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TAXES IN CELLULAR ECOLOGY

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"Nothing is certain but death and taxes." — B. Franklin

Ecological aspects of chemotaxis in microorganisms has been reviewed by Chet and Mitchell (1976). More recently Carlile (1980) surveyed the implications for microbial ecology of various taxes and tropisms. Considerable material on ecological implications can be found in Levandowsky and Hauser's (1978) review of chemosensory responses in algae and protozoa, while the review by Lapidus and Levandowsky (1981) covers mathematical developments connected with microbial chemotaxis on cellular and population levels. These articles provide an excellent background to the present discussion. Thus, on occasion detailed references will not be cited for various points, when these can be found in the reviews just cited.

Here we shall concentrate on the ecological implications of various kinds of taxes, with emphasis on the possible contribution of theoretical developments. We will include within our purview not only true one-celled microorganisms (and perhaps other small creatures) but also the interaction of cell populations in developing and mature higher organisms.

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The Ubiquity of Taxes

We will define a taxis loosely, in accord with much common usage, as the tendency of an organism to move toward or away from some stimulus. Since the classical work of Frankel and Gunn (1940) many authors have taken pains to give precise definitions to different types of directed motions, but we shall not pursue this matter here.

Chemotaxis is perhaps the most studied variety of taxis. See for example Gerisch's (1982) survey of chemotaxis in the cellular slime mold Dictystelium discoideum. Other common types are phototaxis, thermotaxis, and aerotaxis. Carlile (1980), for example, mentions more exotic varieties such as galvanotaxis (response to electric currents), negative geotaxis (tendency to swim upward), electrotaxis (response to electric fields), rheotaxis (upstream swimming), viscotaxis (tendency to move into regions of high viscosity) and attraction by vibrations (vibrataxis?).

We conjecture that any motile organism is tactic to at least one stimulus. Once motility has evolved, it seems reasonable to suppose that many mutants will arise in which the motility is somewhat altered by certain agents, and that in some cases such alterations will benefit the organism and so will become fixed in the population.

Some Ecological Functions of Taxes

Although it may be difficult to provide conclusive demonstrations, many taxes seem to have fairly clear ecological functions. For example, positive and negative aero- and phototaxes are among the influences that presumably direct organisms to favorable physical environments. Sensory cues appear to guide sessile organisms to settling sites, or may lead parasites to particular hosts [as in the chemotactic migration of trematode miracidia to its intermediate snail host mentioned by Mansour (1979)] or even particular locations within particular hosts. A medically important illustration is the demonstration that Vibrio cholerae is strongly chemotactic toward mucosal surfaces, and that this enhances colonization success (Freter, O'Brien, and Macsai 1979).

The use of taxes to lead organisms to their food can be exemplified by the chemotactic responses of the common marine bacterium Vibrio alginolyticus to material released by algae (Sjoblad and Mitchell 1979), for extracellular algal material serves as nutrient for bacteria. Dictyostelium amoebae are probably attracted to their bacterial prey by means of chemotaxis to a bacterial secretion, folic acid (Gerisch 1982).

Dictyostelium can also serve as an example of the role of taxes in sexual development, for they are attracted by immature macrocysts. A more classical example is "the chemotaxis of the male gametes of Allomyces, which occurs in response to sirenin emitted by the female gametangia and gametes but to no other compound, (and) can only have a role of fertilisation" (Carlile 1980). In discussing chemotaxis of the spermatazoa of Muggiaea kochi (a type of siphonophore) Boon (1983) makes an order of magnitude estimate which indicates that the accumulating sperm have an appreciable stirring effect, thereby enhancing the spread of the putative attractant and facilitating further aggregation.

The functions of some of the more unusual taxes remain speculative. For example Maugh (1982) reports the hypothesis of R.P. Blakemore and R.B. Frankel that *magnetotaxis* along field lines helps marine bacteria locate the oxygen-depleted sediments where they flourish. In support of this notion they found that in the northern (southern) hemisphere the bacteria are predominately north (south) seeking, which indeed guides both sets of microorganisms toward the bottom. In the region of the magnetic equator the field lines are roughly parallel to the bottom, and here there are roughly equal numbers of north and south-seeking magnetotactic bacteria. It is conjectured that in this case magnetotaxis might help bacteria remain in the sediment once they have arrived there.

