt} \tag{5}$$

with W a standard Brownian motion. In the next section we give a result which obtains asymptotic estimates for the average values of the state variables in (2) which is analogous to uniform persistence for the corresponding deterministic model (1). Application to specific $PAZF$ models is incomplete at this time and the subject of ongoing work. Transient behavior of the model may be important whether or not the former result applies. The third section contains a result which gives estimates for first exit location probabilities from certain bounded sets in the feasible region which may indicate initial survival or extinction tendencies of populations. We show that this result can be applied to models of the form (3).

2 Persistence in the mean

Permanence (uniform persistence together with dissipativity) is the most basic general qualitative feature to verify for interacting population models ([11],[20]); it is the model analog of mutual survival and non-explosion of the populations represented in the model. Permanence means that there are positive constants K and L such that for any component population $X(t)$ with any positive initial value $X(0)$

$$K \leq \liminf_{t\to\infty} X(t) \leq \limsup_{t\to\infty} X(t) \leq L. \tag{6}$$

If

$$Y(t) = \ln X(t) \tag{7}$$

or some other transformation of the ray $(0,\infty)$ to the line $(-\infty,\infty)$, permanence of X is equivalent to dissipativity or ultimate boundedness of Y: there is a positive constant M such that for any initial value $Y(0)$

$$\limsup_{t\to\infty} |Y(t)| \leq M. \tag{8}$$

There are well-known theorems in differential equations which give ultimate boundedness if a Liapunov function exists. In this section we will apply an analogous theorem of Miyahara ([14]) for stochastic differential equations. It is convenient to change notation here: let

$$\begin{aligned} X &= (X_1, X_2, X_3, X_4) = (P, A, Z, F), & (9)\\ Y &= \ln(X) \leftrightarrow Y_i = \ln(X_i),\ i = 1,2,3,4. & (10) \end{aligned}$$

Applying Ito's formula to (2) yields a transformed system of the form

$$dY = H(t,Y)dt + \Gamma(t,Y)dW \tag{11}$$

where here $W = (W_P,\ W_A,\ W_Z,\ W_F), H$ is a 4-d vector function, and Γ is a 4×4 diagonal matrix function.

Theorem 1 (Miyahara [14]) *Suppose there exists a scalar function $V(t,y)$ which is $\mathcal{C}^1$ in t and $\mathcal{C}^2$ in y and a number $p \geq 1$ such that for some constants a_1 and a_2 and positive constants c_1 and c_2 and all y*

1. $V(t,y) \geq -a_1 + c_1\|y\|^p$

2. $\mathcal{L}V(t,y) \leq a_2 - c_2 V(t,y)$

where $\mathcal{L}V = V_t + H \cdot \nabla V + \frac{1}{2}\,\mathrm{trace}(\Gamma\Gamma^T V_{yy})$ *and* V_t *is the partial derivative of* V *with respect to* t*,* ∇V *is the* y*-gradient of* V *and* V_{yy} *denotes the matrix of second partial derivatives of* V *with repect to* y*. Then for, any solution* $Y(t)$ *of (11),*

$$\limsup_{t\to\infty} E\|Y(t)\|^p \leq \frac{a_1}{c_1} + \frac{a_2}{c_1 c_2} \tag{12}$$

where $E(\cdot)$ *denotes the expected value or mean.*

Equations (6) - (8) suggest that the conclusion (12) of Theorem 1 could be called persistence (or permanence) in the mean for X. Applying Theorem 1 requires a candidate for the Liapunov function V. It has been shown by the author ([8]) that functions of the form

$$V(y) = \exp\{U(y)\} \tag{13}$$

with

$$U(y) = \sum_{i=1}^{n} \alpha_i [e^{y_i} - y_i - 1] \tag{14}$$

for some positive constants α_i can be applied to predator-prey models. The function U in (14) is Volterra's Liapunov function transformed from the positive cone R^n_+ to all of R^n by (10). Utilizing the 1-norm

$$\|y\| = \sum_{i=1}^{n} |y_i|$$

we obtain

$$U(y) \geq -\beta + \alpha\|y\| \tag{15}$$

where

$$\beta = \sum_{i=1}^{n} \alpha_i \quad \text{and} \quad \alpha = \min\, \alpha_i.$$

