

Clustering in intertidal gastropods and chitons : models and field observations

Autor(en): **Focardi, Stefano / Deneubourg, Jean-Louis / Chelazzi, Guido**

Objektyp: **Article**

Zeitschrift: **Mémoires de la Société Vaudoise des Sciences Naturelles**

Band (Jahr): **18 (1987-1991)**

Heft 3

PDF erstellt am: **21.06.2024**

Persistenter Link: <https://doi.org/10.5169/seals-259822>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern. Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden. Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

MODÈLES DYNAMIQUES EN BIOLOGIE, R. ARDITI (DIR.)
DYNAMICAL MODELS IN BIOLOGY, R. ARDITI (ED.)

Clustering in Intertidal Gastropods and Chitons: Models and Field Observations

BY

STEFANO FOCARDI¹, JEAN-LOUIS DENEUBOURG²
AND GUIDO CHELAZZI³

Summary.—FOCARDI S., DENEUBOURG J.-L. et CHELAZZI G., 1990. Clustering in intertidal gastropods and chitons: models and field observations. *In: Dynamical Models in Biology*, R. Arditi (ed.). *Mém. Soc. vaud. Sc. nat.* 18.3: 181-194.

Communal refuging inside holes and crevices is a very frequent adaptation observed in intertidal organisms. A mathematical model of clustering in intertidal snails has been developed in order to analyse the importance of different homing mechanisms on the dynamics of aggregation and on the habitat selection patterns. The model shows that the interplay between a small number of behavioural and ecological parameters is able to simulate many different strategies observed in the field.

In particular, a quantitative fitting of the model is attempted using data on the clustering behaviour of the intertidal snail *Nerita textilis*. The results show a good agreement of simulations and fields observations.

Finally, a new model is proposed which is able to simulate the dynamic of aggregation when the trail-polymorphism is present inside the population, for instance in the case of species which adopt both communal and solitary strategies.

Résumé.—FOCARDI S., DENEUBOURG J.-L. and CHELAZZI G., 1990. L'agrégation de gastéropodes et chitons intertidaux: modélisation et expérimentation. *In: Modèles dynamiques en biologie*, R. Arditi (dir.). *Mém. Soc. vaud. Sc. nat.* 18.3: 181-194.

¹Istituto Nazionale di Biologia della Selvaggina, via Ca' Fornacetta 9, I-40064 Ozzano dell'Emilia (BO), Italia.

²Service de chimie-physique 2, Université Libre de Bruxelles, B-1050 Bruxelles, Belgique.

³Dipartimento di Biologia Animale e Genetica, via Romana 17, I-50127 Firenze, Italia.

L'agrégation dans des trous et des fentes est une adaptation très commune chez beaucoup d'organismes intertidaux. La dynamique de cette agrégation, les mécanismes de retour au gîte et de sélection de l'habitat sont analysés à l'aide d'un modèle mathématique capable de simuler différentes stratégies comportementales qui ont été observées dans la nature.

En particulier, nous avons vérifié, d'une façon très concluante, les prédictions du modèle avec des données sur le comportement agrégatif du gastéropode littoral *Nerita textilis*.

Un nouveau modèle a été développé pour étudier la dynamique de l'agrégation quand la population de mollusques possède un polymorphisme de traces, par exemple, dans le cas d'espèces qui présentent aussi bien des stratégies solitaires que des stratégies agrégatives.

INTRODUCTION

With respect to its biological and physical features, ecologists divide the littoral environment in zonal belts parallel to the shore-line and characterized by specific physical and biological features. The behavioural adaptations of the free moving gastropods and chitons living in the part of the rocky shore included between the maximal and minimal tidal levels (eulittoral) are the object of the present paper. The models which have been developed are mainly directed to the analysis of the temporal and spatial patterns of activity of such organisms, with special regard for adaptations which involve competitive or cooperative interactions between conspecifics.

The rhythmic activity of intertidal chitons and gastropods includes movements related to seasonal, synodic, tidal and diel fluctuations in the shore ecology. Seasonal and synodic movements usually consist in zonal migrations up and down the shore in order to minimize the exposure to stress factors and to optimize the access to resources. Seasonal migrations related to reproduction have been reported in many intertidal gastropods (SMITH and NEWELL 1955, UNDERWOOD 1973, BRANCH 1975, BRANCH and BRANCH 1981). Limpets avoid dehydration and overheating by moving along the sea-land axis in synchrony with seasonal or spring-neap cycles (BREEN 1972, BRANCH 1975, 1981), but the ethological determinism of these long-term rhythmic migrations has yet to be deeply investigated (HAMILTON 1985).

