

THE EXTERNAL MEMORY OF INTERTIDAL MOLLUSCS: A THEORETICAL
STUDY OF TRAIL-FOLLOWING

S. Focardi

Istituto Nazionale di Biologia della Selvaggina
via Stradelli Guelfi 23/a, Ozzano Emilia, Italy

J.L. Deneubourg

Service de Chimie-Physique II, Campus Plaine, U.L.B.
Bruxelles, Belgium

G. Chelazzi

Istituto di Zoologia dell'Università
via Romana 17, Firenze, Italy

Introduction

The secretion of a slimy mucus from the foot, besides being mechanically essential for the locomotion of many molluscs, seems to constitute a system of external storage of information used for orientation towards biologically significant goals such as hiding places, sexual partners or prey. Field observations and laboratory experiments have shown that many species are able to interpret chemical information contained in their mucous trails. In some cases the trail-following mechanism can involve the recognition of "personal" trails and the detection of trail polarization (Wells & Buckley, 1972; Cook & Cook, 1975).

The trail-following behaviour can also be considered as a mechanism for information exchange between members of a population when it is used for congregating into common shelters or mating aggregates. For some littoral species, at least, it seems reasonable to exclude that the periodical onshore clustering could be based on independent and concordant responses of the different animals to the same environmental cues.

The traditional ethological approach to this problem, consisting in the experimental manipulation of the trail, can be partially flanked by theoretical studies on the validity of different hypotheses concerning the orientation mechanisms. The purpose of such theoretical studies is to link the outputs of the two levels of empirical

analysis: the "micro-analysis" of the physio-ethological aspects of orientation, and the "macro-analysis" of such bulk phenomena as the spacial distribution and diffusion of the population.

The biological phenomenon

Clustering is a common stress reducing behaviour present in many intertidal molluscs species (see, for instance, Vannini & Chelazzi, 1978). Despite the differences in the specific behaviour, this phenomenon may be described as in Fig. 1 (left). During the non-active periods, the population of snails present on the shore can be

Figure 1. Left: schematic representation of the spatial distribution of snails on a rocky shore. Two holes sheltering clusters of different dimensions (AF) and some scattered animals (X) are shown. Right: symbolic representation of the mechanism determining the variation of cluster dimension.

divided into a scattered (X) and a protected population inhabiting a variable number (H_t) of equidimensional protected locations (holes); the total area of the H_t holes present on a given surface constitutes the protected surface (PS). Under natural conditions the clusters disaggregate during each activity phase and the scattered and protected snails melt into a common group of feeding animals. The cluster is re-formed at the end of the feeding period. During each aggregation-disaggregation cycle a dynamic exchange of animals between the two fractions can be observed. This kind of modification in the spatial arrangement of the snail population can be synthetically

represented by the chemical symbolism shown in Fig. 1 (right) where H_i is a cluster containing i snails and N is the carrying capacity of the holes, i.e. the maximum number of animals which one hole can shelter. a_i ($0 \leq i \leq N-1$) and b_i ($1 \leq i \leq N$) are the rate-constants of the process.

Results

The steady-state equations for H_0, \dots, H_n are:

$$\begin{aligned}
 \dot{H}_0 &= -a_0 H_0 X + b_1 H_1 = 0 \\
 \dot{H}_i &= a_{i-1} X H_{i-1} - b_i H_i - a_i X H_i + b_{i+1} H_{i+1} = 0 \\
 \dot{H}_n &= a_{n-1} X H_{n-1} - b_n H_n = 0
 \end{aligned}
 \quad i = 1, \dots, N-1$$

with the total population $P = X + \sum_i i H_i$
and the total number of holes. $H_t = \sum_j H_j$.

The distribution of cluster dimension at the steady-state is given by:

$$(2) \quad H_i = H_0 X^i \left(\prod_{j=0}^{i-1} a_j / \prod_{j=1}^i b_j \right) \quad i = 0, \dots, N$$

This steady-state is unique and stable for every values of the parameters. A general discussion of this class of differential equations may be found in Nicolis & Prigogine (1977).

The following variables are computed and used:

- (i) the protected population. $PP = \sum_{j=1}^n j H_j$.
- (ii) The protected fraction. $PF = 1 - X / P$.
- (iii) The aggregated fraction. $AF = PF - H_1 / P$.
- (iv) The turn-over between X and PP at the steady state. $TO = b_j H_j$.

If individual orientation mechanisms are concerned, the expression of the rate-constants in system (1) are:

$$(3) \quad a_i = a_r (1 - i / N); \quad b_i = i b.$$

where $(1 - i / N)$ is the fraction of free places in a hole while b is the inverse of the mean time of an individual's presence in a cluster. The probability of finding a hole by chance, a_r , can be computed by the expression $(L / S)(D + d) A$, where L is the length of the homeward branch of the feeding excursion, A is the probability of stopping when a hole is found and S is the surface; D and d are the diameters of the hole and the snails respectively (Curio, 1976).

Substituting eqs. (3) in system (2), it is possible to compute the cluster-dimension frequency-distribution which may be recognized as

binomial distribution:

$$(4) \quad H_i / H_t = (N! / (i! (N - i)!)) p^i q^{N-i}$$

where:

$$(5) \quad p = a_r X / (N b + a_r X); \quad q = N b / (N b + a_r X)$$

The turn-over and two derived variables can be computed:

$$(6) \quad TO = b (P - X); \quad TO / P = b PF; \quad TO / PP = b$$

In the case of clustering based on chemical communication between snails, the suitable expressions of the rate constants are:

$$(7) \quad a_i = (a_r + i a_c) (1 - i / N); \quad b_i = b i / (1 + e i)$$

The term a_c is the probability of following a conspecific's trail to a cluster, and $(1 + e i)$ is a simple expression which simulates the trapping effect of a web of trails (in fact each member of a cluster is more likely to find a trail leading to its own cluster than to a different one).