From (15) and (13) it follows that

$$V(y) \geq exp\{-\beta + \alpha\|y\|\} \geq e^{-\beta}(1 + \alpha\|y\|).$$

Condition 1 of Theorem 1 is verified for $p = 1$ with

$$a_1 = 0 \quad \text{and} \quad c_1 = \alpha e^{-\beta}. \tag{16}$$

Obtaining Condition 2 is more difficult. Generally one expects

$$a_2 = a_2(\Gamma), c_2 = c_2(\Gamma) \tag{17}$$

if the function V has negative definite derivative $\dot{V}$ along trajectories of the corresponding deterministic system. The following example shows that Condition 2 can be obtained for a single population dynamics model with a Liapunov function of the form (13) even when Γ is not necessarily small. Consider the stochastic logistic model

$$dX = X(1-X)dt + \frac{1}{\sqrt{2}} X\,dW \tag{18}$$

which transforms to

$$dY = \Big(\frac{3}{4} - e^Y\Big)dt + \frac{1}{\sqrt{2}}dW \tag{19}$$

under $Y = \ln(X)$. The Liapunov function (13) here is

$$V(y) = \exp\{e^y - y - 1\}. \tag{20}$$

It is easy to see that

$$V(y) \geq |y|$$

and so we can actually do a little better than (16): we can take

$$a_1 = 0 \quad \text{and} \quad c_1 = 1. \tag{21}$$

To get Condition 2 we need to estimate

$$\begin{aligned} \mathcal{L}V(y) &= \Big(1 - \frac{1}{4} - e^y\Big)V'(y) + \frac{1}{2}\Big(\frac{1}{2}\Big)V''(y) \\ &= \Big(1 - \frac{1}{4} - e^y\Big)(e^y - 1)V(y) + \frac{1}{4}[(e^y-1)^2 + e^y]V(y). \end{aligned} \tag{22}$$

A brief calculation gives

$$\mathcal{L}V(y) = \frac{1}{4}[1 - 3(e^y - 1)^2]V(y) \leq \frac{1}{2} - \frac{1}{4}V(y), \tag{23}$$

i.e., we have Condition 2 satisfied with

$$a_2 = \frac{1}{2} \quad \text{and} \quad c_2 = \frac{1}{4}. \tag{24}$$

Using (21) and (24), the conclusion of the theorem yields

$$\limsup_{t\to\infty} E\|\ln(X(t))\| \leq \frac{1/2}{1/4} = 2. \tag{25}$$

Volterra's Liapunov function does not seem to work for resource-consumer models; the counterpart to inequality (23) does not hold. So there remain some problems in applying Miyahara's result to stochastic $PAZF$ models. We conclude this section by summarizing the conditions which would have to be met in order to get a specific result here. For clarity in stating the conditions, we will consider only the following simplified version of (2)

$$\begin{aligned} dP &= [\delta(P_I - P) + P f_P(P, A)]dt + (P_I - P)\mu_P(P)\, dW_P \\ dA &= [A f_A(P, A, Z) - \delta A]dt + A\mu_A(A)\, dW_A \\ dZ &= [Z f_Z(A, Z, F) - \delta Z]dt + Z\mu_Z(Z)\, dW_Z \\ dF &= [F f_F(Z, F) + F_I]dt + F\mu_F(F)\, dW_F\,. \end{aligned} \tag{26}$$

