Analysis of Movement Patterns and Orientation Mechanisms in Intertidal Chitons and Gastropods

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INTRODUCTION

Despite their different organization and biology, chitons (Mollusca, Polyplacophora) and gastropods (Mollusca, Gastropoda) share a large number of adaptations to intertidal life, including morpho-functional and behavioural traits. Communication, clustering, aggressiveness and even simple parental cares have been reported in both classes but, as in other animals, the basis of their behavioural adaptation to the intertidal environment is a proper organization of activity in space and time.

The quantity of reports on these topics is impressive, but the number of satisfactory ethnological analyses is low. The present contribution is not a comprehensive review of chitons' and gastropods' behavioural ecology (partial reviews may be found in Boyle, 1977; Newell, 1979; Underwood, 1979; Branch, 1981; Hawkins and Hartnoll, 1983), but rather an attempt to clear up some conceptual and methodological misunderstandings and shortcomings, and to identify the problems in a field that only recently has been opened to quantitative and experimental investigation.

ACTIVITY ORGANIZATION IN TIME AND SPACE

In approaching the study of activity patterns of intertidal chitons and gastropods we must clearly distinguish between occasional, continuous and rhythmic phenomena. Occasional activity includes movements in response to such unpredictable ecological variations as those produced by storms or the sudden appearance of predators and competitors. It also includes the capacity shown by some neritid (Chelazzi and Vannini, 1976, 1980), trochid (Byers and Mitton, 1981; Doering and Phillips, 1983) and littorinid (Gendron, 1977; Hamilton, 1978a) gastropods to regain their optimal zonation upon experimental displacement. A second class of occasional behaviours is given by the avoidance responses elicited in gastropods by contact with, or the approach by potential predators such as sea-stars (Burke, 1964; Feder, 1967; Branch, 1979) or other gastropods (Hoffmann et al., 1978).
Onthogenetic shifting of the population members along the shore produces an evident size-gradient in many gastropods (Branch, 1975b; Underwood, 1979) but the relative importance of individual behaviour (continuous, progressive migration along the sea-land axis) and selective mortality in producing it has not been fully clarified.

Rhythmic activity 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 including limpets (Branch, 1975b), trochids (Underwood, 1973) and littorinids (Smith and Newell, 1955; 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, 1975b, 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 determined by tidal and diel variations of physical and biological factors on the shore. In general, intertidal animals may adopt one of two alternative strategies (Chelazzi and Vannini, 1985). The "isophasic" pattern, typical of such mobile groups as arthropods and vertebrates, consists in rhythmic zonal migrations synchronous and concordant with the tides. These animals perform a dynamic colonization of the intertidal environment, following oscillations in the medium (air or water) to which they are primarily adapted. Some sandy beach wheelers, such as Bulila digitalis and B. rhodostoma (McLachlan et al., 1979; Brown, 1982) adopt this isophasic pattern, performing wide "Donax like" migrations. On a shorter scale the isophasic pattern is also shown by some littorinids as the marsh periwinkle Littorina irrata (Hamilton, 1977) and the cerithid Cerithidea decollata climbing on mangrove trunks (Cockcroft and Forbes, 1981).

On the contrary, most typical rocky shore chitons and gastropods, due to the high energy cost of their locomotion (Denny, 1980; Horn, 1986) and low speed, adopt an "isospatial" strategy, remaining within a more or less narrow belt along the sea-land axis, with alternating exposure to air and water. The activity of these animals is limited to the time when the condition of their zone is suitable for moving and feeding. Timing of unit phase of activity (u.p.a.) is limited by the morpho-functional organization of the different species, but the very local structure of the environment, including complex relationships with other species is determinant as well (Thain, 1971; Spight, 1982). For this reason a generalization is not possible (Hawkins and Hartnoll, 1983). Among the few chitons studied, the timing of u.p.a. includes tidal and diel components. While the latter seem to predominate in Nuttalina Californica (Nishi, 1975), a tidal rhythm has been reported in Mopalia lignosa (Fulton, 1975). In gastropods the relative importance of diel and tidal components may depend on their zonation on the shore (Zann, 1973a).

