

How Shore Morphology and Orientation Mechanisms Can Affect the Spatial Organization of Intertidal Molluscs

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(Received 25 March 1983, and in revised form 20 June 1984)

Homing behaviour and clustering are very common in intertidal molluscs. A large number of observations stressed the importance of trail following in the orientation of each snail to its home and its cluster.

The aim of this paper is to provide a mathematical model of the clustering and homing behaviours of *Nerita textilis*, adopting different hypotheses about the mechanisms employed by snails to find their way back home after each feeding excursion. Moreover, the model is able to simulate similar processes in other species on the basis of their specific behavioural ecology. The results given by the model confirm some hypotheses about the nature of the orientation cues and suggest some new aspects of the adaptive value of trail-following in molluscs.

Introduction

Several species of littoral molluscs have been reported as performing short-term looped excursions centred to a more or less constant rest site (Newell, 1979; Underwood, 1979). Besides the examples of homing to individual scars as found in limpets and chitons (Stimpson, 1973; Chelazzi *et al.*, 1983*b*; Chelazzi, Focardi & Deneubourg, 1983*a*), resting in collective homes has been reported in some species (Arey & Crozier, 1921; Abe, 1933; Millard, 1968; Willoughby, 1973).

Also three species of the gastropod genus *Nerita* have been reported as forming clusters: *N. japonica* (Suzuki, 1935), *N. polita* (Vilenkin, 1977) and

N. textilis (Vannini & Chelazzi, 1978). Some populations of the latter species show a clear intraspecific variability with respect to this behaviour: a part of the population rests dispersed in the upper-eulittoral while other snails form large clusters on the lower belt of the rocky cliff. During the activity phase both groups migrate downward to feed on epilithic algae.

The present model deals with the homing and the clustering behaviour of snails in sheltered parts of the shore because the typical location for clusters of *N. textilis* and other species are rocky pools and crevices well protected from wave-action and sun-irradiation, though occasional clustering on flat areas has also been observed.

It is admitted that clustering reduces the exposure of littoral snails to such stress sources as wave-action and desiccation (Feare, 1971; Willoughby, 1973; Underwood, 1979; Branch, 1981). When clustering occurs in physically unprotected areas the adaptive value of this behaviour is even more evident since the mutual contact reduces the probability of being displaced by waves (Carstens, in Feare, 1971) or of overheating (Manning, in Moulton, 1962). This clustering enables snails whose shell (unlike limpets) is not adapted to resist wave-action to exploit flat exposed surfaces.

A number of orientation mechanisms have been suggested for the homing capacity of the littoral molluscs (Chelazzi, 1980), but most of these remain hypothetical since no critical experiments have been performed. In particular, aggregation may result from individual or collective orientation. Snails moving at random or performing individual kinetic or tactic responses to some environmental parameters (Fraenkel & Gunn, 1961) may cluster if, finding a suitable rest area, they stop moving. Also personal trail-following as demonstrated in many intertidal molluscs (Funke, 1968; MacFarlane, 1980, 1982) or other individual mechanisms such as kinesthetic orientation (Pieron, 1909; Thorpe, 1963) can lead to aggregation if the availability of sheltering places is the limiting factor.

Nevertheless, a higher efficiency in aggregative behaviour may be obtained by mutual interaction between snails. Besides short-range physical or chemical interactions (Simpson, Thomas & Townsend, 1973), long-range information exchange has also been suggested. This latter concerns the capacity to follow a trail laid by conspecifics (Cook & Cook, 1975; Lowe & Turner, 1976; Trott & Dimock, 1978), or to follow a chemical gradient originating from the clustering area (Rhode & Sandland, 1975).

The aim of the model which is developed in this paper is to test the effects of different orientation cues employed by the snails to find their way back after each feeding excursion. The model includes the short-term rhythm of aggregation-disaggregation found in *N. textilis* and in many other species, while it does not take into account the long-term cyclic variations (synodic

and seasonal) which have been observed in the clustering of *N. textilis* (Vannini & Chelazzi, 1978), *Nucella lapillus* (Feare, 1971) and *Acmea dorsuosa* (Abe, 1933). Moreover the importance of shore morphology and population density on the clustering behaviour has been tested.