The variation of the TO / PP ratio and PF as a function of the density of population (P) is shown in Fig. 2 (a and b, respectively). Line b shows the existence of two values of P deserving special attention: firstly TD, the threshold value producing an abrupt rise in the PF, secondly MD, is the density giving the maximum value of PF.

Figure 2. Variation of TO / PP (a) and PF (b) as a function of P. $N = 50$, $a_r = 10^{-4} (N^{0.5} + 1)$, $a_c = .01$, $b = 1 / 3$, $e = .05$.

Figure 3. Variation of TO / PP (a) and PF (b) as a function of N. $P = 25$. The other parameter values as in Fig. 1.

In Fig. 3 TO / PP (a) and PF (b) are plotted as a function of the hole dimension. It is interesting to note that line b is U-shaped. The PF decreases as N becomes larger than 1, reaching a minimum value after which the PF monotonally increases. This result appears only if a_r in eq. (8) is relatively large, i.e. when the efficiency of the individual component of the orientation mechanism is high, while the second is given by the occurrence of cooperative behaviour.

Interestingly enough, the cluster dimensions distribution given with increasing values of N is clearly non-binomial (Fig. 4). For large values of N the binomial distribution approaches the normal distribution, while the distribution relative to the cooperative orientation mechanisms shows either a marked bimodality (Fig. 4, b) or a strong kurtosis (Fig. 4, c).

Figure 4. Distribution of cluster dimension for different N values $\overline{PS} = 60$, $P = 75$ and the other parameter values as in Fig. 1.

Discussion

An interesting result of the model is the different frequency-distribution of cluster dimension when assuming individual (e.g. self-trailing, idiotetic mechanisms or topographic memory) or cooperative (inter-individual trail-following) orientation mechanisms. This constitutes a useful tool for the interpretation of data obtained in the field because the difference between simulated and empirical distributions can be statistically tested by the use of non-parametric tests (Siegel, 1956). A second aid to the study of the orientation mechanisms involved in the aggregation of intertidal molluscs is given by the analysis of the turn-over between the scattered and aggregated fractions. Preliminary analysis of the

turn-over in a natural population of Nerita textilis have showed a strong negative correlation to the value of the aggregated population present in the study area, which is in agreement with the model's output in the case of cooperative orientation.

Also relevant is the capacity of the model to reproduce the influence of shore morphology on the behaviour. Individual or collective orientation mechanisms are selected under different shore conformations to maximize the protected fraction of population, as is observed in the field when snails shift from clustering to non-clustering as they move from areas with small holes to areas with large holes (Vannini & Chelazzi, 1978).

The need to quantify physical and behavioural parameters present in the model may guide future experimental analysis of the gregarious behaviour of intertidal molluscs. In particular, the importance of the quantification of the population density - which can strongly affects the behaviour of different populations of the same species in different environments - has to be stressed.

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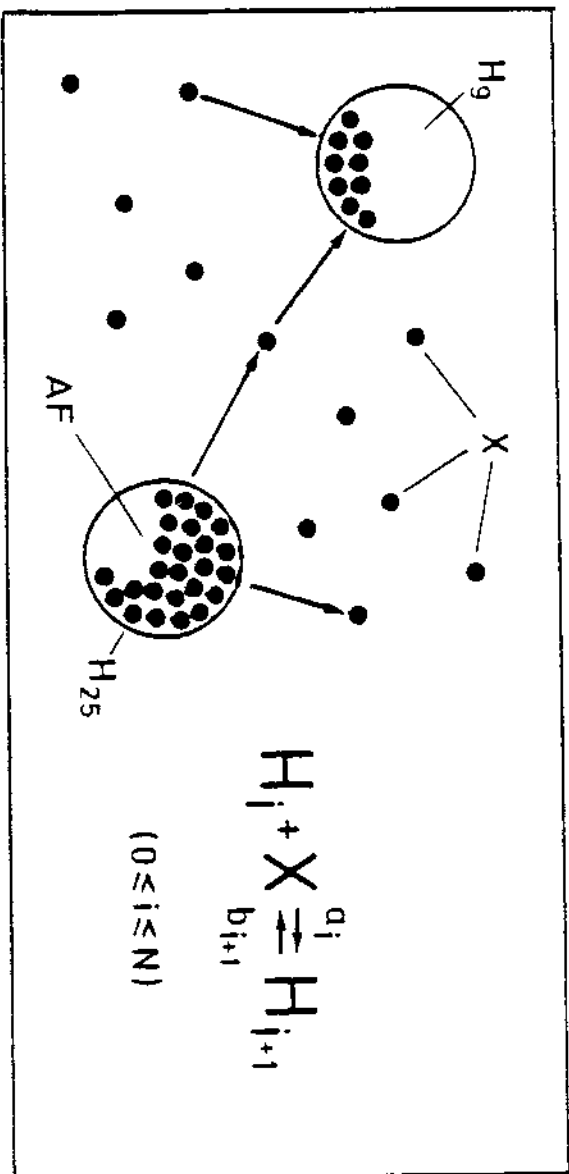
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