Particularly exotically named is *necrotaxis*, the tendency of certain white cells to move toward dead blood cells as a prelude to eating the corpses. Hu and Barnes (1970) provide a simple theory for necrotaxis, enabling certain parameter estimates to be made. The theory is subsumed in the works of Lauffenberger and his associates, to be mentioned below. What is relevant at this point is a first illustration of another reason for taxis by isolated cells. In one sense, the taxis provides preferential motion in the direction of food, but there is also a larger consideration, the survival of the organism of which the cell in question is a part.

Equations for Population Taxis

Phenomenological equations for population chemotaxis were put forward by Keller and Segel (1970). A more fully explained phenomenological derivation is given in the book edited by Segel (1980), Section 6.5. The equations were also derived from various models for individual cell behavior by investigators such as Patlak (1953), Segel (1977) and Alt (1980). For certain models corrections to the original phenomenological equations are required. In some cases measurements show the corrections to be negligible (Rothman and Lauffenburger, 1982).

The phenomenological derivation is based on the fundamental conservation equation for the population density b of the microorganism:

$$\partial b/\partial t = -\nabla \cdot J + Q \,. \qquad (1)$$

The two terms on the right side provide contributions to the change in b that arise respectively from net flux J into a volume element, and net birth rate Q. If the motion is completely random then one expects a flux of the form

$$J = J_{\text{random}} = -\mu \nabla b \,. \qquad (2)$$

The combination of (1) and (2) yields the usual diffusion equation, with the addition of the net creation term Q. The "motility" μ is a diffusion coefficient that can be estimated for microorganisms by simple experiments (Segel, Chet and Hennis, 1977). Effects of (1) and (2) with non-constant μ (when $Q = 0$) have been examined by Lapidus (1980a).

If there is an attractant of density c, one expects an additional chemotactic flux that is proportional to the gradient of c (for sufficiently small fluxes):

$$J = J_{\text{random}} + J_{\text{chemotactic}}, \quad J_{\text{chemotactic}} = \chi b \nabla c \; . \tag{3a,b}$$

For a given gradient of c, the flux should be proportional to the local density of microorganisms, when the density is sufficiently small. This explains the presence of the factor b in (3b). The chemotactic sensitivity χ measures the intrinsic response of a bacterium to a given gradient. Sometimes the chemotactic flux is written

$$J_{\text{chemotactic}} = Vb \tag{4}$$

where V is a drift velocity, annalogous to convection. It should be borne in mind that $V = \chi \nabla c$ and so combines the effects of the environment (∇c) and of cellular behavior (χ).

A fairly general equation for the attractant concentration includes the possibilities (i) that attractant is consumed at a rate $r(c)$ per cell, (ii) that there is a net production of c by chemical reaction at rate $k(c)$, and (iii) that the attractant diffuses with diffusivity D (assumed constant for simplicity). These considerations lead to the following phenomenological equations for gross changes due to chemotaxis:

$$\partial b/\partial t = \nabla \cdot [\mu(c) \nabla b - \chi(c) b \nabla c] + Q \; , \tag{5a}$$

$$\partial c/\partial t = -br(c) + k(c) + D \nabla^2 c \; . \tag{5b}$$

There is a mild controversy as to the correct form of equation to use when the motility μ is not constant. Our remarks on this matter will provide views that may perhaps be regarded as in opposition to those of Lapidus and Levandowsky (1981) but it is better to think of them as an attempt to clarify the issues.