Nevertheless, most intertidal chitons and gastropods show combined diel-tidal rhythms of high complexity (Zann, 1973b). As diel and tidal cycles have not the same period, a short-term survey is generally not sufficient to understand the interlocking of the two components in u.p.a. timing (Cook and Cook, 1978) and a satisfactory analysis may require a complete synodic period (about 29 days). Moreover, a marked variation in u.p.a. timing can occur in taxonomically related species, and between different populations of the same species, as in Patella vulgata (Hawkins and Hartnoll, 1983). Careful investigation of u.p.a. timing, including the
different sources of variability is very important, because the time actually devoted to feeding is a critical parameter in the energy balance of intertidal gastropods and chitons; in addition, u.p.a. definition is necessary for proper scheduling of position sampling for movement analysis.

On the basis of the existing heterogeneous evidence, the feeding excursions performed by rocky shore chitons and gastropods during each u.p.a. are generally classified into three distinct models of increasing complexity: ranging pattern, zonal shuttling and central place foraging.

Ranging pattern. In the first model, sometimes reported as "random pattern", feeding excursions are not oriented toward constant directions and the animals do not 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 with the caribbean Acanthopleura granulata (pers. observation) 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, linked to a solid morpho-functional specialization to stable microhabitats. Nevertheless, ranging does not mean random: the random walk of these animals must be biased at least by kinetic responses, allowing the long-term stability of their zonal distribution.

Zonal shuttling. The second model, sometimes quoted as "tidal migration", has been described in such gastropods as neritids (Vannini & Chelazzi, 1978; Chelazzi, 1982; Chelazzi et al., 1983c), trochids (Wara & Wright, 1964; Micallef, 1969; Thain, 1971), planaxids (Magnus and Haacker, 1968), and some limpets such as Acmaea limatula (Eaton, 1968), A. pelta (Craig, 1968), A. scabra (Rogers, 1968) which loop along the sea-land axis at each u.p.a. That this shuttling is not a true tidal migration typical of isophasic animals is evident from the fact that - despite their upshore climbing for resting - many intertidal gastropods such as Nerita textilis are splashed by waves during high tide. In some species shuttling is paradoxically inverted with respect to the sea level oscillations, with upward movements during low tide, and downward migration prior to high tide, as in N. polita (Chelazzi, 1982). 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 Acanthopleura spp. chitons (Chelazzi et al., 1983a).

Central place foraging. Resting in a definite shelter more or less constant in time and homing to it after each feeding excursion has long since been described in limpets (Davis, 1895) and chitons (Crozier, 1921). Underwood (1979) and Branch (1981) reviewed the occurrence, ecological significance and some operational aspects relative to the so-called "homing behaviour" of limpets, but generalization on the three aspects is again difficult because detailed analysis of movements performed by homer species during each u.p.a., and the modification of individual strategy in time, is often lacking. The sampling of only rest positions is frequent in these studies, since most limpets rest during diurnal low tides, when the shore is accessible for study, while the feeding phase often occurs while the animals are splashed by waves. These sampling limitations produce a fuzzy picture of the spatial behaviour.

Most contributions are concerned with the accuracy of homing performance, scaling the observed behaviour from the "statistical homing" of
e.g. Acmaea digitalis (Frank, 1964) to the deterministic homing of such species as Patella depressa (Cook et al., 1969), P. vulgata (Bree, 1959), P. longicosta (Branch, 1971), Cottilella scabra (Hewatt, 1940) and Notoacmea petterdi (Creese, 1980). Similar scaling has been observed between congeneric chitons as well (Focardi and Chelazzi, in prep.). But the following aspects of central place foraging are also important: use of natural shelters or active digging of scars, such as in many limpets (Branch, 1981) and the chiton Acanthopleura gemmata (Chelazzi et al., 1983a); scar-shell complementarity, as in most limpets, or non-individual scar morphology permitting its use by different conspecifics, as in chitons; scar defense from intruders as in Acanthopleura gemmata (Chelazzi et al., 1983b; Chelazzi and Parpaglioli, 1987) or simply abandoned upon intrusion as in A. brevispinosa (personal observation).