Model I: Clustering in Sheltered Locations

A population of snails inhabiting a rocky shore is composed of P individuals freely moving on a surface pierced by H_i holes or crevices. n is the maximum number of snails which each hole can shelter and H_0, H_1, \dots, H_n the number of holes where 0, 1, ..., n snails are found. Thus:

$$H_t = H_0 + H_1 + \dots + H_n \quad (1)$$

$n = 1$ simulates the existence of individual homes. The total population of molluscs (P) is:

$$P = X + H_1 + 2 \cdot H_2 + 3 \cdot H_3 + \dots + n \cdot H_n \quad (2)$$

where X is the number of animals resting outside the holes.

During a feeding excursion a snail, member of a hole H_i , may be unable to come back home and during the next resting phase it will become part of the unprotected population (X). The rate of occurrence of this event is proportional to the density of holes H_i and to a constant b_i . Inversely an unprotected animal can reach a hole containing i animals at a rate proportional to H_i , to X and to a constant a_i . a_i and b_i are eco-ethological parameters taking into account orientation, activity and the reactions of the animals to the environment. Direct exchange of animals between clusters is thought to be negligible as compared with indirect exchange.

The following system of differential equations describes the set of events that modify the value of the variables X, H_0, \dots, H_n :

$$\begin{aligned} \dot{X} &= -X \cdot \sum_{j=0}^{n-1} a_j \cdot H_j + \sum_{j=1}^n b_j \cdot H_j \\ \dot{H}_0 &= -a_0 \cdot H_0 \cdot X + b_1 \cdot H_1 \\ \dot{H}_1 &= a_0 \cdot X \cdot H_0 - b_1 \cdot H_1 - a_1 \cdot X \cdot H_1 + b_2 \cdot H_2 \dots \\ \dot{H}_n &= a_{n-1} \cdot X \cdot H_{n-1} - b_n \cdot H_n \end{aligned} \quad (3)$$

System (3) is discussed using different expressions for each of the parameters a_i and b_i , corresponding to the actual mechanisms of orientation. The protected ($PF = 1 - X/P$), the aggregated ($AF = PF - H_1/P$) fractions of the population and the mean cluster dimension ($MA = (P - X - H_1)/(H_t - H_0 - H_1)$) are calculated as functions of the population density and the hole size (n).

RANDOM MOVEMENTS AND INDIVIDUAL ORIENTATION

Unlike the probability of entering a hole, the probabilities of finding a hole by chance and of stopping are independent of the number of snails living in the hole. It is assumed that a_i is given by:

$$a_i = f_r \cdot (1 - i/n) \quad (4)$$

where $(1 - i/n)$ is the proportion of empty places in the hole. The carrying capacity of a hole (n) is given by $(D/d)^2$ where D is the diameter of a hole and d the diameter of the snails. f_r is the frequency of crossing one hole during the homeward branch of the feeding excursion:

$$f_r = (L/S) \cdot (D + d) \cdot Q \quad (5)$$

where L is the excursion length, S is the surface and Q the probability of stopping. b_i is given by:

$$b_i = i \cdot g = i/t \quad (6)$$

where t is the mean resting time of one snail in a well-defined cluster (or a hole). g may easily be computed and related to the animals' walking pattern.

In this kind of orientation it is assumed that, the first time, the animals find a hole by chance and so the value of a_i is the same as in the case of random movement, whereas the random movement and the individual mechanisms of orientation have widely different values for b_i .

It is evident that the number of consecutive days during which snails stay in the same hole is much larger if they use an individual memory. This implies that the b_i corresponding to a strategy with "memory" are smaller.