The short-term activity of intertidal chitons and gastropods is organized into temporal units of activity (u.p.a.) determined by tidal and diel variations of physical and biological factors on the shore.

The feeding excursions during each u.p.a. are generally classified into three distinct models of increasing complexity: ranging pattern, zonal shuttling and central place foraging (CHELAZZI and VANNINI 1985).

In the ranging pattern feeding excursions are not orientated toward constant directions and the animals do not use to return to their previous shelter or to the same shore level. This model has been reported by UNDERWOOD

(1977) in some Australian gastropods and seems to be present in some littorinids as well (MCQUAID 1981, PETRAITIS 1982). An example of ranging pattern in chitons has been found in the Caribbean *Acanthopleura granulata* (FOCARDI and CHELAZZI, in press) showing highly meandering feeding paths and no long-term preferential rest sites. More generally, this model may be common in species living on non-tidal shores, or when adaptation to the littoral environment is based on the temporal more than spatial organization of activity. Zonal shuttling has been described in many gastropods (WARA and WRIGHT 1964, CRAIG 1968, EATON 1968, MAGNUS and HAACKER 1968, ROGER 1968, MICALLEF 1969, THAIN 1971, VANNINI and CHELAZZI 1978, CHELAZZI 1982, CHELAZZI *et al.* 1983 b) which loop along the sea-land axis at each u.p.a. Zonal shuttling is due to the separation of feeding and resting zones along the sea-land axis, not simply dependent upon obvious physical factors: predation and competition more often than a simple escape from air or water are probably involved in the evolution of this pattern in such shuttlers as many trochid and neritid gastropods (THAIN 1971) and chitons (CHELAZZI *et al.* 1983 a).

Central place foragers rest in a definite shelter more or less constantly in time and home to it after each feeding excursion. Most contributions are concerned with the accuracy of homing performance, scaling the observed behaviour from the "statistical homing" of e.g. *Acmaea digitalis* (FRANCK 1964) to the deterministic homing of such species as *Patella depressa* (COOK *et al.* 1969), *P. vulgata* (BREE 1959), *P. longicosta* (BRANCH 1971), *Collisella scabra* (HEWATT 1940) and *Notoacmea petterdi* (CREESE 1980). Similar scaling has been observed between congeneric chitons as well (FOCARDI and CHELAZZI, in press).

All these studies are devoted to solitary foragers but there is increased evidence that resting in collective homes is a common adaptation between intertidal chitons and gastropods (ABE 1933, SUZUKI 1935, MILLARD 1968, FEAR 1971, WILLOUGHBY 1973, RHODE and SANDLAND 1975, VILENKIN 1977, VANNINI and CHELAZZI 1978, CHELAZZI *et al.* 1984). The homing mechanisms to the collective shelters have not been specifically analyzed but the existing evidence (CHELAZZI *et al.* 1989) support the idea that the trail-following mechanism better accounts for the homing ability of both solitary and communal central place foragers.

Collective refuger species are expected to release and follow non-individual trails for homing. In fact this is the case for *Ilyanassa obsoleta* (TROT and DIMOCK 1978) and *Nerita textilis* (CHELAZZI *et al.* 1983 b). On the contrary, some mechanisms for own-trail recognition must exist in solitary homers, given the possible interindividual crossing of different feeding paths under natural conditions. FUNKE (1968) showed discrimination between personal and conspecific trails in *Patella vulgata* and the same is true for

Onchidium verruculatum (MCFARLANE 1980). Cross-trailing tests in *Acanthopleura gemmata* (CHELAZZI *et al.* 1987) showed that this solitary-homer chiton has a quasi-personal trail: a low trail polymorphism in the population tested would allow the reduction of inter-individual mistakes in following the outward trail for homing. A detailed analysis on the trail-personality in congeneric *Acanthopleura* species (DENEUBOURG *et al.* 1989) has revealed a high trail-polymorphism in *A. gemmata* and a lower one in *A. brevispinosa* and *A. granulata* which may account for their different home fidelity.

The small number of trail types observed in *A. brevispinosa* accounts for the observation that this species is able to shift from a solitary strategy, used in the typical exposed rocky shores inhabited by the species, to a communal strategy in the peculiar ecological conditions of intertidal caves where the presence of strong tangential forces increases the adaptive value of communal resting (personal observations).