In particular, we are ignoring nutrient recycling and we are assuming that parameters are constants. Under the log transformation:

$$Y_1 = \ln(P/P_I), Y_2 = \ln(A), Y_3 = \ln(Z), Y_4 = \ln(F) \tag{27}$$

the system becomes

$$\begin{aligned} dY_1 &= [\delta(e^{-Y_1} - 1) - \frac{\mu_P^2}{2}(e^{-Y_1} - 1)^2 + f_P]dt + (e^{-Y_1} - 1)\mu_P\, dW_P \\ > dY_2 &= [f_A - \delta - \frac{\mu_A^2}{2}]dt + \mu_A\, dW_A \\ > dY_3 &= [f_Z - \delta - \frac{\mu_Z^2}{2}]dt + \mu_Z\, dW_Z \\ dY_4 &= [f_F + F_I e^{-Y_4} - \frac{\mu_F^2}{2}]dt + \mu_F\, dW_F\,, \end{aligned} \tag{28}$$

where in (28) $f_P = f_P(P_I e^{Y_1}, e^{Y_2})$, $\mu_P = \mu_P(P_I e^{Y_1}), \ldots$. If we choose a $\mathcal{C}^2$ function V which satisfies Condition 1 of Miyahara's Theorem: for some number $p \geq 1$ there is a constant a_1 and a positive constant c_1 such that

$$V(y) \geq -a_1 + c_1 \|y\|^p \tag{29}$$

we need to verify Condition 2. Condition 2 in Miyahara's Theorem is, for some positive constant c

$$\begin{aligned} \mathcal{L}V + cV &= \frac{\partial V}{\partial y_1}[\delta(e^{-y_1} - 1) + f_P] + \frac{\partial V}{\partial y_2}[f_A - \delta] \\ &\quad + \frac{\partial V}{\partial y_3}[f_Z - \delta] + \frac{\partial V}{\partial y_4}[f_F + F_I e^{-y_4}] \\ &\quad + \frac{1}{2}\Big\{\mu_P^2\Big(\frac{\partial^2 V}{\partial y_1^2} - \frac{\partial V}{\partial y_1}\Big)(e^{-y_1} - 1)^2 + \mu_A^2\Big(\frac{\partial^2 V}{\partial y_2^2} - \frac{\partial V}{\partial y_2}\Big) \\ &\quad + \mu_Z^2\Big(\frac{\partial^2 V}{\partial y_3^2} - \frac{\partial V}{\partial y_3}\Big) + \mu_F^2\Big(\frac{\partial^2 V}{\partial y_4^2} - \frac{\partial V}{\partial y_4}\Big)\Big\} + cV \end{aligned} \tag{30}$$

is bounded. The result then is

Theorem 2 *Suppose there exists a $\mathcal{C}^2$ function V defined on R^4 which satisfies (29) and (30). Then, for any solution $Y(t)$ of (28),*

$$\limsup_{t\to\infty} E\|Y(t)\|^p \leq \frac{a_1}{c_1} + \frac{b}{c_1 c} \tag{31}$$

where b is a bound for $\mathcal{L}V + cV$ i. e., for any solution $(P(t), A(t), Z(t), F(t))$ of (26) and any positive number ϵ,

$$E\|(\ln(P(t)/P_I), \ln(A(t)), \ln(Z(t)), \ln(F(t)))\|^p \leq \frac{a_1}{c_1} + \frac{b}{c_1 c} + \epsilon \tag{32}$$

for all sufficiently large t.

3 Exit probabilities

Even when some form of stability can be verified for a model, transient behavior may still be important to investigate. If trajectories enter a region of state space where one or more model components are small, features neglected in the model could lead to collapse before a predicted recovery can occur. For models which attempt to account for random effects, the situation is particularly critical. Estimating certain exit statistics is a natural first approach to deal with this problem ([6],[7],[9],[13]). Suppose

$$X = (X_1, X_2, \ldots, X_n) \tag{33}$$

represents the n components of a stochastic dynamical population model taking values in the usual positive cone

$$R_+^n = \{x = (x_1, x_2, \ldots, x_n) : x_i > 0, i = 1, 2, \ldots, n\} \tag{34}$$

in n-dimensional space, and $B \subseteq R_+^n$ is a bounded set. Then for any fixed $x \in B$, we can consider the realization

$$X = X(t, x), t \geq 0$$

of the model with $X(0, x) = x \in B$, and the corresponding first exit time of X,

