

CHEMORECEPTION, ODOR LANDSCAPES, AND FORAGING IN ANCIENT MARINE LANDSCAPES

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ABSTRACT

For many organisms, chemoreception is critical for activities such as foraging, the detection of potential mates, and the avoidance of possible predators. The spatial pattern of odors, the odor landscape, is a function of the distribution of the odor sources and of fluid dynamics. Microscopic organisms, and probably most infaunal organisms, are in a physical realm where the detection of distant odor sources is controlled by diffusion and movement that takes place in response to chemical gradients. For larger organisms, chemical detection of distant sources is largely controlled by turbulence and thus by spatially and temporally complex odor plumes.

An individual-based, spatially explicit movement model allows the examination of the importance of contact and distant chemoreception for foraging movements in spatially heterogeneous and patchy environments. Gain curves allow the importance of sensory range in settings of differing degrees of patchiness to be compared. As patchiness increases, distant chemoreception becomes increasingly important for efficient foraging.

Movement patterns within patches are different from those between patches. The spatial distribution of resources, therefore, should be a major control of trace geometry.

During the Ediacaran-Cambrian interval, the spatial complexity and patchiness of the marine odor landscape may have increased due to disruption of Neoproterozoic-style microbially bound substrates and the packaging of biomass into spatially discrete carcasses and fecal pellets. At the same time, larger and non-infaunal mobile bilaterians would have entered a fluid regime dominated by turbulence. These changes may be partially responsible for the evolution of external bilateral sensory organs.

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INTRODUCTION

Many studies of animal behavior and ecology

implicitly presume that metazoans possess the ability to obtain, process, retain, and act upon information about the spatial properties of their environ-

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ment, including the presence and location of resources, potential mates or competitors, and possible predators. For example, the habitat selection models described by Pulliam and Danielson (1991) assume that individuals are capable of finding the best available site among an array of choices.

In particular, foraging theory seeks to predict an animal's behavioral choices, based on its knowledge of resource availability, competition, and predation risk (Kramer 2001; Leighton, 2002; Koy and Plotnick 2007). Foragers are hypothesized to continuously compare the net energy gains and costs of continuing to forage in a currently exploited patch with those associated with searching for or moving to another patch. The resulting movements, and the potential corresponding traces, are largely a consequence of interplay of the spatial structure of the environment and the organism's ability to perceive this structure. Foraging traces, as used here, are produced both by exploiting a patch and by locating and moving to a new patch (i.e., they could include both repichnia and pas-cichnia).

Although vision is important in many organisms, the principal means by which marine animals of all sizes obtain this information is through chemoreception (Phillips 1978; Weissburg 2000; Riordan and Lindsay 2002). The detection of chemicals, their discrimination, and the behavioral reactions they evoke may well be the most primitive of all activities of living organisms.

Recent molecular and neurobiological studies of chemoreception have identified striking similarities in the cellular and neurobiological mechanisms of odor detection and transduction in diverse metazoan taxa, including vertebrates, arthropods, terrestrial gastropods, echinoids, and nematodes (Hildebrand and Shepard 1997; Eisthen 2002; Gaillard et al. 2004; Ache and Young 2005; Raible et al. 2006). These similarities include the functional anatomy of olfactory receptor (OR) neurons, the use of G protein-coupled receptors with seven membrane spanning domains as odorant receptors, the pathways used for olfactory signal transduction, and the nature of odor coding by receptors.

Chemoreception can be divided into contact chemoreception (also called: near-field, gustatory, or taste), in which the organism is in direct physical contact with the source of the chemicals, and distant chemoreception (also called: far-field, olfactory, smell), where chemicals (odorants) are transported through a medium to the chemosen-

sory cells. For example, asteroids may use distant chemoreception to locate and discriminate among food sources (Brewer and Konar 2005; Thompson et al. 2005), but also employ contact chemoreception for choosing among prey items (Beddingfield and McClintock 1993). Similarly, sessile deposit feeding spionid polychaetes respond both to dissolved chemicals and to chemicals bound to particle surfaces (Riordan and Lindsay 2002).

The spatial pattern of odor distribution has been termed the "odor landscape" (Atema 1996; Moore and Crimaldi 2004). Chemicals produced by odor sources, usually due to the metabolic activities of organisms, are transported and mixed by diffusion and turbulent fluid movement. The concentrations of odorants that reach chemoreceptors depend both on the location of these sources and the nature of fluid flow between the sources and the sensing organism.