In discussing the random flux Lapidus and Levandowsky (1981) state that "to the extent that the motion of each cell is a random walk, with no interactions with other cells and no response to external sensory cues, ...the appropriate continuous expression" (in our notation) for the flux J is

$$J = -\nabla \cdot (\mu b) \; . \tag{6}$$

This assertion is backed up by a (completely correct) derivation where a diffusion limit is taken of a random walk with a probability of moving from a given point that is a given function of a spatial variable x. The word "from" has been emphasized (and it was not by Lapidus and Levandowsky 1981) for the results would be quite different if it were replaced by "to". Indeed, Skellam (1951) pointed out some years ago that (6) results from an unbiased walk where the probability of taking a step depends on conditions at the beginning of a step while the commonly used diffusive flux (2) is appropriate where conditions at the termination of a step determine the probability of moving.

There is no dispute as to the correct diffusion limit of a given biased random walk model. What remains is a difference in taste as to the most revealing way to arrange the terms. Lapidus and Levandowsky (1981) prefer to call (6) a random flux because it arises wholly "from differences in the isotropic motility at neighboring points of space". They reserve the notion of a drift for situations where at a given point there are different probabilities for motions in different directions. My view is that more understanding is gained if (6) is expanded to

$$J = -\mu \nabla b + bV, \quad V = -\nabla \mu \; . \tag{7}$$

The term $-\mu \nabla b$ is an isotropic flux, which is the same whether or not steps are influenced by conditions at their onset or their termination. The remaining term bV is an effective drift, indeed not brought about by intrinsic directional preferences at point x, but rather due to spatial differences in the vigor of random motion. For example, there will be a net drift in the positive x direction if organisms move randomly but with decreasing vigor as x increases ($d\mu/dx < 0$) — because of smaller "steps" or more time between "steps".

A contribution to the drift velocity V can of course arise from fluid convection -- see the experimental study by Walsh and Mitchell and the related theoretical discussion, using (5), by Lapidus (1980b).

The phenomenological chemotaxis equation (5a) is expected to be valid only when (i) cell and nutrient densities are not high enough to promote interference effects, (ii) the gradients of these densities are small enough to permit linearization, and (iii) longer range effects are negligible so that higher derivative terms can be neglected. With respect to (i), Fu et al (1982) conclude that cell interactions are in fact important in their experiments on combined thermo- and chemotaxis in leukocytes. Relevant to (ii) are experiments by Dahlquist, Elwell and Lovely (1976) on the chemotaxis of Salmonella typhimurium to L. serine. These authors found that the drift velocity V could be related to the attractant gradient ∇c by an expression of the form

$$V = V_{max} \nabla c/(K + \nabla c) ,$$

where $V_{max} = 7\mu/\mathrm{sec}$ and $K = 0.25\mathrm{mm}^{-1}$. According to these measurements, our assumption of proportionality between the drift velocity and the gradient ($V = \chi\nabla c$) is suitable for situations in which the attractant concentration takes somewhat more than one centimeter to double.

Two other effects limit the accuracy of the chemotaxis equation (5a). One is that "memory" must be sufficiently short; otherwise the flux cannot be explicitly given as in (3), but instead requires an integration over past history (Segel 1977). A second restriction is that members of the population must behave sufficiently similarly (Segel and Jackson 1973). In this connection it has been found (Koshland 1978) that "a bacterial culture that is genetically homogeneous and grown in homogeneous nutrient conditions nevertheless produces characteristically different individuals" in that they retain individual adaptations to pulses of chemoattractant. No estimates have been made as to whether the error in (5a) induced by the resulting dispersion of motilities and chemotactic response coefficients significantly affects population behavior.

Of interest in itself is speculation concerning the function of the built-in nongenetic variability. Koshland (1978) suggests that the advantage lies in the possibility that in rare circumstances, bacteria on the tails of the probability distribution would survive in some unusual distribution of toxins or nutrients.

We shall now survey some applications of system (5b), and suitable generalizations thereof, to band formation, to aggregation, and to the general understanding of the ecological roles of motility and taxes.

Bands

Research concerning travelling bands of tactic bacteria has become a major area of interaction between theory and experiment. Adler (1966) began the modern study of this subject, in the course of developing assays for chemotaxis. His work initiated what has proved to be an enormous effort in the molecular biological study of chemotaxis as an example of sensory transduction. For a recent review see Koshland (1980).

