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M. CANTARELLI and G. DI COLA (*)

Identification of a stochastic model of the rhythmic activity of an estuarine population (**)

1 - Introduction

Many animal populations living in estuarine environments show a periodical activity [5]; this rhythmic behaviour is often a strategical adaptation of the animals to cyclic changes of environmental factors promptly and with high efficiency.

Therefore it could be of some interest to understand the processes giving rise to these behaviours. In particular it is interesting to know how some critical environmental factors can control the rhythmic behaviour of these organisms and modify their role in the estuarine environment.

In this paper we consider the exploratory activity of *Cyclope neritea*, a gastropod prosobranch playing the important role of scavenger in the trophic web of Po Delta brackish lagoons.

C. neritea generally stays under the sand and moves to water in search of food, prevalently during night (fig. 1).

It has a strong tendency to aggregation: in fact its spatial distribution is patchy with tendency to aggregation especially on food sources.

It shows this behaviour mainly at sunrise and at sunset when most of population get out or move into the sand. Consequently in these periods the processes of interface (sediment-water) crossing are dependent on the number

(*) Indirizzo: Istituto di Matematica, Università, Via Università 12, 43100 Parma, Italy.

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of individuals in emersion, while during the whole of the day and more evidently during the night the probability of interface crossing is independent on the number of the individuals in emersion (random walk) [**2**].

Exploratory activity is very important because it is strictly related to the trophic role and it is highly affected by environmental factors [**6**].

We represent the processes of interface crossing by means of a stochastic process; particularly we choose a generalized logistic model based on the analogy of birth and death processes with migration.

2 - Mathematical formulation

In this model we represent the number of individuals in emersion at a fixed time by means of a Markovian process in continuous time and discrete space, i.e. the state of the system at time t depends only on the state at time $t - \Delta t$.

The transition probabilities are of two kinds:

(a) one density dependent, defined as follows

$$(a_1 - b_1 n)\, n\, \Delta t + o(\Delta t)\,, \qquad (a_2 + b_2 n)\, n\, \Delta t + o(\Delta t);$$

(b) another density independent

$$k\, \Delta t + o(\Delta t).$$

In particular we refer to the phase of emersion of individuals from the sand.

Let $x(t)$ be the number of individuals in emersion at time t, n_0 the number of individuals in emersion at time $t = t_0$ and $n_{\max}$ the greatest number of observable individuals.

We consider $\{x(t): t \geqslant t_0\}$ as a Markov process with state space $S = \{n: 0 \leqslant n \leqslant n_{\max}\}$, where n is a nonnegative integer.

We can formulate the model assumed in terms of infinitesimal transition probabilities as follows:

$$(1)_1 \qquad p(n \to n+1) = \lambda_n \Delta t + o(\Delta t) = (a_1 n - b_1 n^2 + k)\, \Delta t + o(\Delta t)\,,$$

$$(1)_2 \qquad p(n \to n-1) = \mu_n \Delta t + o(\Delta t) = (a_2 n + b_2 n^2 + k)\, \Delta t + o(\Delta t)\,,$$

$$(1)_3 \qquad p(n \to n) = 1 - (\lambda_n + \mu_n)\, \Delta t\,.$$

We attempt the solution in probability of model (1) through the formulation and solution of the differential form of the Chapman-Kolmogorov equations [4] that, for the process we consider, can be written as follow

$$(2)_1 \qquad \frac{dP_{n,n_0}(t)}{dt} = [a_1(n-1) - b_1(n-1)^2 + k]P_{n-1,n_0}(t)$$

$$-[(a_1+a_2)n - (b_1 - b_2)n^2 + 2k]P_{n,n_0}(t) + [a_2(n+1) + b_2(n+1)^2 + k]P_{n+1,n_0}(t)\,,$$

$$(2)_2 \qquad \frac{dP_{0,n_0}(t)}{dt} = 2kP_{0,n_0}(t) + (a_2 + b_2 + k)P_{1,n_0}(t)\,,$$

with the initial condition

$$P_{n,n_0}(0) = \delta_{n,n_0}$$

and the boundary conditions of $n = 0$ and $n = n_{max}$ as reflecting states.