Studies of the fluid biomechanics of chemoreception have shown that scale is clearly important in how organisms perceive and move within odor landscapes (Ache and Young 2005; Moore and Crimaldi 2004; Koehl 2006). In general, microscopic organisms are in a physical realm where the odor landscape is relatively simple; resource detection and body movement are controlled by diffusion and viscosity. They react only to changes in concentration gradients experienced over time (Fenchel 2002) and move their entire bodies to detect changes in concentrations. For example, the bacterium *E. coli* moves through a combination of straight-line "runs" and random "tumbles," with tumbles producing a slight bias in the forward direction (Berg 2000). By increasing the length of runs, the cell can move up a chemical gradient. Smaller protozoa show similar behavior (Blackburn and Fenchel 1999). Small and simple organisms also usually have "taste" and "smell" combined, rather than separate as in more complex organisms (Ache and Young 2005).

In contrast, larger organisms, such as lobsters or snails, are in a physical realm where chemical detection and movement are controlled by turbulence and thus by spatially and temporally complex odor plumes. The "odor landscape" at these scales is thus complex and dynamic (Atema 1996; Moore and Crimaldi 2004), with odor sources potentially being located at a considerable distance from the organism. Organisms generally react to changes in concentration over space, using sensory organs that are often bilateral and are moved to detect changes in concentrations in the odor plumes and

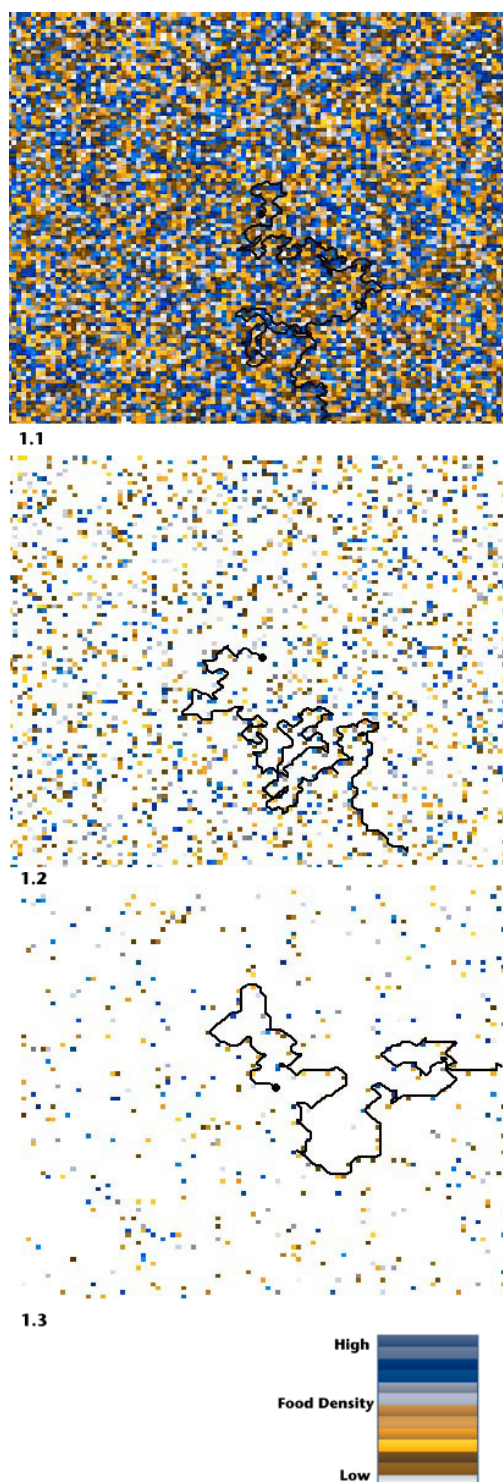


Figure 1. Simulations were run on 100 x 100 two-dimensional square lattices (maps). Map types were 1.1:: all nodes containing resource (continuous), 1.2: 20% of nodes occupied, and 1.3: 5% of nodes occupied. Node occupation sites were chosen randomly; resource per node varied randomly from 0.00 to 1.00 (color legend). Representative movement trails are shown on each map ($R = 4$, no currents).

to increase the rate of fluid flow past them (Webster et al. 2001).