Repeating more quantitatively some 19th century experiments, Adler observed that bacteria inoculated into one end of a capillary tube would consume nutrient in their vicinity, creating a gradient. Pursuit of higher nutrient concentrations and continued consumption resulted in the formation of a band that moved steadily down the tube. In conditions of substrate excess, aerotaxis would bring about band formation.

Keller and Segel (1971) analyzed this phenomenon by looking for travelling wave solutions

$$b = b(x-\xi t),\ c = c(x-\xi t),\quad \xi \text{ a constant "wave speed"},$$

to selected special cases of (5). Several other authors also examined conditions that would permit exact travelling wave solutions, and still others provided numerical analyses of representative problems. Novick-Cohen and Segel (1982) cite the earlier work in an analytic study which shows that deviations from conditions for exact travelling waves can be permitted at low nutrient concentrations, thereby admitting certain biologically realistic hypothesis that were previously excluded. Such deviations have the consequence that the band no longer exactly retains its shape and constant speed. Behavior of this nature is observed, for example in Adler's (1966) original experiments.

Qualitative descriptions of banding phenomena have been given by Smith and Doetsch (1969) in their study of chemotaxis away from acidic domains in Pseudomonas fluorescens, and by Allweis et al (1977) in a demonstration that chemotaxis is important in the interaction of bacterial pathogens with mucosal surfaces. Reasonable agreement with the theory has been reported by Chen and his coworkers (Wang and Chen 1981 is the latest paper in the series) who used laser scattering techniques to obtain accurate density profiles of the moving bacterial band. In an interesting recent investigation that combines absorption photometry measurements with theory, Boon and Herpigny (1982) found that the basic theoretical framework (5) had to be extended in order to explain events when a uniform distribution of E. coli are placed in a step gradient of glucose. The developing spatial inhomogeneity in the bacterial distribution brings about an inhomogeneity in oxygen concentration. This in turn affects glucose consumption -- and all this must be taken into account to explain the observed formation first of a broad band and later of a second sharp band. That chemotaxis is not necessary for band formation has been shown by Kennedy and Aris (1980). Just substrate-dependent growth and random motility suffice. Lauffenburger, Kennedy and Aris (1982) consider the combined effects of net growth, random motility, and chemotaxis with emphasis on band formation as a mechanism for effective utilization of nutrient. Puzzling aspects remain after comparison with the experimental work of Chapman (1973).

In unpublished work Odell (1982) has made several contributions to the theoretical study of bands. In particular he examined a situation where exploiters and victims assume the roles of bacteria and substrate in (5), with $Q = 0$, $D = 0$, $\chi(s) = \delta/s$, $K(c) = \alpha c(\beta - c)$; $\delta, \alpha, \beta, \mu, r$ constants. Thus the "victaxis" function χ was assumed to obey the Weber-Fechner law and the victim reproduction was taken as logistic. Odell found conditions under which there are exact solutions that take the form of travelling wave trains. Here a group of exploiters nearly wipes out the victim population — which then grows up from its low level only to be nearly consumed again by the next band of exploiters, etc. It would be interesting to know whether there are concrete examples of this multiple-herd behavior.

Aggregation

After their food suuply runs out, free-living cellular slime mold amoebae (such as Dictyostelia) aggregate as the first step in the eventual formation of a multicellular organism. In its multicellular state, a typical cellular slime mold consists of a spherical collection of spores perched atop a slender, tapering stalk composed of dead cellulose filled cells. The aggregation is mediated by a chemoattractant (identified for several species as cyclic-AMP) that the amoebae secrete in the hours following starvation. Keller and Segel (1970) showed how a version of equations (5) could produce aggregation as an instability of a uniform layer of cells and attractant. Further studies along this line are cited by Lapidus and Levandowsky (1981). Noteworthy recent contributions include Hagan and Cohen's (1981) treatment of spiral and target aggregation patterns, and Childress and Percus's (1981) examination of whether chemotactic collapse according to the Keller-Segel (1971) version of (5) can result in total aggregation to a delta-function distribution of cells.

