Is diffusion-induced chaos robust?

Vikas Rai* and Girija Jayaraman[†,#]

*Department of Applied Mathematics, Delhi College of Engineering, Delhi 110 042, India
†Centre for Atmospheric Sciences, Indian Institute of Technology, New Delhi 110 016, India

We examine the robustness of diffusion-induced chaos in spatial predator–prey systems with a view to ascertain likelihood of its occurrence in natural systems. Our study of two models with spatial gradient in the prey growth rate and random (diffusive) movements of both species suggests that the chaotic behaviour generated through this mechanism is robust and therefore may be observed in natural systems. Another useful result that has emerged out of our simulation studies is that migratory behaviour of predators suppresses chaos, but cannot eliminate it. We suggest that chaos should be looked for in places where these necessary ingredients, viz. spatial gradient, diffusive movement of species and oscillatory predator–prey dynamics, are present.

IN nonlinear dissipative dynamical systems, a peculiar type of behaviour is observed when a crucial parameter crosses a certain value. System trajectories, in this case, are not attracted to a sink; instead, they meander aimlessly on a bounded phase space. The system's evolution is such that two nearby points in the space diverge exponentially. If one takes it to be the error in specifying the initial conditions, then this exponential magnification means that the system loses predictability after a certain amount of time has elapsed. This dependence of a system's trajectory on initial conditions in deterministic dynamical systems is known as chaos. Chaotic systems do not possess reproducibility property and therefore, are not amenable to any scientific verification.

An ecological model displaying chaotic dynamics at an isolated point in a parameter space has no meaning. Unless this chaotic behaviour is robust, there does not exist a possibility that the same will be realized in an experiment or it can be captured in a natural setting. What is meant by robust chaos is that for every parameter value there exists a range of other parameter(s), wherein the chaotic behaviour is preserved. In addition to this, the attractor's basin should not have complicated boundary structure. Only smooth boundaries are allowed.

Chaos was first observed by May[1] in models of populations with non-overlapping generations. Later, in 1976, he established that simple mathematical models could display complicated dynamical behaviour including chaos. Since then, many investigators have attempted to study this mode of the system's dynamics in model terrestrial systems[2–6]. All these studies indicated that field ecologists can easily capture chaos out in the field. Studies by McCann and Yodzis[7] and by Ruxton[8] critically examined the findings of earlier investigators and made the following key observations: (1) productive environment is a prerequisite for a system to support a dynamical behaviour such as chaos, (2) any reduction in chaos caused by immigration or refuge can be compensated by a sufficient increase in the resource renewal rate and (3) highly enriched systems are the most prospective candidates for chaotic dynamics to exist[8].

Unfortunately, attempts to observe chaos in natural populations have largely been a failure. In the early part of the last decade, Sugihara et al.[9] reported that the variability in marine diatoms in Scripps Pier, San Diego, as recorded by Allen, can be partly described by deterministic chaos. Later on, Hanski et al.[10] discovered chaotic dynamics in rodent populations of Fennoscandia. In the light of the criticism of such approaches by Morris[11], and keeping in view the noisy character of population systems, this cannot be regarded as an unequivocal evidence of chaos in a natural population. Recently, Costantino et al.[12] established the occurrence of chaotic dynamics in an insect population, flour beetle tribolium in the laboratory. But, the conditions in which the chaotic attractor was observed are far from reality. Absence of a spatial dimension and biological interaction, and presence of cannibalism (which acts as a potent feedback mechanism) make it unrealistic. Therefore, it can be understood that no unambiguous evidence of chaos exists till date. The investigations by Upadhyay and Rai[13,14] and Upadhyay et al.[15] into reasons why chaos had been rarely observed in natural populations concluded that natural terrestrial systems are not suitable candidates for the exploration of chaotic dynamics. This is paradoxical, since ecological systems have all the necessary characteristics (nonlinearity, high-dimensions, etc.) to be able to support chaotic dynamics. Since almost all the other forms 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 evolving on chaotic attractors. It is with this motivation that the present study was undertaken.

We describe in the following, two model systems: (a) model 1 by Pascual[16], and (b) model 2 incorporating feeding by the specialist predator on the alternative prey.