Although little studied, it is likely that the odor landscape for mobile infaunal organisms is also dominated by movement within chemical gradients, since they are not exposed to turbulent flow conditions. Movement in chemical gradients by the soil nematode *C. elegans* is characterized by straight runs and reorienting turns (Pierce-Shimomura et al. 1999). As in bacteria, the number of turns decreases as an animal moves up a gradient. Experiments with spionids by Riordan and Lindsay (2002) also suggest that contact chemoreception with sediment particles is important for infaunal forms.

In this paper, I describe a simulation model for foraging that demonstrates the importance of distant chemoreception in spatially complex and patchy environments. These results are then discussed in the context of changes in environmental complexity and animal evolution associated with the Ediacaran-Cambrian transition.

MODEL DESCRIPTION

The model TraceFossil is a form of “individual based model” (IBM) in which autonomous simulated animals make decisions based on spatially explicit aspects of their environment (Grimm and Railsback 2005). These models are widely used in wildlife ecology, urban planning, and other fields, where they are frequently termed “agent models.”

TraceFossil is based on the model first used in Plotnick (2003) and is described in more detail in Koy and Plotnick (2007), which focused on patterns of movement within patches as a consequence of contact chemoreception. The latter paper discussed simulated movement patterns that were the consequence of different spatial distributions of resources within patches and resembled many random, spiral, and meandering traces. The current paper examines movements among patches, rather than movement within patches. The primary focus is on the importance of distance chemoreception to locating spatially isolated resource sites.

Space in TraceFossil is represented as a two-dimensional (2-D) or three-dimensional (3-D) square lattice. The distribution of resources in the space is represented as real numbers, ranging from 0.00 to 1.00, assigned to each node in the lattice. The model provides numerous options for the spatial distribution of these resources. This paper focuses on 2-D patterns, which simulate spatial distributions at or parallel to the sediment-water

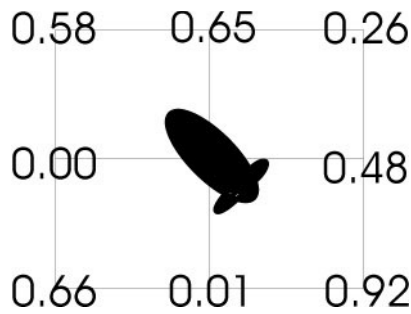


Figure 2. Contact chemotaxis algorithm. Each surrounding node has a resource value ranging from 0.00 to 1.00. Organism moves toward the node having the highest value (“southeast”).

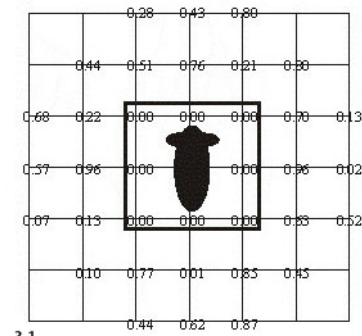
interface with different degrees of patchiness. A later paper will consider movements in three dimensions.

In the simplest case, all nodes have some level of resource chosen from an even random distribution (Figure 1.1); i.e., the resources are heterogeneous but not patchy. In the remaining cases, the level of resources at each node is again selected from an even distribution but a fixed proportion of nodes are randomly set to zero. This produces a pattern of isolated resource patches of random size and shape; the greater the proportion of the nodes set to zero, the greater the patchiness of the resource distribution. A map showing a pattern where 95% of the nodes are empty is shown in Figure 1.3.

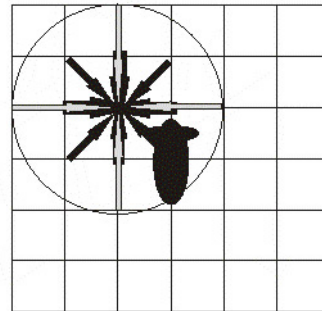
Each node releases a chemical signal proportional to the amount of resource it contains. Detection of the signal can be either through contact or distant chemoreception. The node containing the organism is at zero; that is, all its resources are assumed to have been consumed.

For contact chemoreception, the animal is in direct contact with the adjacent eight nodes (Figure 2). The chemical signal S_{contact} detected at a node is assumed to be linear with the amount of resource at each node.