In this model the number of individuals in emersion is represented by the first moment $\langle n\rangle$ defined as $\langle n\rangle = \sum_{\text{allowed states}} nP_{n,n_0}(t)$ and satisfying the following equation

$$(3) \qquad \frac{dn}{dt} = \langle\lambda_n\rangle - \langle\mu_n\rangle = (a_1 - a_2)\langle n\rangle - (b_1 + b_2)\langle n^2\rangle\,.$$

This equation is equivalent to the logistic deterministic model when $\langle n^2\rangle = \langle n\rangle^2$ is assumed.

It must be noticed how the deterministic formulation can be misleading not showing the stochastic fluctuations.

3 - Parameter estimation

Once a realization of the process (the experimental observations $x_0, x_1, \dots, x_n$ taken at discrete timepoints $t_0, t_1, \dots, t_n$) is avaible we are interested in the problem of estimating the parameters of the model.

This problem of parameter estimation is approached in the present study by the maximum likelihood method consisting on the maximization of the likelihood functional taking into account the probability differential model.

If the set $\{x(t): t \geqslant t_0\}$ is observed at $(N+1)$ distinct and equidistant time points then the likelihood functional can be written as follows

$$L = P\{x(t_0) = n_0,\, u\} \prod_{j=0}^{N} P\{x(t_j) = n_j \,|\, x(t_{j-1}) = n_{j-1},\, u\}\,, \tag{4}$$

where $P\{x(t_j) = n_j \,|\, x(t_{j-1}) = n_{j-1}\}$ is the conditional probability that the experimental value $x(t_j)$ observed at the j-th time falls in state n_j when the experimental value $x(t_{j-1})$ observed at the $(j-1)$-th time falled in state n_{j-1} and u is the parameter vector.

Generally the problem of finding the maximum of the likelihood functional is transformed into a minimization problem introducing the support functional

$$g = -\log L\,. \tag{4$'$}$$

The support functional is subject to the following differential constraints

$$\frac{\mathrm{d}P_i(t)}{\mathrm{d}t} = f_i(P(t),\, u)\,, \tag{5}$$

with the initial and interface conditions

$$P_i(t_j^+) = \delta_{in_j} \qquad (j = 0, 1, \ldots, N)\,, \tag{5$'$}$$

so that the probability distribution functions $P_i(t)$ are generally continuous functions with discontinuities of first kind at the points $t = t_j$, $j = 0, 1, \ldots, N$. $P(t)$ is a vector with dimension $n_{\max}$ given by the number of possible states and u is the parameter vector with dimension m.

The solution of this problem may not be unique, therefore we have added to the functional g a stabilizing term $\Omega(u)$ which takes into account of some apriori informations on the solution, for instance given by equations (7), then we have considered the extended functional

$$g^* = g + \alpha\Omega(u)\,. \tag{4$''$}$$

In our case f_i has the following form

$$f_i = \lambda_{i-1} P_{i-1}(t) - (\lambda_i - \mu_i)\, P_i(t) + \mu_{i+1} P_{i+1}(t)\,,$$

$$\lambda_i = (u_1 + u_2\, i - u_3\, i^2)\,, \qquad \mu_i = (u_1 + u_4\, i + u_5\, i^2)\,,$$

$$u_1 = k\,, \quad u_2 = a_1\,, \quad u_3 = b_1\,, \quad u_4 = a_2\,, \quad u_5 = b_2\,.$$

Our estimation problem will be that of minimizing the functional (4)″ under the differential constraints (5) and (5)′.

This minimization problem, through the calculus of variations [3], gives rise to the following system of equations

(A)
$$\dot{P} - f(P, u) = 0\,, \qquad \dot{\eta} = -\,\eta f_p\,,$$
$$\operatorname{grad} g^* = \eta f_u + \alpha \operatorname{grad} \Omega = 0\,,$$

where f_p is the matrix $(\partial f_i/\partial P_j)$ $(i, j = 1, ..., n_{\max})$, f_u is the matrix $(\partial f_i/\partial u_j)$ $(i = 1, ..., n_{\max},\ j = 1, ..., m)$, and η is a row vector with $n_{\max}$ components; the state variable P and the adjoint variable η are subject to the following interface and terminal conditions

(6)
$$P_i(t_j^+) = \delta_{in_j}\,, \qquad \eta_i(t_j^-) = \delta_{in_j}/P\big(x(t_j) = n_j\big)\,.$$

Such conditions express the fact that the state variable and the adjoint variable are piecewise continuous functions with discontinuities of first kind at the points $t = t_j$, $j = 0, 1, ..., N$.