THE MODEL

A population of P snails lives over a rock surface of area S pierced by a total of H_T holes or crevices. We denote with H_1, \dots, H_N the number of holes sheltering $1, \dots, N$ individuals where N is the carrying capacity of holes. During each resting phase X snails are unable to find a hole and remain scattered, and unprotected, on the flat part of the rocky shore. During each u.p.a. the scattered and clustered snails move away from their resting positions to feed. During the return branch of the feeding excursion a clustered snail has a positive probability not to be able to recover the cluster, so becoming a scattered one, inversely some scattered snails are able to locate a cluster.

The following set of differential equations modelizes the process (FOCARDI *et al.* 1985 a, b):

$$\begin{aligned} \dot{H}_0 &= -a_0 X H_0 + b_1 H_1 \\ \dot{H}_1 &= a_{i-1} X H_{i-1} - b_i H_i - a_i X H_i + b_{i+1} H_{i+1} \\ \dot{H}_N &= a_{N-1} X H_{N-1} - b_N H_N, \quad i = 1, \dots, N-1 \end{aligned} \quad (1)$$

$$\dot{X} = -X \sum_0^{N-1} a_j H_j + \sum_i^N b_j H_j .$$

The possibility of discovering a hole (for an X snail) or coming back to its hole (for a protected snail) depends on the orientation mechanisms used by the animals during the return branch of their feeding excursions. Here both individual and collective mechanisms of orientation shall be studied.

Random and individual orientation. The probability of finding a hole by chance and of stopping there is

$$f_r = (L/S)(D + d)Q, \quad (2)$$

where L is the excursion length, Q the probability of stopping when a hole is found and D , d are the diameters of the hole and snail, respectively. The recruitment parameter a_i is

$$a_i = f_r(1 - i/N) \quad (3)$$

where the term in brackets takes into account the saturation of the holes.

The rate of escaping from a cluster sheltering i snails is

$$b_i = ig, \quad (4)$$

where g is the per-snail escape rate. The numerical values of g , depends by the efficiency of the homing mechanism(s).

Collective orientation. The animal is able to find the hole using informations originating from other members of that cluster, for instance on the basis of inter-individual trail-following. We have

$$a_i = (f_r + f_c i)(1 - i/N), \quad (5)$$

where

$$f_c = iL^2C/S, \quad (6)$$

supposing that out- and back-ward branches of the feeding excursions have the same length L . Accordingly, b becomes

$$b_i = gi/(1 + ei), \quad (7)$$

where e is an empirical constant which takes into account the trapping effect of the web of trails around the hole.

It has been possible to obtain the steady state distributions of cluster size to understand the protective value of a determined orientation mechanisms in an environment characterized by a given N value. Moreover the study of such distributions permits an easy comparison between model predictions and observational data.

The cluster size distribution is obtained by

$$H_i = \frac{H_T U_i}{\sum_0^N U_j}, \quad i = 0, \dots, N \quad (8)$$

$$\text{with } U_i = X^i \left(\frac{\prod_0^{i-1} a_j}{\prod_1^i b_j} \right), \quad i = 1, \dots, N \quad (9)$$

$$\text{and } U_0 = 0.$$

The steady state analysis of model (1) has been able to reproduce qualitatively a part of the variability observed in intertidal molluscs. The model shows what are the ecological conditions where individual or collective orientation are selected for: when the shore is rich in small holes the individual strategy results more efficient than the collective one. In some range of f_r and f_c values the trail-following mechanism is able to select the environments where the protected population ($PP = P - X$) is larger. A first maximum of PP is observed on rocky shore with small holes and a second where large shelters are present, intermediate situations being unfavourable.

In the case of collective orientation mechanisms there is a threshold in the population size, P , which maximizes the fraction of protected snails and the ownership of cluster, in other words, which reduces the per-snail probability of leaving the cluster.

In species with individual orientation mechanisms, the cluster size distribution is binomial, while in the case of collective orientation it is possible to have different cluster size distributions depending on the parameter values, with the appearance of bimodality and strong kurtosis. When the cumulative carrying capacity of the holes (NH_T) becomes large in front of P , the scattered snails are very few and almost all population is clustered.

Small variations of the behavioural parameters (e.g. of f_c) may greatly change the behaviour of system (1). Some authors (e.g. COOK and COOK 1978) have attributed the high behavioural plasticity observed in intertidal gastropods to the evolution of local races: these results suggest instead that marked changes in behaviour may be due to interactions between a basically constant behavioural element (trail-following) and varying physical parameters such as the coastal morphology.

A FIELD TEST OF THE MODEL

A very striking instance of behavioural plasticity is exhibited by the Indian Ocean populations of the gastropod *Nerita textilis*. This snail lives on exposed rocky shore experiencing large tidal excursions. In the upper littoral *N. textilis* adopts a solitary strategy while the animals resting in the

mid-littoral live only in big clusters. Moreover the two populations are not separated: during the activity phases (at low tide between noon and midnight) both groups migrate downward to feed. At neap tide a large part of snails become members of the cluster system while at spring tide clusters disappear and all the population moves upward (VANNINI and CHELAZZI 1978).