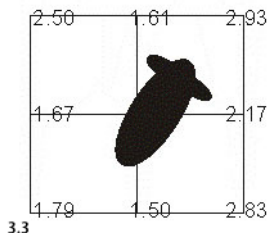
Distant chemoreception is modeled by assuming that each of the eight adjacent nodes (Figure 3.1) receives a summed chemical signal from N neighborhood sites that are within a defined distance R and that the organism can sense the relative signal in each of those neighboring sites. In Figure 3.2, the signal in each adjacent node comes from the $N = 12$ sites within $R = 2$; arrows represent the signal from some of these cells. A total of 34 sites are within the chemosensory range of the organism (Figure 3.1). The signal from each of



3.1



3.2



3.3

Figure 3. Distant chemotaxis algorithm. 3.1. Organism shown in center of an area of the lattice, each value indicates the amount of resource present at each node. The box indicates the area within which a waterborne signal can be directly detected. Numbered nodes are within the “detection range” of the organism. 3.2. Sources of summed chemical signal at location “northwest” of organism, assuming no net current direction. Thickness of arrows represents attenuation with distance D . 3.3. Signal at each location at which the waterborne signal is detected; assuming $1/D^2$ attenuation. Organism moves in the direction of the greatest signal (“northeast”).

these more distant cells is a function of the amount of resource it contains and attenuation due to distance (width of the arrows in Figure 3.2); that is, a nearby cell with less resource can produce more detectable chemicals than a more distant cell with greater resources.

Specifically, the signal S_{dist} in one of the eight adjacent cells can be written as:

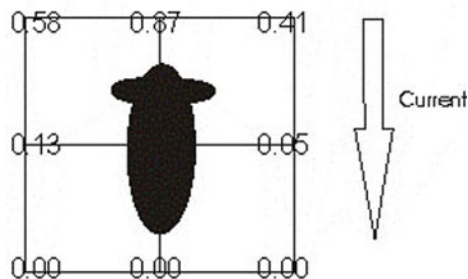


Figure 4. Distant chemotaxis algorithm, modified for directional currents. Only nodes directly upstream (“north”) contribute to the received signal. Organism moves upcurrent; i.e., rheotaxis.

$$S_{dist} = \sum_{i=1}^N s_i a(d_i)$$

where s_i is the amount of resource in the i th node within the neighborhood and $a(d_i)$ is the signal received from that node as a function of its distance. The algorithm postulates that the chemical signals become mixed as they approach the animal. The simulated organism cannot determine directly where a node with the greatest amount of resource is located; instead it can only determine in what direction the greatest and/or closest concentrations exist.

The higher the value of R , the more likely the simulated organism is to detect distant resources; it is a proxy for the detection range of the organism. However, because the number of cells N included increases proportional to R^2 , this number rapidly becomes very large. In addition, due to attenuation the contribution from distant nodes is very small. For these reasons, the maximum value of R utilized was 7 in nearly all cases.

Several functions are available in TraceFossil to represent signal attenuation; they are designed to include a wide range of realistic representations of chemical dispersal. The functions are based on those used to model seed dispersal by Plotnick and Gardner (2002) and are fully described therein. In this paper, attenuation is assumed to be a function of the inverse square root of distance; e.g., doubling the distance decreases the signal received by 25%. Using this function, the signal distribution detected by the example organism is shown in Figure 3.3.

Simulations with a circular neighborhood represent situations with little or no directional current. Currents are easily represented, however, by setting the attenuation functions for sites in certain

directions to zero. This is equivalent to restricting the neighborhood to only those sites lying in a particular direction. For example, in Figure 4, the nodes contain a signal only from the sites directly “North” of it.

For the simulations described here, contact chemoreception has precedence over distant chemoreception; i.e., if an organism is in direct contact with a resource site, it will exploit it prior to searching for more distant resources.

During each step of a simulation, the organism:

1. Examines the eight adjacent nodes and the node with the highest value of $S_{contact}$ is determined.
2. If this maximum value is not zero, then the organism moves into the node with the maximum value and “ingests” the resource in that node, reducing its level to zero.
3. If the maximum value of $S_{contact}$ is zero, then all of the adjacent nodes are empty. The organism examines the eight adjacent nodes and finds the one with the highest value of S_{dist} . It then moves into that node.
4. If the maximum value of S_{dist} is zero, then there are no resources within the detection range of the organism. In that case, it moves one step in a random direction (another available option is to continue to move in the same direction as it did in the previous step).