Moreover, the knowledge of actual movement pattern between two rest events is critical, giving a great deal of information on the spatial relationships between rest site and feeding grounds. It is evident that feeding loops are usually orientated in the different species and in the different populations of the same species: radially distributed around the shelter, as in Patella vulgata (Hartnoll and Wright, 1977), or biased along the sea-land axis as in Acanthopleura gemmata (Chelazzi et al., 1983a). Moreover, some species are territorial, defending their feeding ground (Stimson, 1970; Branch, 1981), while in others the feeding grounds are not personal. The long-term strategy of homers is very interesting as well, as stressed by Cook and Cook (1981): do the animals intensively exploit a good algal patch or is their feeding conservative, shifting to different places on different excursions? Reiteration in time of individual route recording may reveal interesting aspects of homing pattern, but so far this kind of analysis has been limited to two chitons (Chelazzi et al., 1983a) and two sipholanid limpets (Cook and Cook, 1981). A more detailed analysis of movements may help to interpret the shifting from solitary homing to collective refuging, as observed in many intertidal gastropods and some chitons. This transition often seems intraspecific and dynamic: the mechanism for shifting from solitary to collective resting must be searched for in the amplification of minimal variations in individual behaviour, depending on variations in shore morphology and tidal regime (Chelazzi et al., 1985; Focardi et al., 1985a, 1985b).

An ethological approach to all the above aspects is more necessary than a blind classification of homing performance to understand the homing phenomenon in terms of "central place foraging" theory (Orians and Pearson, 1979). One of the methods which may open some ethological black boxes of the homing phenomenon in chitons and gastropods is LED tracking (or motographic method) (Chelazzi et al., 1983c; 1987). This simple technique permits the integral recording of the spatial strategy of the single animals, provided that the diel component of their u.p.a. is nocturnal. If exported to other species LED tracking may overcome many of the methodological shortcomings indicated by Hamilton (1978b): "absence of data on individuals, lack of multiple position records for individuals, impreciseness of direction and distance measurements, small sample size, short-term observations, and lack of statistical analysis". The last point is a very critical one, as recently stressed by Underwood and Chapman (1985).

But establishing three very distinct models (ranging, zonal and homing) may be misleading. In fact, the zonal pattern is frequently linked to solitary or collective homing (Magna and Haacker, 1968; Vannini and Chelazzi, 1978) and, conversely, excursions of typical homers are sometime zonally polarized (Chelazzi et al., 1983c), while deterministic homing can alternate with dispersive (ranging) excursions such as observed in the chiton Acanthopleura granulata (personal observation).
ANALYSIS OF ORIENTATION MECHANISMS

A frequent outcome of the study on movement patterns is the analysis of underlying orientation mechanisms. Intertidal molluscs have not escaped this trend and some work has been done on mechanisms controlling the behaviours described above. Nevertheless, the quality of information available on chitons and gastropods is disappointing in comparison to that on other groups such as crustaceans (Herrmann, 1983; Pardi and Ercolini, 1986), with the result that chitons and gastropods make only a timid appearance in recent important reviews on animal orientation (Jander, 1975; Schone, 1984).

Directional orientation. Under the distinct sea-land asymmetry faced by many rocky shore chitons and gastropods, there is probably no pressure to evolve such complex directional mechanisms as the astronomical and magnetic orientation used by some sandy beach arthropods. Some speculations about the existence of "solar orientation" in gastropods (Warburton, 1973) must be discarded on the basis of experiments conducted on neritids (Chelazzi and Vannini, 1976, 1980) and littorinids (Hamilton, 1978a). Also evidence for the use of magnetic field by gastropods (Brown, 1963) and chitons (Ratner, 1976) is very slim. On the contrary, the importance of gravity, light and wave movement in the directional orientation of these groups is evident (Newell, 1979; Creutzberg, 1975; Gendron, 1977) but will not be reviewed here.

The real problem with these intertidal animals lies elsewhere: besides orienting cues, their directional orientation requires a correct modulation of movement polarity to be ecologically adaptive. There is early and recent evidence that zonal movements of molluscs are not based on simple responses to a single cue, but depend on complex regulation of taxis by arrays of releasing stimuli (Chelazzi and Focardi, 1982; Underwood and Chapman, 1985). Some contributions, most on littorinids, demonstrate the dependence of photo- and geotaxis polarity on such external factors as hydration (Gowanloch and Hayes, 1926; Kristensen, 1965) and temperature (Bingham, 1972; Janssen, 1960; Bock and Johnson, 1957), but other physical and biological releasers may be involved as well. Endogenous reversing of taxis is suggested by observations of movements in such shuttlers as Nerita polita (Chelazzi, 1982), but while the internal rhythm of general motor activity has been demonstrated in some gastropods (Zann, 1963b; Rohde and Sandland, 1976) the endogenous control of cyclic reversing in photo- and geotaxis polarity is a field open to future research.