COLLECTIVE ORIENTATION

a_i now has two components:

$$a_i = (f_r + i \cdot f_c) \cdot (1 - i/n) \quad (7)$$

f_r , which corresponds to random search (equation (4)) and $f_c \cdot i$, where i is the number of outward trails, assumed to be equal to the number of animals present in the cluster the precedent resting period. f_c is proportional to the length of the feeding excursion (L) and to the probability of following a trail and stopping in a hole (C):

$$f_c = i \cdot L^2 \cdot C/S \quad (8)$$

The outward and the homeward branches of the feeding excursion are supposed to be equal.

Similarly we redefine b_i . For a given snail the probability of its leaving its own trail during a feeding excursion is the same as in the individual-trail orientation but now the snail can meet the trail of a snail coming from the same cluster and follow it home. An expression for this is:

$$b_i = g \cdot i / (1 + e \cdot i) \quad (9)$$

where e is an arbitrary constant which takes into account the trapping force of the web of trails.

Model II: Clustering in Unprotected Locations

When detectable resting-sites are not present on the shore the snails stop their movement only if a conspecific is encountered. These aggregations are described by:

$$\begin{aligned} \dot{X} &= -X \cdot \sum_{j=2}^{n-1} a_j \cdot X_j + \sum_{j=3}^n b_j \cdot X_j - 2a_1 X^2 + 2b_2 X_2 \\ \dot{X}_2 &= a_1 X^2 - b_2 X_2 - a_2 X X_2 + b_3 X_3 \\ \dot{X}_i &= a_{i-1} \cdot X \cdot X_{i-1} - b_i \cdot X_i - a_i \cdot X \cdot X_i + b_{i+1} \cdot X_{i+1}, \quad i = 3, \dots, n-1 \\ \dot{X}_n &= a_{n-1} X X_{n-1} - b_n X_n. \end{aligned} \quad (10)$$

X is the population of scattered snails and X_2, \dots, X_n the number of cluster containing 2, ..., n snails. n is considered to be large but not infinite in order to simulate the limiting effect that the food-abundance around the cluster, have on the number of clustered snails.

The expression for a_i and b_i is the same as reported in equations (7) and (8). The contribution of the random search (f_r) is considered to be null.

Results

MODEL I: RANDOM MOVEMENTS AND INDIVIDUAL ORIENTATION

The steady-state frequency-distribution of the hole population is given by a binomial distribution:

$$H_i / H_t = n! \cdot p^i \cdot q^{n-i} / (i! \cdot (n-i)!) \quad (11)$$

where

$$p = f_r \cdot X / (n \cdot g + f_r \cdot X); \quad q = n \cdot g / (n \cdot g + f_r \cdot X).$$

From equation (11) it is possible to compute the protected fraction PF :

$$PF = (B - (B^2 - 4 \cdot PS / P)^{0.5}) / 2 \quad (12)$$

where:

$$B = 1 + n \cdot g / (f_r P) + PS / P$$

and $PS = n \cdot H_i$, i.e. the largest number of snails that the area S can shelter.

PF as a function of n and P is monotonically decreasing for every parameter value (Fig. 1). It appears clearly that the individual strategy yields the best results when the holes are small and their number is large. Similarly PF decreases as the density increases. This is because the presence of other animals decreases each animal's probability of finding empty holes.

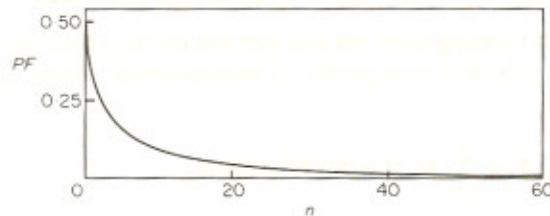


FIG. 1. Individual mechanisms of orientation. The PF is plotted as a function of n . $PS = 80$, $g = 0.1$, $P = 50$, $f_r = 2 \cdot 10^{-4} \cdot (n^{0.5} + 1)$.

These preceding observations lead us to imagine special behaviours which can be selected in the case of individual homing: an aggressive behaviour, which in fact was observed only in species having individual homes, and an avoidance of conspecific trails. This latter mechanism is useful when the hole-density is high compared to the snail density.