The behavior described by this model is simple: the organism detects a chemical signal and moves in the direction of its highest value. If it encounters a food source, it ingests it. In other words, the only behaviors are chemotaxis and feeding. Examples of trails corresponding to the studied resource distributions are shown in Figures 1.1-1.3.

As with all models, there is an unavoidable trade-off of generality with specificity. It is not the goal of TraceFossil to reproduce the morphology of specific ichnotaxa (although it can potentially be modified to do so), but instead to act as a heuristic tool (sensu Hammer 1998) for understanding the behavioral and environmental control of trace-producing movements. Similarly, it is also recognized that additional factors, such as the presence of predators or substrate consistency, may also influence movement patterns (Phillips 1978). These factors will be included in subsequent versions of the model.

Table 1. Results of simulations. Simulated chemosensory behavior was no chemosensory ability, moving randomly (None) or in a straight line (Straight – single run); contact chemoreception only (Contact); contact and short-range distance chemoreception, range $R = 4$ (Short); contact and longer-range distance chemoreception, $R = 7$ (Long); contact and directional current (Current) Values are average and standard deviation of 10 runs for mean resource gained/step. For continuous maps, results were the same for all runs with chemoreception.

Map Type	Chemosensory Behavior	Mean Resource Gained Per Step	
		Mean	standard deviation
Continuous	None	0.253	0.031
	Straight	0.464	---
	Contact/Short/Long	0.759	0.000
20% Occupied	None	0.044	0.012
	Contact	0.171	0.040
	Short	0.360	0.013
	Long	0.354	0.000
5% Occupied	None	0.012	0.005
	Contact	0.036	0.014
	Short	0.139	0.029
	Long	0.184	0.016
	Currents ($R = 7$)	0.174	0.009
	Currents ($R = 10$)	0.189	0.000

Gain Curves

Gain curves are plots of cumulative amounts of resource harvested over time (Olsson et al. 2001). The shape of a gain curve should relate to a forager's decision when to abandon a food patch; i.e., a flattening of the gain curve may signal depletion of the patch. On a landscape scale, the shape of the gain curve gives a measure of the forager's ability to locate high quality patches. An organism with a greater ability to locate and discriminate among patches should have a steeper gain curve than an organism that accounts patches by chance or that does not distinguish poor from rich patches. This difference should become more pronounced as patchiness increases.

Gain curves, therefore, should discriminate among foraging model organisms with different ranges of sensory ability in environments of different degrees of patchiness.

Simulations

Three sets of simulations were run. Each set possessed a different amount of patchiness - Set 1: all sites randomly occupied by resource (Figure 1.1); Set 2: 20% of the sites randomly occupied by resources (Figure 1.2), for this map, the average nearest neighbor distance between occupied sites is 1.3; Set 3: 5% of the sites randomly occupied by resources (Figure 1.3), with a mean nearest neighbor distance of 2.3. The map generated for each

set was saved and reused. All maps were 100 x 100 pixels, resource values per node randomly ranged from 0.00 to 1.00, so that the average resource per node was 0.5.

Four "species" of digital organism were run on each map. Species A simply wandered randomly; it had no outside knowledge of the resource distribution. Species B possessed only contact chemoreception. Species C and D possessed both contact and distant chemoreception, but the detection range of C was $R = 4$ and for D it was $R = 7$. Average gain curves for 10 multiple runs were determined for each species and map combination.

Each run was initialized in the middle of the map. Runs were terminated when the digital organism's sensory range encountered the edge or after 200 steps. For each set of runs, the mean resource gained per step was determined (Table 1).

An additional set of runs was performed on the 5% map to evaluate the role of directional currents. For these runs, the signal attenuated linearly with distance and that the detection range was longer ($R = 7$ and $R = 10$). Only nodes to the northeast, north, and northwest contributed to the signal. The goal was to at least crudely mimic turbulent mixing upstream and the reduced attenuation associated with mass fluid transport. Because of the directionality of the current, the run was initialized at the bottom of the map.