Homing mechanisms. Three sets of orienting cues have been suggested to be involved in the homing of chitons and gastropods: internal to the animal (Pierou, 1909), pertaining to the macrosystem (Bohn, 1909) or related to the microsystem onto which the animal moves. Once discarded the importance of idiotiochic mechanisms, and of path-integration based on gravity or sun (Cook, 1959), two possible mechanisms of piloting by local information have remained: memotaxis, i.e. memorization of micro-landmarks intrinsic to the substrate, and trail following. The memotaxis hypothesis (Ohgushi, 1955; Thorpe, 1963; Galbraith, 1965; Jessee, 1968) rises where trail following falls and no direct proof of its validity has been obtained. On the contrary, evidence in support of trail following in solitary (Funke, 1968; Cook et al., 1969; Chelazzi et al., 1987) and collective homers (Lowe and Turner, 1976; Gilly and Swenson, 1978; Trott and Dimock, 1978; Raftery, 1983; Chelazzi et al., 1985) is solid, but incomplete according to some authors.

The following observations are usually reported as disproving the unique importance of trail following in the homing of intertidal chitons and gastropods: 1) in some homer species the return and outgoing paths during each feeding loop do not overlap (Beckett, 1968; Cook et al., 1969; Thomas,
1973); ii) some chitons and limpets passively displaced from their scars are nonetheless able to home (Thorne, 1968; Cook, 1969); iii) different methods of trail interruption — including rock chiselling, brushing, or washing with various chemicals — fail sometimes to extinguish the homing performance (Calbraith, 1965; Jesse, 1968; Cook et al., 1969). But the first two counter-proofs fail by admitting that the trail associated information is long lasting and that animals are able to detect a previous, old trail. In fact, there is increasing evidence that this is true in siphonarid limpets (Cook, 1969; 1971) and in neritids (Chelazzi et al., 1985). Concerning the third point, it is interesting what has been observed in the opisthobranch \textit{Onchidium verruculatum} (Mcfarlane, 1980, 1981) and in the chiton \textit{Acanthopleura gemmata} (Chelazzi et al., 1987): upon reaching the experimental trail interruption these animals perform explorative movements which allow them to re-contact the outward trail and home safely.

**Trail associated orienting cues.** Although these considerations strongly support the importance of trail following in the homing of chitons and gastropods, the nature of orienting cues contained in their trails and the actual orientation mechanism are still unknown. Cook (1971) quotes three possibilities: radular scrapings on the algal cover; textural discontinuities provided by the mucus; attached or diffusible chemicals. Many authors favour the chemical hypothesis and Funke (1968) admits also that a complex chemical "footprint" is left by \textit{Patella vulgata} in the scar, in order to correctly orientate while resting. Contact chemoreception using pedal receptors has been claimed for \textit{Ilyanassa obsolenta} (Trott and Dimock, 1978), while the cephalic tentacles would be sensitive to trail associated chemicals in littorinids (Peters, 1964; Hall, 1973). Raftery (1983) maintains that chemical information could be important in \textit{Littorina planaxis}, but in his opinion physical properties cannot be ruled out. On the other hand, Bretz and Dimock (1983), on the basis of one of the most complete surveys of trail cues in gastropods, conclude that \textit{Ilyanassa obsolenta} uses mechanical information (textural properties of the mucus) and not such chemicals as proteins. But in a similar analysis, performed on the freshwater snail \textit{ Biomphalaria glabrata}, Bousfield et al., (1981) reached the opposite conclusion that "chemical, as opposed to physical factors, play a dominant role in trail following behaviour". The physical hypothesis is indirectly supported by the observation of micro- and macro-pattern of the mucus trail of gastropods (Cook, 1971; Bretz and Dimock, 1983; Stirling and Hamilton, 1986). But chemical content of the trail is even more complex, including such different classes of light and heavy molecules as free aminoacids, lipids, carbohydrates, free proteins and glycoproteins (Wilson, 1968; Hunt, 1970; Grenon and Walker, 1980, Bretz and Dimock, 1983). Future research must proceed both ways but chemical hypothesis seems more attractive upon recognition that the trail associated information is complex, including individual cues and polarity.