MODEL I: COLLECTIVE ORIENTATION

The shape of the curves shown in Fig. 2(a, c) is part of the characteristic behaviour resulting from a collective orientation mechanism. The first observation is that the PF and AF have practically the same values. Secondly there is a threshold in the density of the population (TD) necessary to obtain a significant clustering. Thirdly, there is a density (MD) which maximizes the PF and AF . The comparison between Figs 2(a) and 2(c) shows the influence of n on the dynamics of the system. If n increases the values of TD and MD are reduced while the maximum values of the PF and AF increases.

The variation of the MA as a function of the population density is shown in Figs 2(b) and 2(d). Both graphs show that the system reaches a plateau corresponding to the holes' carrying capacity. This growth is markedly non-linear when the holes are large: the first sudden change in the rate of

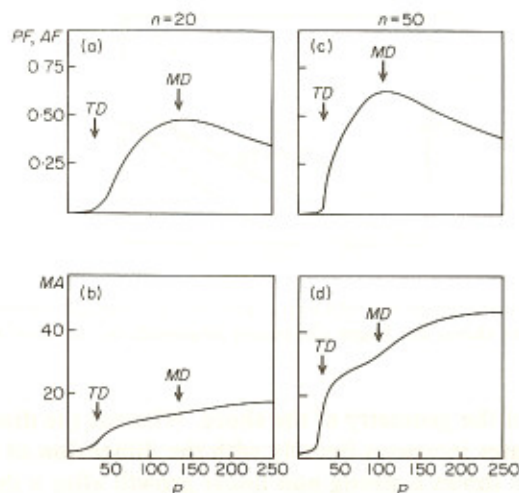


FIG. 2. Collective orientation. The *PF* and *AF* (a, c) and the *MA* (b, d) are plotted as functions of *P*. In Figs (a) and (c) the *PF* and *AF* have almost coincident values and no graphical discrimination is possible. The influence of the physical environment is analysed comparing two different *n* values. $f_r = 10^{-5} \cdot (n^{0.5} + 1)$, $f_c = 0.01$, $g = 1/3$, $e = 0.05$.

growth of the *PF* appears when the density reaches *TD*. A second, less abrupt, change appears when the density reaches *MD*.

Figure 3 shows the behaviour of system (3), with two different values of f_c . As expected, when f_c increases, the efficiency of the system (i.e. the *AF*) increases. This difference is clear for lower values of the density while the curves converge when the density increases.

New information about system (3) appears when one plots the *MA* as a function of *n* keeping the population density and the *PS* constant (Fig. 4). The clustering of snails is greatly influenced by the environment but is not

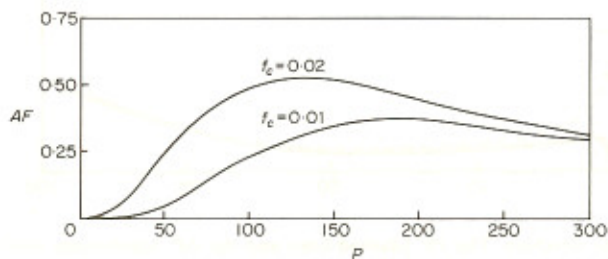


FIG. 3. Collective orientation. The influence of different values of parameter f_c in equation (3) on the *AF*, plotted as a function of *P*, is shown.

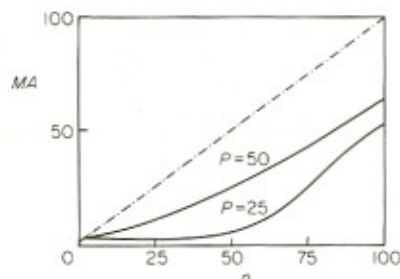


FIG. 4. Collective orientation. The *MA* as function of *n* is computed for two different values of *P*. The broken line shows the larger dimension attainable by the cluster. The parameter values as in Fig. 3.

a passive result of the geometry of the shore. Whereas the dimension of the potential aggregates increases linearly with the dimension of the holes, the mean cluster-size shows a strong non-linear growth after a threshold value in the hole dimension.