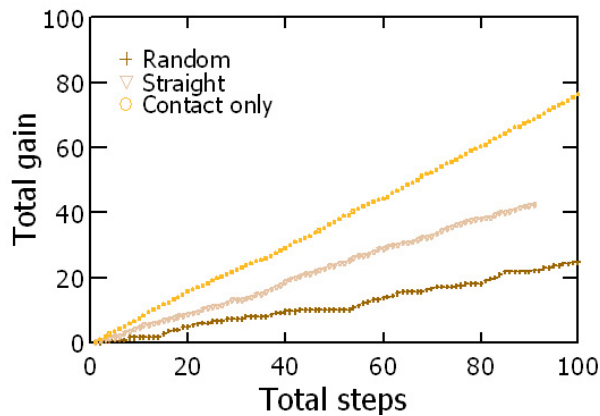


Figure 5. Gain curves for continuous random map (Figure 1.1). All chemotaxis simulations gave identical results; moving in a straight line is preferable to random movements, but less favorable than at least contact chemoreception.

RESULTS

The simulations show, not surprisingly, that even a little knowledge of the outside chemical environment is tremendously advantageous (Table 1, Figures 5-7). In all cases, contact chemoreception alone produced an approximately threefold increase in the amount of resource gained, as compared to “blind wandering.”

For comparison, an additional run was made on the set 1 (fully occupied) map. In this run, the organism followed a simple straight path. This is the case labeled “straight” in Table 1 and Figure 5. Moving in a straight path increases the gain per step over random movements because it does not revisit already harvested nodes.

What are more interesting are the relationships among contact and distant chemoreception and the patchiness of the map. In the case of a map where all nodes contained at least some resource, all runs with chemoreception produced exactly the same movement path (Figure 1.1), regardless of whether distant chemoreception was active. This was due to the organism never being out of direct contact with at least some resource. As discussed in Koy and Plotnick (2007) paths on resource distributions of this type will avoid crossing themselves (i.e., show “phobotaxis”), because they do not move to already exploited areas. Because the distribution of resources is essentially the same in all directions, movement choice is governed by information of variation on very local scales.

When resources become patchier (Figures 1.2 and 1.3) the advantage of some form of distant

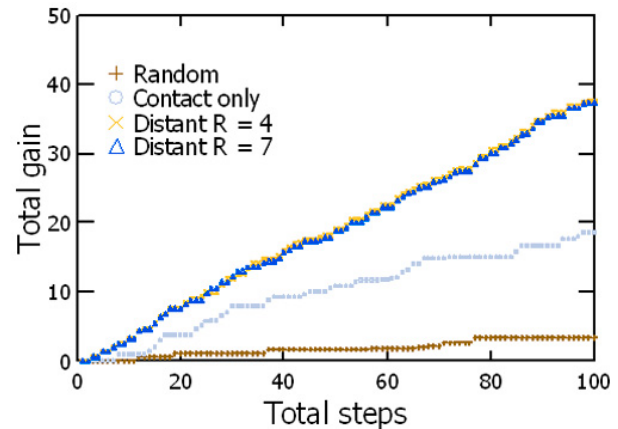


Figure 6. Gain curves for 20% occupied map. Rate of acquisition of resources is far more rapid for simulations with distant chemoreception.

chemoreception becomes clear. For the 20% occupied map, distant chemoreception produces a doubling of the average resource gained by step (Table 1, Figure 6). For the 5% occupied map, short range distant chemoreception ($R = 4$) nearly quadruples the gain rate, whereas longer range distant chemoreception ($R = 7$) increases it fivefold (Table 1, Figure 7).

Self-crossing is also infrequent on patchy resource maps. This is expected, since the simulated organisms will tend not to revisit regions that have already been harvested. When self-crossing does occur on the sparser maps, it is usually when the organism is out of sensory range of any resource and thus moves randomly in a small area.