Model 1: The model based on the paper by Pascual[16] takes into account the diffusion along a spatial gradient of both the species – predator and prey. It is analysed for temporal chaos at a fixed point in space. The model, in non-dimensional form, is given as follows:

$$\frac{\partial p}{\partial t} = r_x p(1-p) - \left[\frac{ap}{1+bp}\right]h + d\frac{\partial^2 p}{\partial x^2}, \qquad (1)$$

#For correspondence. (e-mail: jgirija@cas.iitd.ernet.in)

$$\frac{\partial h}{\partial t} = \left[\frac{ap}{1+bp}\right]h - mh + d\frac{\partial^2 h}{\partial x^2}, \tag{2}$$

where the non-dimensionalization is given by

$$p = P/K, \quad h = AH/K, \quad x = X/L, \quad t = \overline{R}T$$

$$r_x = R_x/\overline{R}, \quad m = M/\overline{R}.$$

$P(X, T)$, $H(X, T)$ are respectively, the prey and predator populations at any point X and time T; $\overline{R}$, K, M and $1/A$ denote the intrinsic growth rate of the predator and the yield coefficient of prey to predator respectively. L is the total length of the gradient, $\overline{R}$ is a characteristic value of the prey growth rate and d is the diffusion coefficient assumed to be same for both prey and predator. a, b are non-dimensional constants parameterizing the saturating functional response, environmental heterogeneity (R_x) is introduced by considering the non-dimensional prey rate of increase r_x as a linear function of x, say $e + fx$. Assuming zero flux at the boundaries, the boundary conditions are written as

$$\frac{\partial p}{\partial x} = \frac{\partial h}{\partial x} = 0 \quad \text{for all } t. \tag{3}$$

Model 2: In situations when it is hard to find the most preferred prey, specialist predators switch to other preys. In such a situation, model 1 needs to be modified to include switching behaviour of some individuals of predators by subtracting a constant term from the specialist predator's mortality term. This new model is based on the rationale that no predator is a specialist predator in the sense of eq. (2), according to which h will decline exponentially, when p is absent. Inclusion of a term to represent switching behaviour takes care of the fact that the prey feeds on alternative prey when its most favourite prey is scarce.

The resulting equations are given by:

$$\frac{\partial p}{\partial t} = r_x p(1-p) - \left[\frac{ap}{1+bp}\right]h + d\frac{\partial^2 p}{\partial x^2}, \tag{4}$$

$$\frac{\partial h}{\partial t} = \left[\frac{aph}{1+bp}\right] - m(h-h^*) + d\frac{\partial^2 h}{\partial x^2}, \tag{5}$$

where h^* is a constant. As before, eq. (3) provides the boundary conditions. Such a modification was first introduced by Blasius *et al.*[17]. Equations (1)–(5) were solved using Crank–Nicolson finite difference scheme. The resulting algebraic equations involve a tridiagonal matrix and hence the system could be solved easily using Thomas algorithm.

The models contain various parameters, which correspond to intrinsic attributes of the system. The two models are solved to test the robustness of the chaotic behaviour if it exists; and the discussions are carried out for the two-dimensional parameter spaces, e.g. b and d, f and d.

The motivation behind the analysis is the fact that any single change in the physical conditions of the system brings corresponding changes in, at least, two system parameters.

It is well known that minimum number of degrees of freedom required for chaos is three. This is the reason why two-species systems do not display chaotic solutions. Pascual[16] examined the possibility if the spatial gradient, affecting the growth rate of the prey species, can provide the coupling mechanism for the oscillatory predator–prey dynamics. Two coupled non-chaotic oscillators are known to admit chaotic dynamics. He found that the diffusive movements of the species create a system of coupled oscillators that mutually force each other at incommensurate frequencies. This results in chaos. The period of cycles of these oscillators is determined by the parameter r_x, which is given by

$$r_x = 2 - 1.4\,x,$$

and thus varies along the spatial gradient.

The parameter values for model 1 were taken from Pascual[16]. Apart from confirming all the results of Pascual, our analysis extends them to a discussion corresponding to two-dimensional parameter spaces. Model 2 introduces switching behaviour explicitly through the parameter h^* whose value is fixed at 0.1.

A scalar time series was generated by solving the equations numerically with a given set of parametric values. The dynamics was analysed with the help of Chaos Data Analyser, a software tool from AIP. In order to diagnose a model generated time-series data as chaotic, various tasks were performed. No single test (e.g. phase space reconstruction or Lyapunov exponent calculation) gave an unambiguous result. Therefore, outcomes from various tasks were combined to arrive at a conclusion. Keeping all other parameters fixed, calculations were mostly done for variations of the two parameters b and d. The chosen set of parameter values is the one which yields stable limit cycle solutions in the absence of diffusion. The two critical parameters b and d were varied in their biologically plausible range. Figure 1 a and b shows two time series plots for $x = 0$ and for $x = 0.85$. Figure 1 a shows the time series corresponding to regular cycles. Figure 1 b displays a chaotic time history at the high end of the spatial gradient.