Usually the problem (A) cannot be solved directly and an iterative procedure must be used.

In this case we have proceeded as follows.

(1) An initial evaluation for the model's parameters is obtained by a least square estimate of the following semi-stochastic model of logistic type

$$\frac{\mathrm{d}n}{\mathrm{d}t} = (1 - n/N_{\max})\, rn + \varepsilon(t)\,,$$

where $\varepsilon(t)$ is a random term which takes into account the environmental variability and

(7)
$$N_{\max} = (a_1 - a_2)/(b_1 + b_2)\,, \qquad r = (a_1 - a_2)\,.$$

(2) When a set of parameter values is achieved the o.d.e. system is solved; since an analytical solution is not possible a numerical solution via the Crank-Nicholson method is obtained.

At each iteration we assume the following initial conditions

$$P\{x(t_j) = n_j\} = \begin{cases} 1 & \text{for } j = n_j\,, \\ 0 & \text{for } j \neq n_j\,. \end{cases}$$

(3) The adjoint equations are solved in order to obtain the value of η. The system to be solved is

(8)
$$\dot{\eta} = -\,\eta A\,,$$

that is integrated in the reversed time ($\tau = -t$); so the system becomes $\dot{\eta} = \eta A$ and is solved as the state equations system.

(4) The gradient is computed.

Then we search the values of the parameters minimizing the functional g^* in a range containing the initial value u_0 in the parameter space through a gradient method.

4 – The results obtained for a particular set of observations are shown in Fig. 2 where a simulation of the Markovian process (1) is compared with the set of experimental data.

The proposed stochastic model allowed to clarify how the characteristic parameters could depend on the various environmental factors. Particularly we saw that the emersion rate is mainly dependent on the light intensity variations and the fluctuations about the average values are strictly related to temperature in that the second moment's value increases when the k's value increases.

This work is a first attempt to get a quantitative description of the exploratory activity of some estuarine populations which can allow to understand how the trophic web can be affected by environmental pollution. In particular the knowledge of these processes may be of some relevance in the control of environmental factors related to thermal pollution.

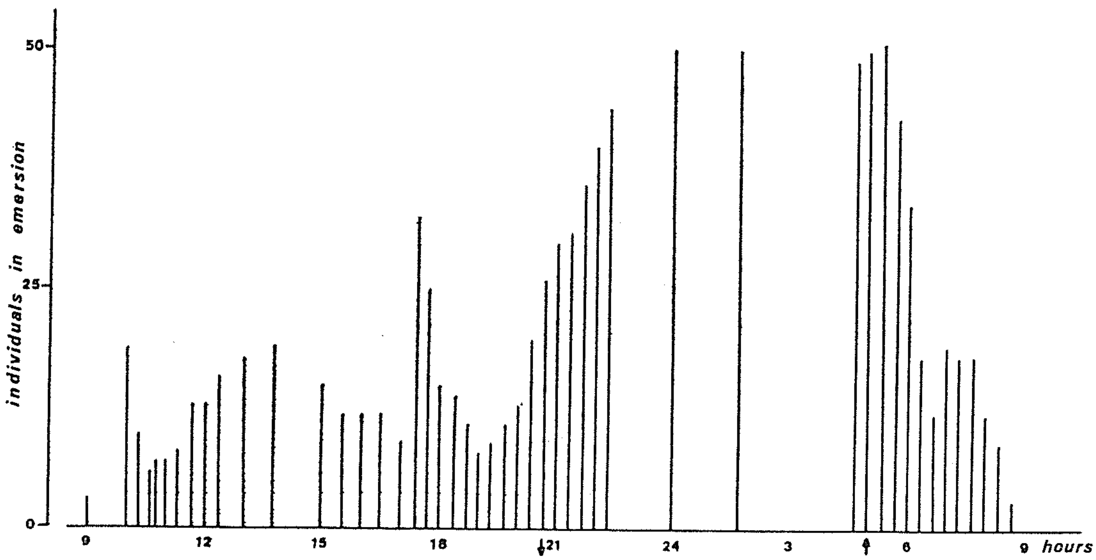

Fig. 1. – Exploratory activity of *Cyclope neritea*: experimental data.