**Trail individuality.** Collective refugio species are expected to release and follow non-individual trails for homing. In fact this is the case for \textit{Ilyanassa obsolenta} (Trott and Dimock, 1978) and \textit{Nerita textillis} (Chelazzi et al., 1985). 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. Some widely quoted experiments of Funke (1968) show discrimination between personal and conspecific trails in \textit{Patella vulgata} and the same is true for \textit{Onchidium verruculatum} (Mcfarlane, 1980). Cross-trailing tests in \textit{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. Nevertheless, other solitary-homers such as \textit{Patella vulgata} (Cook et al., 1969) and \textit{Siphoaria alternata} (Cook, 1971) if transplanted onto conspecific trails do follow them up to the scar. The
possibility remains that in these species trail contains both individual- and species-specific information, but in some cases the normal recognition of own trail during the homing could be based on mechanisms external to the trail, such as memorization of the direction taken during the outward journey.

**Trail polarity.** That trail following is not performed at random concerning polarity has been documented in many gastropods (Stirling and Hamilton, 1986). When central place foraging is combined with zonal shuttling as in Nerita textile (Chelazzi et al., 1985), correct following may be due to directional mechanisms based on cues external to the trail. Nevertheless, some experiments have ruled out the possibility that polarized trail following is based on such external cues as light or gravity (Cook and Cook, 1975), but the intrinsic mechanisms involved in polarized trail following have not been discovered. Cook (1971) speculates four hypotheses for this capacity in siphonarid limpets: i) chemical macro-gradient along the trail; ii) polarized sequence of different chemicals; iii) polarized physical structure of the trail; iv) differential friction upon retracing the trail in the two opposite directions. Stirling and Hamilton (1986) listed three more: v) chemical micro-gradient; vi) bilateral asymmetry in chemical or physical properties of the trail; vii) differential light reflection in the two opposite directions of the trail. By excluding other mechanisms, the last Authors conclude that a micro-structural polarization of trail is possibly detected by Littorina irrorata. This agrees with the findings of Breetz and Dimock (1983) on Lyanassä obsolata, but contrasts those of Gilly and Swenson (1978) who claimed the importance of a chemical macro-gradient as polarity mechanism in Littorina sitkana and L. littorea. Finally, Cook and Cook (1975) obtained the interesting evidence that in Siphonaria alternata trail polarity is lost after retracing.

**Trail complexity and multiple use of trail following.** That trail following may be used by intertidal gastropods in functional contexts different from homing, such as prey location (Gonor, 1965; Snyder and Snyder, 1971) and mate searching (Hirano and Inaba, 1980) is well known, but in the context of central place foraging it has been usually regarded as a homing mechanism. Recent findings demonstrate that this is an oversimplified view. That homing gastropods and chitons may discriminate between outgoing and return trail has been argued by McFarlane (1981) for Onchidium verruculatum, and by Chelazzi et al., (1987) for the chiton Acanthopleura gemmata. In O. verruculatum displacement tests lead to the conclusion that outward and return trails have different information content. Field observations using LED tracking showed that A. gemmata, besides performing the usual homing-related following of own trail, may reach the feeding place by following its own trail released on the previous night. What is worthy is that where the outward and return trails of the previous night do not overlap, the animal counter-follows the return one. This may be based on a different information content of the two branches as in O. verruculatum, or on the intrinsic polarization of the trail.

Whatever the discrimination mechanisms are, the ecological importance of this foodward auto-trailing is evident, allowing the animal to optimize the exploitation of algal grounds. In fact the foodward trail following is not as deterministic as the homeward one. We have hypothesized (Chelazzi et al., 1987) that the amount of foodward trail following may depend on the quality of return trail, which in turn may depend upon the quantity or quality of ingested food. In the same species there is also preliminary evidence for inter-individual trail following in the retrieval of the feeding grounds (Chelazzi et al., 1987), which is tuned at minimal levels thus avoiding local overexploitation of algal patches. In this case communication via trail following may represent a mechanism of ecological regulation for the whole population.
These aspects of chitons' behaviour deserve further work and the study on these particular topics must be extended to intertidal gastropods as well. Nonetheless, they suggest that the trail is a complex eternal memory of multiple ecological significance, which may regulate the different aspects of central place foraging in intertidal molluscs. Besides ants, where trail following play a major role in controlling the ecological relationships of the population, intertidal chitons and gastropods may represent a second study case for this important class of problems in behavioural ecology.

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