A preliminary comparison between the behaviour of this species and model outputs shows that collective mechanisms of orientation are involved: the model predicts a negative correlation between the output flow from the cluster ($\sum_1^N b_j H_j$) and the aggregated fraction of population ($\sum_2^N i H_i$). This was fully confirmed by our field observations (CHELAZZI *et al.* 1984).

In order to simulate in detail the aggregative behaviour of *N. textilis* we had to introduce some modifications in the expression of parameters of system (1), relative to the time-dependence of the recruitment parameter $a_i(t)$. On the basis of field observations, we tested the most simple hypothesis that the excursion length of the scattered population is the behavioural parameter mainly influenced by the synodic rhythm. Under this assumption we set (FOCARDI *et al.* 1989)

$$f_r(t) = (L(t)/S)(D + d)Q, \quad (10)$$

$$f_c(t) = L_0 L(t) C/S, \quad (11)$$

where L_0 is the time-independent length of the outward branch of the feeding excursion of clustered animals and $L(t)$ is the same for the scattered snails. It results

$$a_i(t) = (f_r(t) + f_c(t)i)(1 - i/N). \quad (12)$$

The escape rate b_i was considered to be time-independent.

The synodic tidal rhythm has a fortnightly periodicity and can be represented by a sinusoidal wave: spring tide is the maximum of the cycle (new and full moon) and neap tide its minimum. They are separated by a 7-day interval.

Concerning the dependence of $L(t)$ on the cycle we set

$$L(t) = L_0 V(t), \quad (13)$$

where $V(t)$ is a periodical function. To test the type of signal detection used by *N. textilis* two different models have been developed: (i) a linear response of snails to the tide level variations

$$V(t) = V + A \sin(2\pi t/T), \quad (14)$$

(ii) a non-linear, on/off, response

$$V(t) = V - A, \quad T/2 < t \leq T, \quad (15 \text{ a})$$

$$V(t) = V + A, \quad 0 < t \leq T/2, \quad (15 \text{ b})$$

where T is the period, A the amplitude and V the mean value of the cycle.

The factors which most determine the adaptive value of the clustering behaviour change with the ecological constraints acting on the studied population. Very often the limiting factors are different also in close parts of the rocky shore. In oscillating environments the intensity of the ecological constraints rhythmically changes with the phase of the synodic cycle.

At spring tide the mid-eulittoral is very unfavourable for *N. textilis* because its globular shell makes the probability of dislodging very high: the wave action is dangerous also for snails resting in clusters. On the contrary, clusters are efficient shelters against the lighter waves at neap tide. For this species it seems useful to try to maximize the difference between the cluster size at neap and spring tide.

When the stress level is not very large a better strategy could be to maximize the mean aggregation level during the cycle. Finally, for species or populations where competition for food is higher than in the precedent instances, it may be convenient to try to maximize the cluster number, at least in the cases where the protection given by small clusters is high enough with respect to the situation of being scattered.

The main effects of population density on clustering behaviour in constant and oscillating environments have been analyzed in details by FOCARDI *et al.* (1989). Relevant differences in the aggregation dynamics have been shown between sine and square waves and also larger between snails in constant and oscillating environments. An important behavioural parameter in the clustering process is the trail-following level. Its effect on the mean aggregation is relevant: there is a threshold level of C which induces an abrupt increase in the efficiency of the mechanism of interindividual trail-following. Larger C values are unable to increase significantly the level of protection. The physiological adaptations relative to the trail-following behaviour are energetically expensive and it is probably useful to limit the trail-following performance to the minimal levels which yield good results. This fact can probably account for many relatively disappointing results of trail-following experiments.

While all parameter values were assessed in the field we had no information on the trail-following response (C) in this population. We tried to estimate it from the model: the best agreement of the model with the field data is obtained when the square wave (eq. 15) is used with a C value of 0.04. Interestingly, with this value we observe a large difference between maximal and minimal mean cluster size.

The comparison between field data and simulations has shown a good agreement when the time evolution of mean cluster size and cluster number through the synodic cycle is studied: expected and observed distributions are not statistically different.

In conclusion, the model seems able to model the dynamics of homing and clustering in intertidal molluscs, and it has permitted to estimate the value of a parameter, such as the trail-following response, for which there are not quantitative field observations. The analysis of clustering in *N. textilis* has confirmed the result of the precedent section showing that trail-following may constitute an adaptive mechanisms for habitat selection in intertidal molluscs.