The theoretical framework (5) has been used by Edelstein (1971) to provide an explanation for aggregation-like cell sorting in morphogenesis. This framework has also been employed by Lauffenburger and Keller (1982) in a model for the mutual approach of swarms of Chondromyces apiculatus, and for the coherence of individual swarms.

We will soon describe another study of aggregation, in a medical context.

Models for Ecological Functions of Motility

Earlier we mentioned some ecological functions for taxes such as the guidance of organisms toward food, favorable habitats, and sexual partners. Leaving aside the question of the experimental verification of these ideas, their very reasonableness seems to leave little scope for the theoretician. Thus we now turn to situations of more subtlety, where modelling has contributed or promises to contribute something to our understanding.

Purely random motility can be included within our discussion of taxes as a limiting case of completely undirected motion. It seems intuitively clear that motility in itself would be advantageous to an organism, but theoretical investigations have shown that this is not necessarily so. For example, one might think that the diffusive flux of nutrient into an organism would be enhanced by motion, for then the organism would continually leave behind areas depleted by its own feeding. Berg and Purcell (1977) pointed out, however, that for organisms as small as bacteria this effect has a negligible influence on uptake. The reason is that in the associated low Reynolds number flow the microorganism continually drags along an appreciable portion of its fluid environment.

When nutrients are inhomogeneously distributed, motility can indeed affect the feeding rate of microorganisms, by bringing them into regions of differing nutrient concentrations. Here one's intuition might be that motility is certainly beneficial for it will scatter concentrations of organisms and thereby provide a better average environment for each. That this is not necessarily correct is shown by Lauffenburger, Aris and Keller (1981) in their examination of bacterial growth in a confined region $0 \leq x \leq L$ with a fixed nutrient concentration c_0 at $x = L$ and a wall impermeable to nutrient c at $x = 0$. Assuming an interaction between equations for uptake, growth, and death (rate d) that are familiar from chemostat theory, and postulating boundaries that are impermeable to bacteria, Lauffenburger et al (1981) study the mathematical problem

$$\partial b/\partial t = [r(c) - d]b + \mu \partial^2 b/\partial x^2 ; \qquad (8a)$$

$$\partial c/\partial t = -Y^{-1} r(c) b + D \partial^2 c/\partial x^2 ; \qquad (8b)$$

$$\text{at } x = 0, \quad \partial b/\partial x = \partial c/\partial x = 0 ; \qquad (8c,d)$$

$$\text{at } x = L, \quad \partial b/\partial x = 0, \quad s = s_0 . \qquad (8e,f)$$

The rate $r(c)$, expected to be a saturating function with $r(0) = 0$, is approximated by the step function

$$r(c) = k, \quad c \geq c^* ; \; r(c) = 0, \quad c \leq c^* . \qquad (9)$$

The governing problem is thus piecewise linear and can be explicitly solved. The major result is that at steady state the total bacterial population is a *decreasing* function of the bacterial motility parameter μ. This is because random motility disperses bacteria from the nutrient-rich fast growth zone near the substrate source at $x = L$. The effect is found to be significant when $(Dk)^{\frac{1}{2}} < L$, i.e. when in a time of order one generation bacteria can move into a significantly different nutrient environment.

Possible effects of motility on competition between two species has been examined by Lauffenburger and Calcagno (1982), for the same consumption and growth type of assumptions, under the same geometric conditions, that were postulated in (8). The authors remark that the model could "represent situations as diverse as bacteria growing in water films, around soil particles or hydrocarbon droplets, or in the mammalian gastrointestinal tract". As was to have been anticipated in view of the earlier results it is shown that steady coexistence is possible even though one species has a smaller growth rate, providing that its motility is sufficiently weak. An investigation of the stability of coexistence is promised in a future paper.

Models for Ecological Functions of Chemotaxis

It is to be expected that chemotaxis can override the deleterious effects of motility in moving bacteria away from peak nutrient concentrations. This is demonstrated by Lauffenburger, Aris and Keller (1982) in an analysis wherein the bacterial equation (8a) is supplemented by a chemotactic term of the form (3b). The analysis shows how strong the chemotaxis must be before its effect is significant. This paper also makes the non-obvious point (that seems consistent with observations) that populations are larger if the motility μ decreases at higher nutrient concentrations.