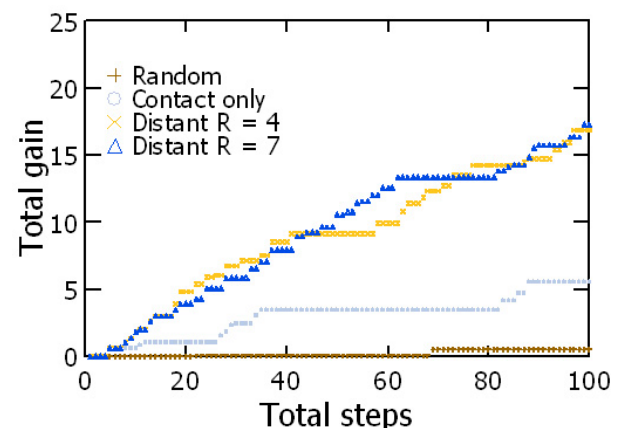
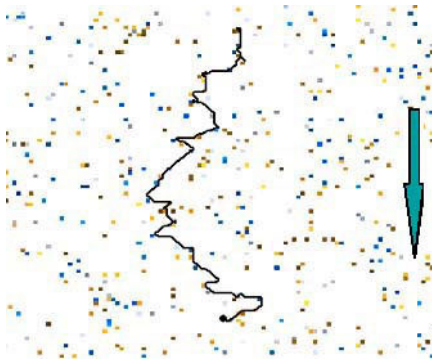
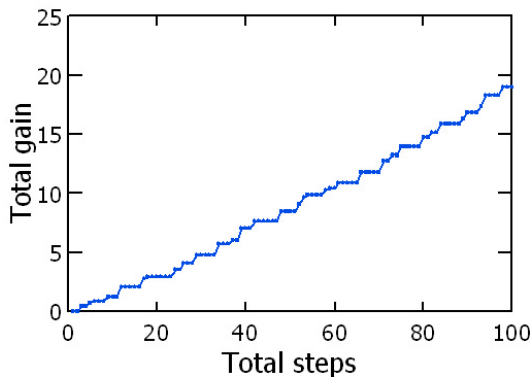


Figure 7. Gain curves for 5% occupied map. Rate of acquisition of resources is far more rapid for simulations with distant chemoreception. Lower detection ranges, by allowing some randomness in search, favor finding globally higher resource patches (see text).



8.1.



8.2

Figure 8. 8.1. Representative movement path on 5% occupied map, “currents” moving top to bottom; $R = 10$. 8.2. Corresponding gain curve.

Many runs on the 20% map produced higher gain curves for short-range chemoreception than for long-range. Similarly, some runs on the 5% map also produced higher gains, at least for short periods, for short-range over long-range.

This seeming conundrum can be understood by looking at the standard deviations of the mean resources gained at the end of the run. Every long-range run on the 20% map produced exactly the same path; because the detection-range was so long, it always located the “best” sites within this local range. Better sites in other parts of the map were missed. On the other hand, the shorter-range chemoreception produced a greater randomness to the search. As a result, parts of the map that had slightly higher levels of resource were encountered. Some randomness in a search may lead to greater efficiency of resource acquisition. This result is consistent with theoretical studies of search strategies during foraging (Viswanathan et al. 1999), which suggest random movements increase search efficiency when the desired objective is not in direct sight.



Figure 9. Change in movement pattern when encountering a patch. Shown here is part of a path on a fractal map (Koy and Plotnick 2007). The simulated animal switches from distant to contact chemoreception as it enters the patch from the left.

Introducing currents had only a minor effect on the search efficiency (Figure 8.2). The probability of detecting “upstream” sites was increased, but potentially better sites perpendicular to the current direction were missed.

DISCUSSION

Discussions of the behavior of trace fossils have generally hypothesized that movement patterns are “hard-wired,” e.g., they result from some innate set of behaviors. For example, Raup and Seilacher (1969) hypothesized that spiral and meandering trails resulted from a combination of phototaxis (avoidance of crossing a previous trail), thigmotaxis (staying close to older parts of the trail) and strophotaxis (periodic sharp turns). These movement patterns may instead result from simple chemotaxis interacting with heterogeneities of resource distribution and encounters with patch boundaries (Kitchell 1979; Koy and Plotnick 2006). If correct, phototaxis, strophotaxis, and thigmotaxis are thus consequences, and not the causes, of the observed movements.

The results for inter-patch behavior discussed here also support the importance of resource distributions as a major control of movement and thus of trace morphology. For example, Figure 9 illustrates a portion of the movement trail of a simulated organism approaching an isolated patch within which the distribution of resources is fractally distributed (Plotnick and Gardner 2003; Koy and Plotnick 2006). The relatively simple trace geometry outside of the patch becomes far more complicated within the patch.