As noted earlier, model 2 is a modified version of model 1. Hence comparing the two models should bring out the effects of switching on population dynamics. Table 1 is based on several runs carried out by varying the two parameters b and d in the range $2 < b < 12$; $10^{-8} < d < 10^{-3}$. For all values in this range other than those presented in Table 1, chaos found in model 1 was found suppressed in model 2. It is surprising that switching has the ability to contain chaos.

An investigation of the question of robustness is not complete unless one ensures that a given dynamical
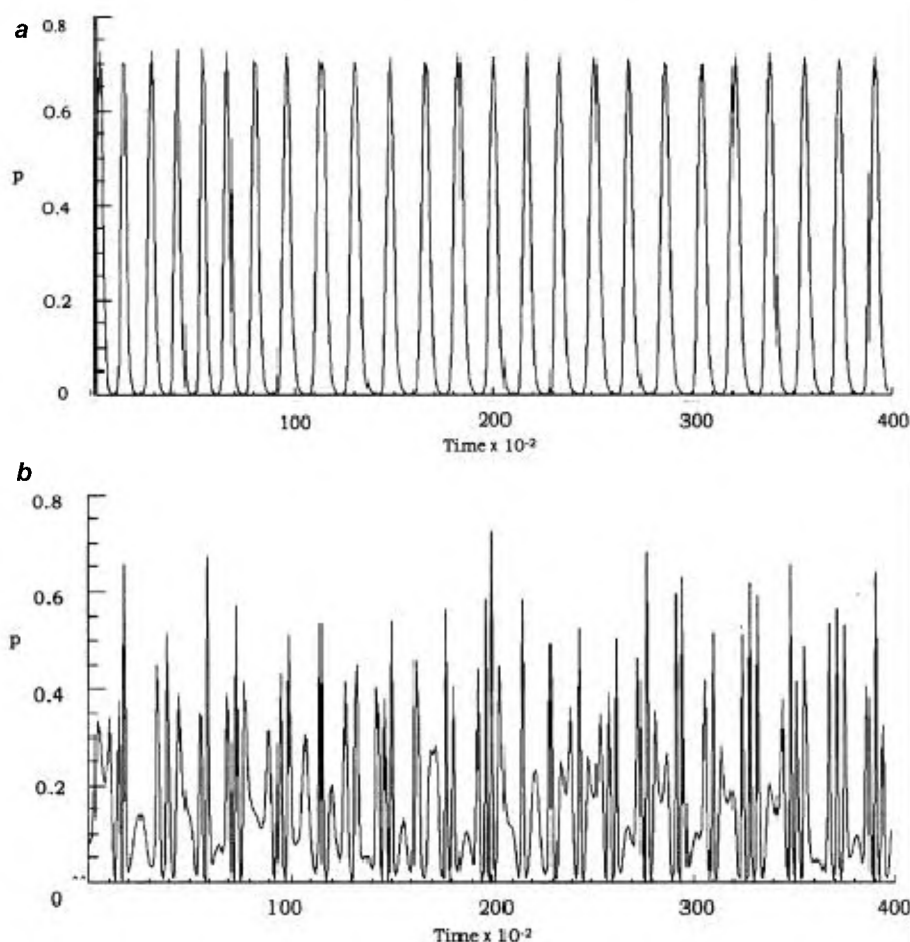
Figure 1. Time-series plots for model 1 at *a*, $x = 0$ and, *b*, $x = 0.85$. Parameter values used to generate these time histories are: $a = 5$, $b = 2$, $e = 2$, $f = -1.4$, $m = 0.5$.

Table 1. Comparison of models 1 and 2 for appearance of chaos

b	d	Remarks on chaos
5	10^{-4}	Chaos preserved in models 1 and 2
6	10^{-4}	Chaos absent in model 1, present in model 2
6	10^{-5}	Chaos absent in model 1, present in model 2
7	10^{-4}	Chaos absent in model 1, present in model 2
7	10^{-5}	Chaos absent in model 1, present in model 2

behaviour is observed for almost all the sets of initial conditions forming a sufficiently large area in the initial condition space. Chaos was observed at $b = 2$, 4 and 5 for all the sets of initial conditions sampled from their range $0 \le p$, $h \le 1$. The parametric values $b = 2$ and $b = 5$ are the edges of the parameter region. No other competing behaviour was found.