TRAIL-POLYMORPHISM AND CLUSTERING

The models of clustering have shown the effects of two different systems of orientation with respect to variable ecological conditions. The analysis assumed that the trail-personality was absolute in the case of individual mechanisms and null in the case of inter-individual trail-following. The available evidence (in spite of its relatively hypothetical character) suggests indeed that in some species there is a quasi-personality of trail with a certain number of trail types inside a population.

It is interesting to wonder what is the influence of trail polymorphism on the aggregative dynamics in species exhibiting a shift from a solitary to a communal strategy: the advantages of trail-polymorphism during the solitary phase are in competition with the costs of polymorphism during the clustering phase.

To study this topics we have modified eq. (1) to introduce two different trail types inside a population.

We denote with the superscripts 1 and 2 the different trail types. Let H_{ij} be the number of clusters with i snails of type 1 and j snails of type 2. Variations of cluster size are produced by two processes

$$H_{ij} + X^1 \frac{a_{ij}^1}{b_{ij}^1} H_{i+1,j}$$

$$H_{ij} + X^2 \frac{a_{ij}^2}{b_{ij}^2} H_{i,j+1} \quad \text{where}$$

$$a_{ij}^1 = (f_r + i f_c)(1 - (i + j)/N) , \quad (16 \text{ a})$$

$$a_{ij}^2 = (f_r + j f_c)(1 - (i + j)/N) . \quad (16 \text{ b})$$

The escape constants, b_{ij}^1 and b_{ij}^2 , have been modified accordingly.

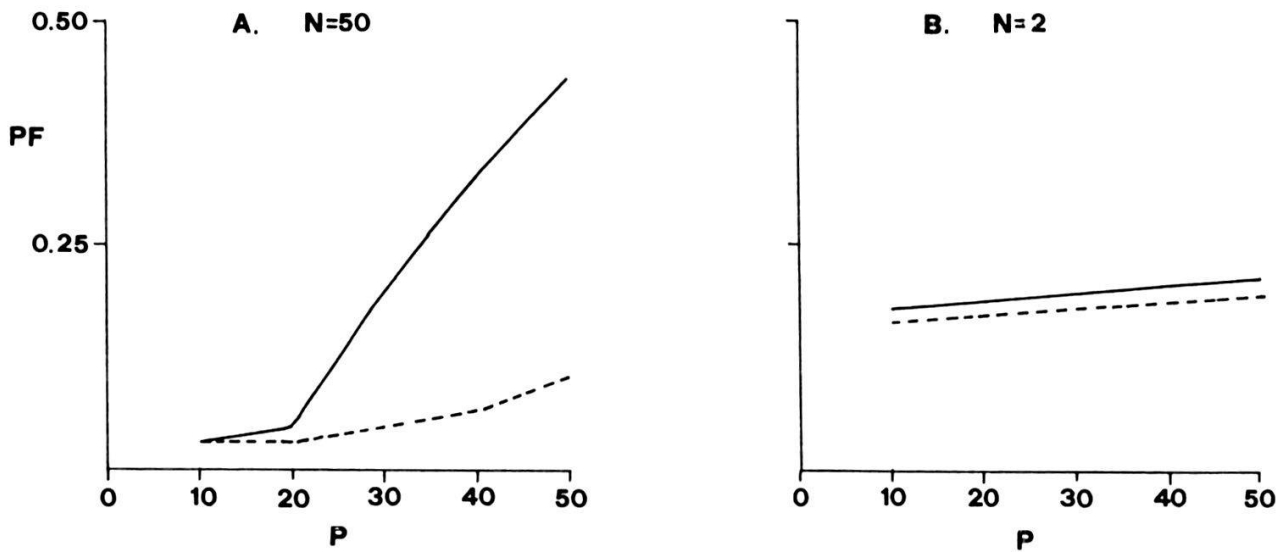


Figure 1.—The protected fraction of population as function of population size (P) at two different values of holes' carrying capacity, for populations with one (*continuous line*) and two trail types (*broken line*). $f_r = 0.0005$, $f_c = 0.01$, $e = 0.05$, $g = 0.33$, $NH_T = 100$.