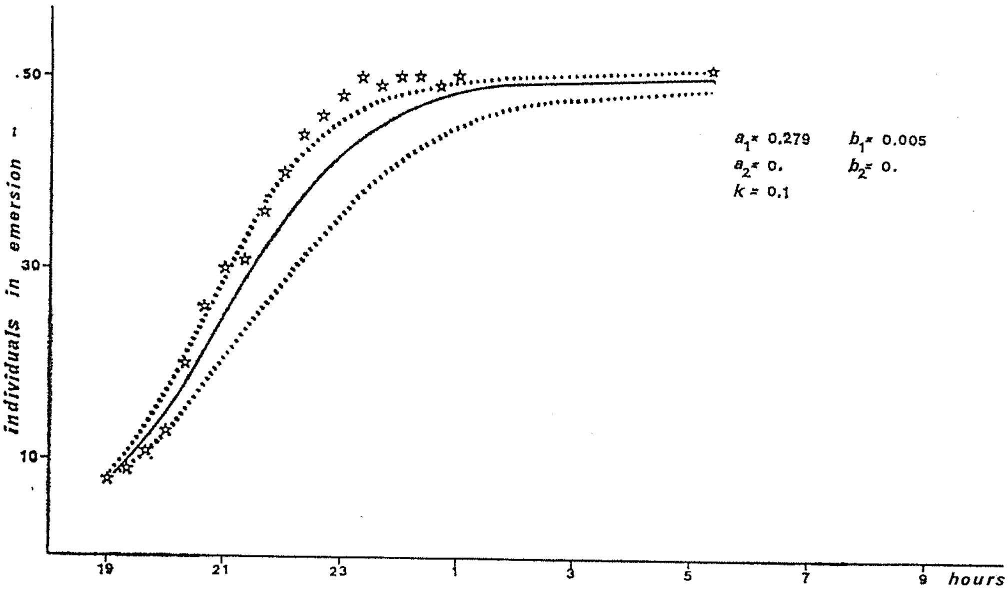

Fig. 2. – Exploratory activity of *Cyclope neritea*: comparison between a simulation of the Markovian process with the set of experimental data.

Bibliography

[1] M. S. Bartlett, *An introduction to stochastic processes with special reference to methods and applications*, Cambridge University Press, Cambridge 1978.

[2] M. Cantarelli, G. Di Cola, M. G. Mezzadri, V. Parisi e P. Poli, *Analisi dell'attività esploratoria di una popolazione di prosobranchi*, Atti del II Simposio di Dinamica di Popolazioni, Pallanza, 6-8 settembre 1979.

[3] L. E. Elsgolc, *Calculus of variations*, Pergamon Press 1961.

[4] S. Goel Narendra e e N. Richter-Dyn, *Stochastic models in biology*, Academic Press, New York 1974.

[5] J. D. Palmer, *Biological clocks in marine organisms*, Wiley Interscience Publication, New York 1974.

[6] P. Poli, V. Parisi, M. G. Mezzadri e D. Bedulli, *Trophic behaviour and thermobiology of estuarine molluscs in an experimental model*, part II: *Exploratory activity in « Cyclope neritea »*, J. Therm. Biol. (1979) (submitted for publication).

Abstract

Many animal species living in estuarine environments show a periodical activity; this rhythmic behaviour is often a strategical adaptation of the animals to changes of environmental factors. Then it is of some interest to know how critical environmental factors can affect these processes.

In this paper the exploratory activity of Cyclope neritea, a gastropod prosobranch playing the important role of scavenger in the trophic web of the Po Delta brackish lagoons, is considered.

A logistic stochastic model based on the analogy of the birth and death processes with migration is proposed in order to represent the processes of interface (sediment-water) crossing.

The parameter estimation problem and the model identification are approached by means of the maximum likelihood method.

The data analysis of experimental observations seems to confirm the relation between some environmental factors, such as light intensity and temperature, and exploratory activity.

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