In this study, we have analysed two different model aquatic ecosystems. Each one of them has a distinct characteristic: model 1 corresponds to a specialist predator, model 2 modifies model 1 by allowing feeding on the alternative prey available to the specialist predator, as and when the population density of its most favourite prey

declines to a critical value. For example, in an aquatic environment, the zooplanktons, which prey on the phytoplankton, can switch to alternative preys like their own fellow populations, when the algae is in short-supply.

Our simulation experiments and subsequent analyses reveal that chaotic behaviour displayed by model 1 is robust. Model 2 is found to be largely non-chaotic, but it also supports chaotic dynamics in a narrow strip of the b–d parametric space. In any case, existence of robust chaos has been found in a model ecosystem. Previous studies have not focused their attention on the requirement that any dynamical behaviour should exist in a considerably large area of the two-parameter space in order to correspond to any realistic situation.

From Figures 2 and 3 it is evident that low-to-moderate values of the parameter $b = k/c_2$, where k is the carrying capacity for the prey and c_2 parametrizes the saturating functional *response of the predator* favours existence of chaotic dynamics when the diffusion coefficient is relatively high. Our analysis also shows that chaos exists in a range of the parameter f, for these values of diffusion coefficients (Figure 3). This is what we mean by robust
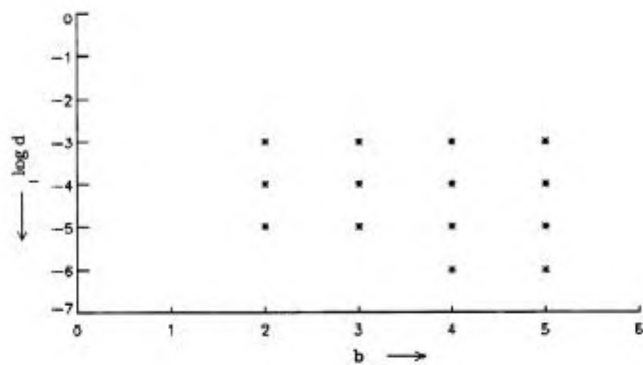
Figure 2. Points in the b–d parameter space where chaos was observed in model 1. The rest of the parameters are: $a = 5$, $e = 2$, $f = -1.4$, $m = 0.5$.
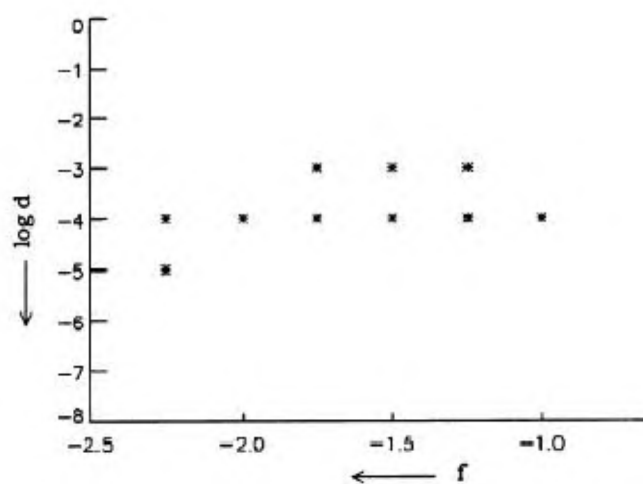

Figure 3. Points in the f–d parameter space where chaos was observed for model 1. The other parameters were fixed at: $a = 5$, $b = 5$, $e = 2$, $m = 0.5$.

Figure 4. Points in p–h initial condition space where chaos was observed in model 1. The parameters were taken to be: $a = 5$, $b = 2$, $e = 2$, $f = -1.4$, $m = 0.5$, $d = 10^{-4}$.

chaos. If field studies are performed in real systems, one is most likely to be able to observe chaos. Figure 4 gives sets of initial conditions that were used to run the model 1 at $b = 2$.