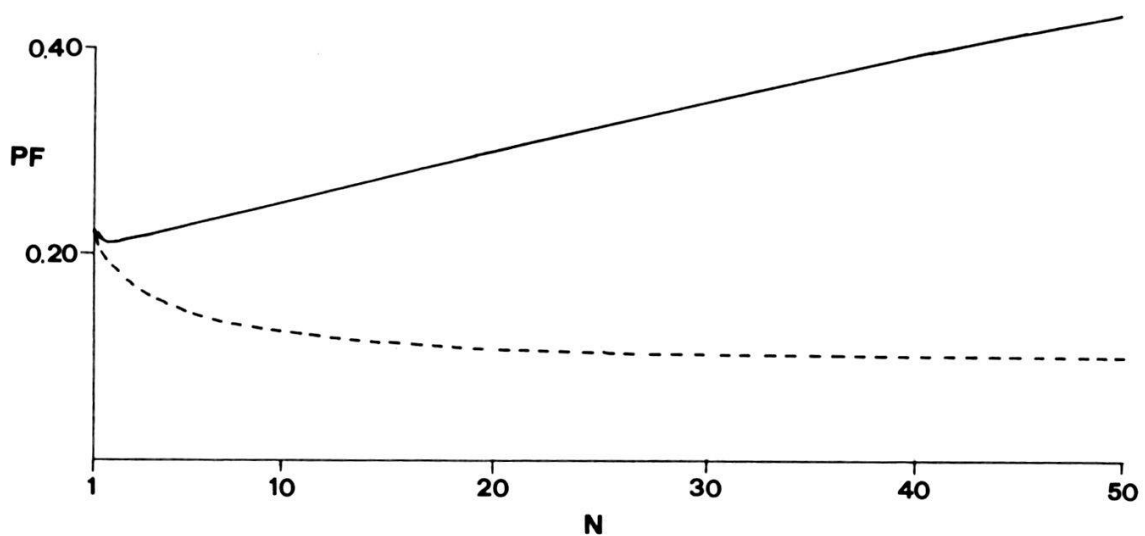


Figure 2.—The protected function of population as function of carrying capacity of holes. $P=50$. Symbols and other parameter values as in Fig. 1.

The modifications introduced by the existence of two trail types on the protected fraction of population ($PF = PP/P$) are shown in fig. 1 in two different environmental contexts. When the hole size is large (fig. 1a) the presence of two trail types reduces the number of protected snails. In the case where the carrying capacity of the holes is small (fig. 1b), no evident

modification is introduced.

These results are summarized in fig. 2 where the protected fraction is plotted as function of N , for one and two trail types. The decrease of the protected fraction is particularly evident for small N , while for large hole sizes P_F reaches a plateau value.

DISCUSSION

The models developed for the study of clustering behaviour in intertidal chitons and gastropods can reproduce a large number of phenomena observed in the field. It is noteworthy that these results were obtained with the use of parameters measurable in the field with classical observational methods. The number of hypotheses which were introduced is very small and this fact increases the possibility of using critical experiments for testing the model.

The approach used in the studies which have been summarized in the present report presents a certain number of shortcomings. First, the model is deterministic so that it cannot be properly used, for instance, in situations where population size is small or a high variability in hole size is present. The model does not take into account the actual movement of animals: in the studied situation this effect is probably not very important, but in many cases an ethological analysis of the paths followed by the animals (CHELAZZI *et al.* 1983b, 1987) can be necessary to calculate correctly recruitment and escape rates.

The original results presented in this paper are not surprising at all, but they could be relevant when the ecology and the problem of sympatric evolution of intertidal gastropods and chitons are studied.

The consequence of the reduced efficiency of the mechanism of aggregation with more than one trail type can lead to different ecological consequences. In some cases the species with polymorphic trails will become unable to colonize those shores where clustering is necessary to survive, in other words the ecological niche of the species is reduced.

In organisms where a pelagic larval stage and external fecundation are common the possibility of having short-scale allopatric evolution is remote: the interruptions of the rocky shore along the continental coasts are not, in general, so large to isolate populations of the same species. Trail polymorphism, linked to a behavioural shift from solitary to communal lifestyle could produce a fine-grained separation of animals with different trail types during the communal phase. When the mortality rate of scattered snails is large in front of larval recruitment, chitons or snails which have settled in the vicinity of a cluster prevalently composed (e.g. by random events) by animals with another trail type will suffer a higher mortality and are so

excluded by that small area of shore. The long-term effects of such mechanisms have to be analyzed but it seems reasonable that the concentration of individuals with the same trail type inside neighbouring holes can be a precondition for reproductive separation with subsequent selection of new morpho-functional and behavioural characters.