When the value of the term f_r in equation (7) is relatively high *PF* is U-shaped (Fig. 5). In this particular situation the snails are able to protect themselves by individual strategy, if in their habitat there is a large number of small holes, and, by co-operative behaviour, when there is a small number of large holes. With an intermediate number of holes of intermediate size, the protective efficiency is lower.

A study of the distributions and the turn-over between *X* and *PF* with comments on their importance for the interpretation of field data is presented in a related paper (Focardi, Deneubourg & Chelazzi, 1984).

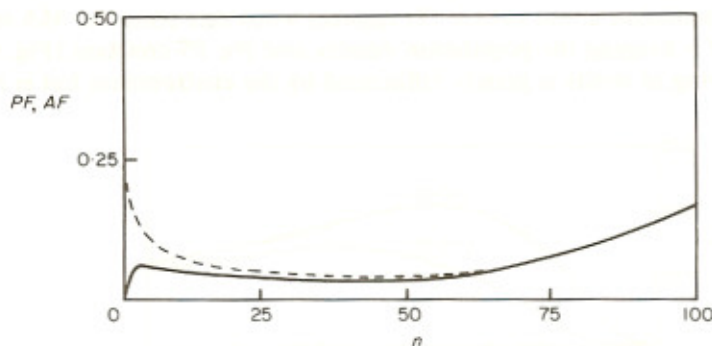


FIG. 5. Habitat selection. The *PF* (dashed line) and the *AF* (continuous line) are plotted as a function of *n*. A good degree of protection results when *n* is equal to 1 (by individual strategy of orientation) or when it is large enough to permit an efficient co-operative behaviour. This result is obtained only when f_r is large. $P=25$, $f_r=5 \cdot 10^{-4} \cdot (n^{0.5}+1)$, $g=1/3$, $e=0.05$.

MODEL II: CLUSTERING IN UNPROTECTED LOCATIONS

Figures 6(a) and 6(b) show the AF and MA when plotted as function of P . AF and MA increase smoothly to their maxima value while critical densities are found (TD and MD) in the case of clustering in holes (Fig. 2(b)). While the AF is higher on flat than on protected areas the cluster-size attained on flat surfaces is always smaller than in holes. This is due to the fact that flat areas favour the development of a larger number of cluster, thereby preventing efficient collective homing.

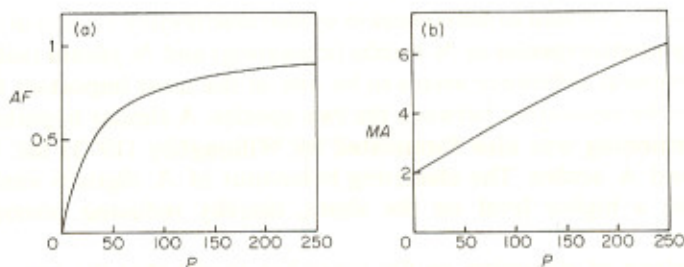


FIG. 6. Unprotected locations. The AF (a) and the MA (b) are plotted as function of P . $f_r = 0$, $n = 50$, $f_c = 0.01$, $g = 1/3$, $e = 0.05$.

The effect of trail-following on aggregation in flat areas is shown in Fig. 7 where the number of cluster is plotted as a function of f_c . A value of f_c appears that maximizes the number of cluster. For greater f_c only a few clusters are formed, being of a larger size.

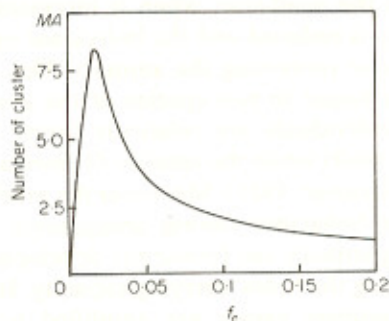


FIG. 7. Unprotected locations. The number of clusters plotted as function of f_c . $P = 50$, $n = 200$, $f_r = 0$, $g = 1/3$, $e = 0.05$.