$$\tau = \tau_x(B) = inf\{t : X(t, x) \notin B\} \tag{35}$$

from B. The first exit time τ or even its mean or expected value

$$u(x) = E(\tau_x) \tag{36}$$

gives an indication of persistence of X relative to the set B ([13]). For example, if $\tau_x = \infty$ for all $x \in B$, then B is positive invariant for X, and if also the boundary ∂B of B is contained in R_+^n, then the set B is a candidate for a practical persistence estimate for the model. If it could also be shown that each realization X which begins at an x outside B hits B in a finite time before hitting the boundary of R_+^n, verification of practical persistence would be complete. If the model for Xtakes the form of a stochastic differential equation

$$dX = G(X)dt + \Lambda(X)dW \tag{37}$$

as discussed in the previous section, then it is known that the expected exit time u solves the boundary value problem

$$\begin{aligned} \mathcal{L}u(x) &= -1, \quad x \in B \\ u(x) &= 0, \quad x \in \partial B\,, \end{aligned} \tag{38}$$

where, as in Theorem 1 above,

$$\mathcal{L}u = G \cdot \nabla u + \frac{1}{2}\,\mathrm{trace}(\Lambda\Lambda^T u_{xx})\,. \tag{39}$$

For example, for the simple scalar problem,

$$dX = \sqrt{\varepsilon}\; dW, X(0) = x \in B = (0,1) \tag{40}$$

with ϵ any positive number, the boundary value problem for $u(x) = E(\tau_x)$ is

$$-1 = \mathcal{L}U(x) = \frac{\varepsilon}{2}u''(x), u(0) = 0 = u(1). \tag{41}$$

The solution is easily calculated:

$$u(x) = \frac{1}{\epsilon}(x - x^2). \tag{42}$$

Note that τ_x is finite almost surely in this example. The unit interval B here is not an estimate for practical persistence; in fact persistence fails in this example. Although the above example is not a very interesting population model, it does exhibit what has become anticipated behavior of randomly perturbed deterministic models - loss of stability. In this situation the size of τ_x or $E(\tau_x)$ still can indicate relative persistence. One can also try to determine other exit statistics such as exit point location probabilities

$$v(x) = P\{X(\tau_x) \in \partial_\eta B\} \tag{43}$$

where $\partial_\eta B$ is some particular subset of the boundary of B. This can be both physically relevant and mathematically tractable if the set B and the boundary portion $\partial_\eta B$ are suitably chosen. Suppose V is a $\mathcal{C}^2$ function, and

$$B \subseteq \{x : \eta \leq V(x) \leq \gamma\} \tag{44}$$

and

$$\partial_\eta B = \partial B \cap \{x : V(x) = \eta\}. \tag{45}$$

We have the following result (See also [8].)

Theorem 3 *Let $p = v(x)$, and $q = u(x) = E(\tau_x)$. Suppose there is a constant $c \geq 0$ such that*

$$\mathcal{L}V(x) \geq c, \text{ for all } x \in B \tag{46}$$

where $\mathcal{L}$ is the operator given by (39). Then

$$p \leq [\gamma - V(x) - cq]/[\gamma - \eta]. \tag{47}$$

Remark 1. Note that, if, for example,

$$V(x) = \frac{\eta + \gamma}{2} \tag{48}$$

then (47) becomes

$$p \leq \frac{1}{2} - cq/[\gamma - \eta] \tag{49}$$

i. e., the term $-cq/[\gamma - \eta]$ gives an estimate of the net bias due to the drift $G(x)$ and diffusion $\Lambda(x)$ terms in (37).