REFERENCES

- ABE N., 1933. The colony of limpet (*Acmaea dorsuosa* Gould). *Sci.Rep. Tohoku Univ. 4th Ser. Biol.* 9: 279-296.
- BRANCH G.M., 1971. The ecology of *Patella* L. from the Cape Peninsula, South Africa. 1. Zonation, movements and feeding. *Zool. Afr.* 6: 1-38.
- BRANCH G.M., 1975. Mechanisms reducing intraspecific competition in *Patella* spp.: Migration, differentiation and territorial behaviour. *J. Anim. Ecol.* 44: 575-600.
- BRANCH G.M., 1981. The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanogr. Mar. Biol. Ann. Rev.* 19: 235-379.
- BRANCH G.M. and BRANCH M.L., 1981. Experimental analysis of intraspecific competition in an intertidal gastropod, *Littorina unifasciata*. *Aust. J. Mar. Freshwat. Res.* 32: 573-589.
- BREE P.J.H., 1959. Homing-gedrag van *Patella vulgata* L., Kon. Ned. Akad. Wetensch. *Versl. Gewone Vergd. Afd. Natuurk.* 68: 106-108.
- BREEN P.A., 1972. Seasonal migration and population regulation in the limpet *Acmaea (Collisella) digitalis*. *Veliger* 15: 133-141.
- CHELAZZI G., 1982. Behavioural adaptation of the gastropod *Nerita polita* L. on different shores at Aldabra atoll. *Proc. R. Soc. Lond. B*, 215: 451-467.
- CHELAZZI G. and VANNINI M., 1985. Space and time in the behavioural ecology of intertidal animals. *S.I.T.E. Atti* 5: 689-692.
- CHELAZZI G., FOCARDI S. and DENEUBOURG J.-L., 1983a. A comparative study on the movement patterns of two sympatric tropical chitons (*Mollusca: Polyplacophora*). *Mar. Biol.* 74: 115-125.
- CHELAZZI G., INNOCENTI R. and DELLA SANTINA P., 1983b. Zonal migration and trail-following of an intertidal gastropod analyzed by LED tracking in the field. *Mar. Behav. Physiol.* 10: 121-136.
- CHELAZZI G., DENEUBOURG J.-L. and FOCARDI S., 1984. Cooperative interactions and environmental control in the intertidal clustering of *Nerita textilis*, (Gastropoda; Prosobranchia). *Behaviour* 90: 151-166.
- CHELAZZI G., DELLA SANTINA P. and PARPAGNOLI D., 1987. Trail-following in the chiton *Acanthopleura gemmata*: operational and ecological problems. *Mar. Biol.* 95: 539-545.
- CHELAZZI G., FOCARDI S. and DENEUBOURG J.L., 1989. The analysis of movement patterns and orientation mechanisms in intertidal chitons and gastropods. *In: Behavioural Adaptations to Intertidal Life*, G. Chelazzi and M. Vannini (eds), Plenum Press, New York, p. 173-184.

- COOK A., BAMFORD O.S., FREEMAN J.D.B. and TEIDMAN D.J., 1969. A study on the homing habit of the limpet. *Anim. Behav.* 17: 330-339.
- COOK S.B. and COOK C.B., 1978. Tidal amplitude and activity in the pulmonate limpets *Siphonaria normalis* (Gould) and *Siphonaria alternata* (Say). *J. Exp. Mar. Biol. Ecol.* 35: 119-136.
- CRAIG P.C., 1968. The activity pattern and food habits of the limpet *Acmaea pelta*. *Veliger (Suppl.)* 11: 13-19.
- CREESE R.G., 1980. An analysis of distribution and abundance of populations of the high-shore limpet *Notoacmaea petterdi* (Tenison-Woods). *Æcologia* 45: 252-260.
- DENEUBOURG J.-L., FOCARDI S. and CHELAZZI G., 1989. Homing mechanisms of intertidal chitons: Field evidence and the hypothesis of trail-polymorphism. In: Behavioural Adaptations to Intertidal Life, G. Chelazzi and M. Vanini (eds), Plenum Press, New York, p. 185-195.
- EATON C.M., 1968. The activity and food of the file limpet *Acmaea limatula*. *Veliger (Suppl.)* 11: 5-12.
- FEAR C.J., 1971. The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillus* (L.). *Æcologia* 7: 117-126.
- FOCARDI S., DENEUBOURG J.-L. and CHELAZZI G., in press. Ecological determinants of bioeconomics in the intertidal chitons (*Acanthopleura spp.*). *J. Animal. Ecol.*
- FOCARDI S., DENEUBOURG J.-L. and CHELAZZI G., 1985 a. How shore morphology and orientation mechanisms can affect spatial organization of intertidal molluscs. *J. Theor. Biol.* 112: 771-782.
- FOCARDI S., DENEUBOURG J.-L. and CHELAZZI G., 1985 b. The external memory of intertidal molluscs: a theoretical study of trail-following. In: Mathematics in Biology and Medicine, V. Capasso, E. Grosso and S.L. Paveri-Fontana (eds), Springer Verlag, Berlin, p. 524.
- FOCARDI S., DENEUBOURG J.-L. and CHELAZZI G., in press. Theoretical analysis of rhythmical clustering in an intertidal gastropod. *Ecol. Model.*
- FRANK P.W., 1964. On home range of limpets. *Am. Nat.* 98: 99-104.
- FUNKE W., 1968. Heimfindevermögen und Ortstreue bei *Patella L.* (Gastropoda, Prosobranchia). *Æcologia* 2: 19-142.
- HAMILTON P.V., 1985. Migratory molluscs, with emphasis on swimming and orientation in the sea sars, *Aplysia*. In: Migration Mechanisms and Adaptive Significance, suppl. to *Contributions to Marine Sciences* 27: 212-226. Hewatt, W. G., 1940, Observations on the homing limpet *Acmaea scabra* Gould. *Am. Midl. Nat.* 24: 205-208.
- MAGNUS D.B.E. and HAACKER U., 1968. Zum Phänomen der ortsunsteten Ruheversammlungen der Strandschnecke *Planaxis sulcatus* (Born) (Mollusca, Prosobranchia). *Sarsia* 34: 137-148.
- MCFARLANE I.D., 1980. Trail-following and trail-searching behaviour in homing of the intertidal gastropod mollusc, *Onchidium verruculatum*. *Mar. Behav. Physiol.* 7: 95-108.
- MCQUAID C.D., 1981. The establishment and maintenance of vertical size Gradient in populations of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. *J. Exp. Mar. Biol. Ecol.* 54: 77-89.