Discussion

The model is able to reproduce a part of the variability present both within each single species and between congeneric species living in quite similar environments.

Firstly, it is able to show the influence of the shore morphology on the homing process: the snails are able to shift from individual to collective strategies following the dimensions of the holes. The collective mechanism of trail-following simulated by the model is itself able to select environments where the degree of protection of the snails is high.

This process can lead to differences in spatial distribution such as observed between sympatric species as *N. textilis* (clustering) and *N. plicata* (solitary). This behavioural difference seems to be one of the most important factors of zonal niche separation between the two species. A similar hypothesis of niche partitioning was also formulated by Willoughby (1973) for *Acmea digitalis* and *A. scabra*. The clustering behaviour of *A. digitalis* enables it to colonize a higher level on the shore, thereby reducing interspecific competition.

The analysis of clustering on flat areas has shown that the presence of holes on the shore is important when the cluster-size determines the adaptive value of clustering. Also if the formation of small aggregates is advantageous, the choice of flat surfaces can be favoured. Moreover, the models forecasts that the snails' spatial distribution on flat surfaces is less aggregated than on sheltered areas having the same value of n .

Secondly, small variations of the behavioural parameters (e.g. f_c in equation (8)) may greatly change the behaviour of system (3) (cf. Fig. 3). For example, variations in the excursions length result in completely different patterns of spatial distribution. The model shows that communal behaviour depends on the snail-size: when it increases, the value of the holes' carrying capacity is reduced and the individual orientation mechanisms are more effective in protecting the animals. This fact could explain the different behaviour found in two species of the genus *Onchidium*: *O. verruculatum*, whose individuals are relatively large, has an individual strategy (MacFarlane, 1980) while the smaller *O. floridanum* is reported to live in groups (Arey & Crozier, 1921). Moreover the model forecasts abrupt changes in the homing behaviour during ontogenesis. In fact, the small dimension of the young animals can favour the development of a high level of clustering by increasing the holes' carrying capacity. In conclusion, small variations in the parameters values are amplified by the co-operative behaviour to give different patterns of spatial distribution.

The existence of a value of f_c maximizing the formation of small clusters on flat surface may be a mechanism selected by snails to allow a large number of reproductive encounters.

When a form of interaction exists, clustering can be regarded as a form of protosocial behaviour, especially if a mutual benefit for the sharers can be proved.

Communal behaviour is very common in arthropods and it is considered the first step towards a higher level of social behaviour (Wilson, 1971). On account of the pelagic larval stages parental care plays a less important role in molluscs than in arthropods in the development of social behaviour. The snails' social behaviour is probably due to the mutual advantages obtained by the clustering animals rather than being related to an altruistic behaviour between genetically related individuals.

The model has been analysed at the steady-state. Its dynamics have not been followed. Moreover one particular important feature is that, in nature, different parameters used in the model are not constant during time (synodic and seasonal variations). Observations and preliminary theoretical estimations show the strong influence of these variations on the temporal evolution of clustering.

Our model does not take into account explicitly the space. Jorné & Safriel (1979) have developed an interesting method, based on long-term measures of the rate of dispersion of snails. This method, tested on *Nerita polita*, allows estimation of the intensity of the interactions between animals. These interactions being due to different factors such as trail-following.

This kind of model helps the understanding of such phenomena by providing quantitative information about the different behavioural mechanisms involved and testing their efficiency.

Aggregational phenomena are good examples of self-organizing processes. Large-scale collective structures result from a multitude of interactions between small-scale units and from the continuous interplay between random events and the deterministic component of the units' behaviour (Nicolis & Prigogine, 1977). We believe that the study of chemical communication in molluscs may contribute to a fuller understanding of the self-organizing processes.

We would like to thank Professor Lefever for many helpful discussions and his invaluable comments. The authors wish to thank Professors Prigogine and Nicolis for their constant interest. Thanks also to Drs Champagne and Goss. This study was supported by the NATO grant 267.81.

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