The simulations also suggest that when resources are continuously distributed, only short-range detection (contact chemoreception) is necessary for efficient foraging in heterogeneous environments. As resource distributions become increasingly patchy, the advantage of possessing the ability to detect these resources at a distance

(distant chemoreception) becomes greater. As a result, there may be morphological and anatomical differences between organisms living in patchy vs. non-patchy settings.

These inferences have potential implications for our understanding of some of the biotic changes occurring during the Ediacaran-early Phanerozoic. During this interval there was a major increase in trace fossil diversity and complexity (Crimes and Fedonkin 1994; Jensen 2003; Droser et al. 2005). Re-analyses of taxa used in these analyses have indicated that many suggested Ediacaran trace fossils, in particular ones purportedly showing complex movement traces, are probably not traces (Droser et al 2005). Nearly all traces currently accepted as valid are small and simple meandering horizontal forms and are presumed to have formed at or near the sediment water interface within or just below microbial mats (Jensen 2003).

Gehling et al. (2005) discussed a conceptual model for feeding on biomats by the larger possible bilaterian *Dickinsonia*, based on preserved traces, which suggest movement to immediately adjacent areas (Fedonkin 2003). In their scenario, *Dickinsonia* absorbed nutrients over its ventral surface. When an area was fully exploited, the organism shifted to exploit the neighboring area. This behavior would have required contact chemoreception only.

In addition, conceptual models and some data also suggest a general increase in mobile bilaterian body size over this interval (Valentine 2002; Novack-Gottshall 2005). Typical body widths suggested by Ediacaran trace fossils are on the order of millimeters (Jensen 2003); Cambrian bilaterians are clearly much larger. An increase in body size, as well as shift from grazing under biomats to foraging over the substrate, would have changed the relevant fluid mechanical environment from one dominated by diffusion to one dominated by convection.

Another change is in the nature of sense organs. As most recently pointed by Marshall (2006), Ediacaran body fossils show a noticeable lack of macroscopic sensory organs of any kind. This is in contrast with the presence of organs such as eyes and antennae in Cambrian animals, in particular the early arthropods.

Finally, there are possible changes in substrate heterogeneity associated with the "agronomic revolution" or "substrate revolution" concept originally proposed by Seilacher and Pflüger (1994), Seilacher (1999), and expanded by Bottjer

et al. (2000). In this concept, matground environments offered relatively low spatial patchiness at scales relevant to the earliest benthic bilaterians. With resources more-or-less continuously distributed, contact chemoreception and accompanying relatively simple movement patterns were appropriate for effective resource exploitation.

The advent of burrowing greatly increased the spatial complexity of the sea floor (Meysman *et al* 2006). The previously extensive subtidal mats became disrupted by bioturbation, scarcer, and perhaps much patchier. Modern supratidal mats described by Hagadorn and Bottjer (1999) are patchy. Resource patchiness was further increased by the advent of macroscopic bilaterians. These would produce spatially discrete carcasses and fecal pellets (McIlroy and Logan 1999). The advent of higher trophic levels likely enhanced spatial resource heterogeneities by producing patches of higher quality food (Bengston 2002). Taken together, this suggests that the spatial heterogeneity of biomass distribution in the benthic environment rapidly increased in the early Paleozoic. Resource distributions became increasingly patchy with an increase in the range of resource concentrations.

As spatial heterogeneity increased, there should have been concomitant changes in the foraging responses of the animals. These changes would be a direct consequence of the increased patchiness and, most probably, of increased rates of predation (Bengston 2002; Dzik 2005). With the increase in patchiness and heterogeneity, the complexity of movement patterns between and within resource patches increased, and thus trace fossil diversity increased. The Cambrian growth of trace fossil diversity, therefore, may be part of a larger cascade within the evolving biosphere (McIlroy and Logan 1999; Bengston 2002; Marshall 2006).

In sum, the critical innovations that would have led to optimal foraging by early mobile marine organisms in an environment of increasing patchiness are directly related to an organism's abilities to obtain, process, and retain information about the spatial properties of its environment, similar to a conclusion reached by Hammer (1998). Selection would have favored the evolution of mechanisms for obtaining the location and richness of resources both close by and at a distance and for the assessment of predation risk. Such mechanisms include chemosensory organs such as the antennae of trilobites and other arthropods and the osphradia of molluscs, and the apparently polyphyletic evolution of complex eyes (Fernald 2004; Nilsson 2005).

These ideas are admittedly speculative and await further analysis and testing.

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