The requirement that an ecosystem should be highly productive in order to be able to support chaotic dynamics[8] is relaxed in the case of systems where diffusion is active. We have observed existence of robust chaos in model 1 for relatively low value of the intristic growth parameter r. Our analysis of model 2 suggests that ability of specialist predators to adjust to their environmental conditions (food availability and capacity of the environment to sustain a specific rate of growth) does not favour chaotic evolution. Instead, it suppresses many of the unstable periodic orbits embedded in a chaotic attractor and, thus, converts it into a stable limit cycle. To be precise, we find that prey-switching in specialist predators does not allow populations to cycle, but in most of the cases, forces the system to rest on a stable focus.

The formulation of the predator's feeding on alternative prey used in model 2 essentially amounts to the pre-
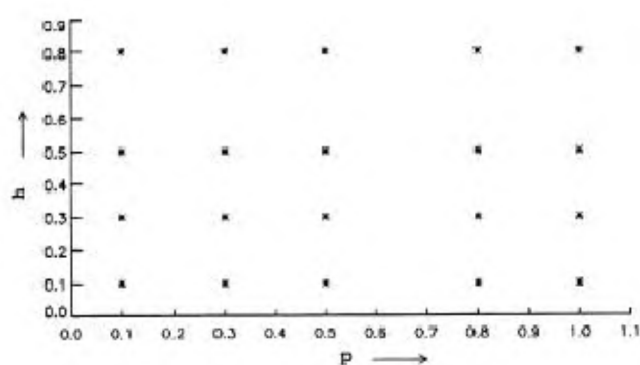
dator's migration from one patch to the other. The patchy nature of the environment is generated by the interaction of diffusion and migration; diffusion representing random movements of both predator and prey. Thus, model 2 describes population dynamics in the wake of patchings generated by diffusive instability. This diffusive instability is driven by migration of predators from one patch to another. Although model 2 displays chaotic behaviour in a thin strip of b–d parameter space, it can be observed in nature, as the basin of attraction for these chaotic attractors is large enough.

Sherratt et al.[18] have proposed a different mechanism for the generation of chaos; invasion waves of predators may have chaotic solutions in their wake in oscillatory predator–prey systems driven unstable by diffusive movements of both species. This mechanism does not require a spatial gradient to couple to diffusion to create chaos. The robustness of this mechanism is yet to be examined. Nevertheless, their study makes an important contribution by providing insight that the destabilization of predator–prey dynamics by diffusion is not an artifact of reaction–diffusion models; instead, it is a general property of oscillatory predator–prey interactions. In our opinion, this mechanism is more likely to be operational in terrestrial ecosystems. This can be verified by designing and conducting field studies.

In conclusion, we note that aquatic systems may be suitable places to look for chaos. There is every reason to believe that carefully designed, long-term field studies will enable ecologists to capture chaos in the wild. If it so happens, then the Eulerian sampling techniques which are currently in vogue in marine ecology, will prove unsuitable and inadequate[19]. More data based on satellite images will be required to obtain spatial averaging of large marine populations.

1. May, R. M., *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ, 1974.
2. Schaffer, W. M. and Kot, M., *BioScience*, 1985, **35**, 342–350.
3. Schaffer, W. M. and Kot, M., *Trends Ecol. Evol.*, 1986, **1**, 58–63.

4. Hastings, A. and Powell, T., *Ecology*, 1991, **72**, 896–903.
5. Rai, V. and Sreenivasan, R., *Ecol. Model.*, 1993, **69**, 63–77.
6. Hastings, A., Hom, C. L., Ellner, S., Turchin, P. and Godfray, H. C. J., *Annu. Rev. Ecol. Syst.*, 1993, **21**, 1–33.
7. McCann, K. and Yodzis, P., *Ecology*, 1994, **75**, 561–564.
8. Ruxton, G. D., *Ecology*, 1996, **77**, 317–319.
9. Sugihara, G., Grenfell, B. and May, R. M., *Philos. Trans. R. Soc. London Ser. B*, 1990, **330**, 235–251.
10. Hanski, I., Turchin, P., Korpimaki, E. and Henttonen, H., *Nature*, 1993, **364**, 232–235.
11. Morris, W. F., *Ecology*, 1990, **71**, 1849–1862.
12. Costantino, R. F., Desharnais, R. A., Cushing, J. M. and Denis, B., *Science*, 1997, **275**, 389–391.
13. Upadhyay, R. K. and Rai, V., *Chaos Solitons Fractals*, 1997, **8**, 1933–1939.
14. Upadhyay, R. K. and Rai, V., *Chaos Solitons Fractals*, 2001, **12**, 205–218.
15. Upadhyay, R. K., Iyengar, S. R. K. and Rai, V., *Int. J. Bifur. Chaos*, 1998, **8**, 1325–1333.
16. Pascual, M., *Proc. R. Soc. London Ser. B*, 1993, **251**, 1–7.
17. Blasius, B., Huppert, A. and Stone Lewi, *Nature*, 1999, **399**, 354–359.
18. Sherratt, J. A., Lewis, M. A. and Fowler, A. C., *Proc. Natl. Acad. Sci. USA*, 1995, **92**, 2524–2528.
19. Little, S. *et al.*, *Physica D*, 1996, **96**, 321–333.