- MICALLEF H., 1969. The zonation of certain trochids under an artificial tidal regime. *Neth. J. Sea Res.* 4: 380-393.
- MILLARD C.S., 1968. The clustering behaviour of *Acmaea digitalis*. *Veliger (Suppl.) 11*: 45-51.
- PETRAITIS P.S., 1982. Occurrence of random and directional movements in the periwinkle *Littorina littorea* (L.). *J. Exp. Mar. Biol. Ecol.* 59: 207-217.
- ROGERS D.A., 1968. The effect of light and tide on movements of the limpet *Acmaea scabra*. *Veliger (Suppl.) 11*: 20-24.
- ROHDE K. and SANDLAND R., 1976. Factors influencing clustering in the intertidal snail *Cerithium moniliferum*. *Mar. Biol.* 30: 203-216.
- SMITH J.E. and NEWELL G.E., 1955. The dynamics of the zonation of the common periwinkle *Littorina littorea* (L.) on a stony beach. *J. Anim. Ecol.* 24: 35-56.
- SUZUKI S., 1935. Notes on the behaviour of *Nerita japonica* Dunker. *Sci. Rep. Tohoku Univ. 4th Ser. Biol.* 9: 297-314.
- THAIN V.M., 1971. Diurnal rhythms in snails and starfish. In: Fourth European Marine Biology Symposium, D.J. Crisp (ed), Cambridge Univ. Press, Cambridge, p. 513-537.
- TROTT T.J. and DIMOCK R.V., 1978. Intraspecific trail-following by the mud snail *Ilyanassa obsoleta*, *Mar. Behav. Physiol.*, 5: 91-101.
- UNDERWOOD A.J., 1973. Studies on the zonation of intertidal prosobranchs (Gastropoda: Prosobranchia) in the region of Heybrook Bay, Plymouth. *J. Anim. Ecol.* 42: 353-372.
- UNDERWOOD A.J., 1977. Movements of intertidal gastropods. *J. Exp. Mar. Biol. Ecol.* 26: 191-201.
- VANNINI M. and CHELAZZI G., 1978. Field observations on the rhythmic behaviour of *Nerita textilis* (Gastropoda: Prosobranchia). *Mar. Biol.*, 45: 113-121.
- VILENKIN B.Y., 1977. On the behaviour of *Amphinerita polita* in a populated territory (Gastropoda, Neritidae) (in Russian). *Zool. Zh.* 56: 303-306.
- WARA W.M. and WRIGHT B.B., 1964. The distribution and movements of *Tegula funebris* in the intertidal region of Monterey Bay, California (Gastropoda). *Veliger (Suppl.) 6*: 30-37.
- WILLOUGHBY J.W., 1973. A field study on the clustering and movement behaviour of the limpet *Acmaea digitalis*. *Veliger 15*: 223-230.

Manuscrit reçu le 1er décembre 1988