Proof of Theorem 3. By Dynkin's formula ([4]) (or by Ito's formula and taking expected values - see [5], for example) applied to the process $V(X(t))$ on the random interval $[0, \tau]$ we have

$$EV(X(\tau)) - V(x) = E\int_0^\tau \mathcal{L}V(X(s))ds \tag{50}$$

and then (46) yields

$$E\int_0^\tau \mathcal{L}V(X(s))ds \geq cE(\tau). \tag{51}$$

From (50) and (51) then we have

$$EV(X(\tau)) \geq V(x) + cE(\tau). \tag{52}$$

On the other hand, taking into account (44) and (45) , we get

$$EV(X(\tau)) \leq p\eta + (1-p)\gamma. \tag{53}$$

Inequalities (52) and (53) give

$$p\eta + (1-p)\gamma \geq V(x) + cE(\tau). \tag{54}$$

or

$$p \leq [\gamma - V(x) - cq]/[\gamma - \eta]. \tag{55}$$

$\diamondsuit$

Returning to the example (40): $dX = \sqrt{\epsilon}\, dW, X(0) = x \in B = (0,1)$ for a simple application of Theorem 3, we take

$$\eta = 0, \gamma = 1, \text{ and } V(x) = x^r,$$

for any number r satisfying $1 < r < 2$. Then, we have

$$\mathcal{L}V(x) = \frac{\epsilon r(r-1)}{2}x^{r-2} \geq \frac{\epsilon r(r-1)}{2}, \tag{56}$$

for $x \in B$. Recalling (42), the conclusion (47) of the theorem is

$$p \leq [1 - x^r - \frac{\epsilon r(r-1)}{2}(\frac{1}{\epsilon}(x - x^2))] = [1 - x^r - \frac{r(r-1)}{2}(x - x^2)]. \tag{57}$$

Further in this case, $p = v(x)$ also can be found exactly, since it solves the BVP

$$0 = \mathcal{L}v(x) = \frac{\epsilon}{2}v''(x), v(0) = 1, v(1) = 0. \tag{58}$$

The solution of (58) is easily seen to be

$$p = v(x) = 1 - x \tag{59}$$

Thus the application of the theorem to this example results in the estimate of the linear function $1 - x$ by a concave function on the interval $(0, 1)$

$$1 - x \le 1 - x^r - \frac{r(r-1)}{2}(x - x^2). \tag{60}$$

We conclude this paper with an application of Theorem 3.1 to the $PAZF$ model

$$\begin{aligned} dP &= [\delta_0(P_I - P) + g_P]dt + \delta_1(P_I - P)\,dW \\ dA &= [g_A - \delta_0 A]dt + \delta_1 A\,dW \\ dZ &= [g_Z - \delta_0 Z]dt + \delta_1 Z\,dW \\ dF &= g_F dt \end{aligned} \tag{61}$$

mentioned in section 1 where we assume g_P, g_A, g_Z and g_F are time independent. Actually all we show here is that the crucial estimate (46) can be obtained. Complete application of this result would also necessitate obtaining at least an estimate of $E(\tau_x)$ which could be accomplished by numerically solving the appropriate BVP (38), mentioned in the last section for the particular set B chosen. We make use of the function

$$V(x) = x_1 \prod_{i=2}^{4} x_i^{r_i}\,, \tag{62}$$

where the r_i are constants. Functions V of the form (62) have been used to verify uniform persistence in deterministic models. (See [1],[2] and references for some examples.) For constants η and γ with $0 < \eta < \gamma$, let

$$B \subseteq \{\eta \le V(x) \le \gamma\}$$

be a bounded set. Then we have, if r_2 and $r_3 > 0$ and δ_1 sufficiently large,

$$\begin{aligned} \mathcal{L}V(x) = \{ &[\delta_0(P_I - x_1) + g_P + \frac{1}{2}(\delta_1(P_I - x_1))^2]/x_1 \\ &+ r_2[g_A - \delta_0 x_2 + \frac{1}{2}(\delta_1 x_2)^2] \\ &+ r_3[g_Z - \delta_0 x_3 + \frac{1}{2}(\delta_1 x_3)^2] \\ &+ r_4 g_F\} V(x) \ \ge \ c \end{aligned} \tag{63}$$

for some positive constant c and for all $x \in B$, since everything in (63) is bounded, and all of the terms involving δ_1 are positive. We remark finally that it should be noted that both c and q in (47) generally will depend on δ_1.

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Thomas C. Gard
Department of Mathematics
The University of Georgia
Athens, GA 30602, USA
e-mail: tgard@uga.edu