Erosion activity on Majuli – the largest river island of the world

P. Kotoky[†,*], D. Bezbaruah[†], J. Baruah[†] and J. N. Sarma[#]

[†]Regional Research Laboratory (CSIR), Jorhat 785 006, India
[#]Dibrugarh University, Dibrugarh 786 004, India

Majuli, a river island within the two arms of the mighty Brahmaputra river, is a site having extreme historical and cultural importance, and warrants immediate exposure to the scientific community. The island faces an acute erosion problem as no permanent anti-erosion measures based on proper geo-hydrological models have been adopted so far. The land area of the island, as evidenced from the IRS satellite imagery of 1998, is 577.65 km² compared to 1245 km² according to available historical records. The available data indicate an erosion rate of 1.9 km²/yr for the period of 1920–98. If the situation remains unattended, the island will soon be engulfed by the Brahmaputra river and will become extinct from the world map.

MAJULI, the largest river island of the world[1,2] (26°45′N to 27°15′N lat.; 93°45′E to 94°30′E long.), is covered by the Survey of India toposheet nos. 83 F/5, F/6, F/9, F/13, I/4, I/8 and J/1 (Figure 1). Majuli Island has a population[3] of 134,395 and an area of 900 km². It is now one of the subdivisions of Jorhat District, Assam, India, with Kamalabari as its subdivision headquarter. It includes 155 villages under three revenue circles (Salmora, Kamalabari and Ahatguri). The famous cultural centres – Auniati, Kamalabari, Garamur and Dakhinpat – have made significant contributions to the Vaisnavite Movement of Assam[4,5].

Geomorphologically, the Majuli Island forms a part of the flood plains of the Brahmaputra river. The Majuli Island suffers from severe bank erosion on its southern side due to the erosive action of Brahmaputra river, and on its northern side due to the Subansiri river. The river island is subjected to severe annual floods under the influence of the SW monsoon. The erosion is mainly attributed to extreme sediment charge[6–9] and to the main river traversing through a series of deep and narrow throats, and formation of sand bar in the midst of the river. Along the channel of the Brahmaputra river, bank material is rarely homogeneous in composition and uneven bank-slumping is a characteristic feature. Often, highly saturated clayey silts liquefy and tend to flow towards the channel. Consequently, the overlying less saturated bank material tends to slump along well-defined shear planes. Thus, there appear two prominent types of slumping: (a) undercutting during flood stage and (b) flowage of highly saturated sediments during the
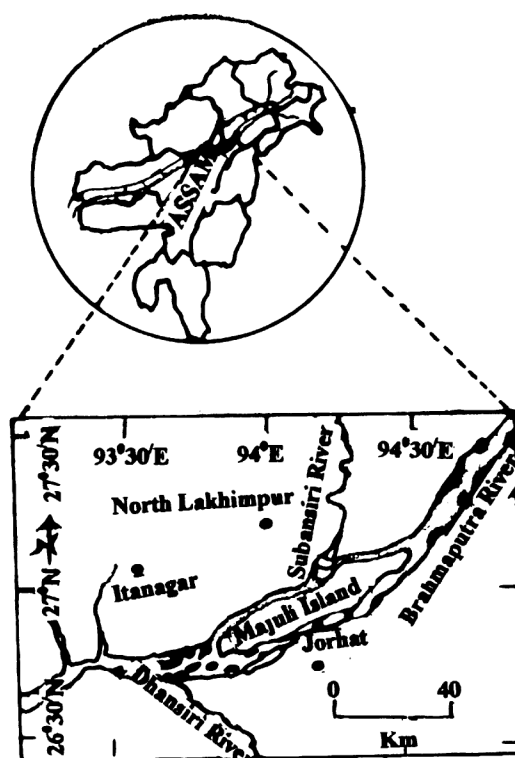

Figure 1. Location map of Majuli Island.

*For correspondence. (e-mail: probhatk@yahoo.com)