There is growing medical interest in cellular chemotaxis. For example, detailed studies have been made of chemotactic response in leukocytes (Zigmond and Sullivan 1979) and granulocytes (Gerisch and Keller 1981). Evidence has been presented that metastasis of malignant cells to bone is mediated by a chemotactic factor (Orr et al 1979).

Particularly elegant is the role of leukocyte chemotaxis in the body's defense against disease (Snyderman 1981). An obvious function can be ascribed to the finding that leukocytes are chemotactic to degradation products of bacteria. The leukocytes are also chemotactic to a fragment C5a of complement, the assemblage of molecules that leukocytes deploy to breach the cell walls of invaders and thereby to kill them. Apparently the "smoke" of an initial skirmish attracts defenders to the scene of an impending battle between them and the invading cells.

The same complement fragment has two further effects. It brings about a contraction of smooth muscle in post capillary venules and promotes the appearance of endothelial gaps. The first effect apparently decreases the dissipative effects of blood flow on the attractant gradient while the second opens the gates for leukocytes to leave the blood stream and move up the gradient.

Lauffenburger and Aris (1978) and Rothman and Lauffenburger (1982) discuss how to estimate the motility and chemotactic parameters μ and χ of the phenomenological equations (5) from the "under-agarose assay" used for leukocyte migration. These parameters play a major role in a study of inflammation by Lauffenburger and Keller (1979) that quantifies the host's ability to overcome bacterial invaders. In an extension of this work, Lauffenburger and Kennedy (1982) postulated the following equations for the concentrations of bacteria $b(x,t)$ and leukocytes $w(x,t)$, where the k_i are constants:

$$\frac{\partial b}{\partial t} = \mu_b \frac{\partial^2 b}{\partial x^2} + \frac{k_1 b}{1+b/k_2} - \frac{k_3 bc}{k_4+b} , \tag{10a}$$

$$\frac{\partial w}{\partial t} = \mu_w \frac{\partial^2 w}{\partial x^2} - \chi \frac{\partial}{\partial x}\left(w \frac{\partial b}{\partial x}\right) - k_6 w + k_7 (1+k_8 b) . \tag{10b}$$

The bacteria are randomly motile, grow with a self-damped birth rate, and are consumed by the leukocytes. Leukocytes possess both random and chemotactic (toward the bacteria) aspects to their motion and they die off at rate k_6. In the macroscopic perspective of the analysis, the last term in (10b) models the entry of leukocytes into the arena of conflict by passage through venular walls, at a rate that increases with bacterial population.

Lauffenburger and Kennedy (1982) show that the uniform solution of (10) can become unstable for realistic parameter values. This can result in a rather strongly nonuniform steady state with pockets of bacteria that are reminiscent of clinical observations. As the authors point out, the aggregation here differs from that found in slime mold amoebae in that the chemotactic cells are agents for stability in the present case while they promote instability in the case of the slime mold.

Need for deeper study of the ecological effects of taxes is suggested by striking results of I. Chet and R. Mitchell (private communication). These investigators checked about 20 different species of motile marine bacteria for chemotaxis to approximately 10 different chemicals. They found that every species responded chemotactically to at least one chemical, but each species seemed to have a different mixture of strong or weak positive responses, no response, and strong or weak negative responses.

These results suggest that there is more to the ecological function of taxes than avoidance of harmful agents and preferential motion in the direction of favorable locations. There appears to be a complex dynamic situation in which a spectrum of taxes enables a community of organisms to exploit different temporal-spatial niches. As a first step in illustrating such a situation I have begun an investigation into the possible coexistence of generalists and specialists. [Heller (1980) found conditions for such coexistence in an interaction between predators and sometimes harmful prey.]

Consider the competition between specialists A and B and generalist C. A and B respectively consume nutrients α and β, and move chemotactically toward relatively high concentrations of these nutrients. Generalist C can handle both nutrients, but in each case less efficiently than the specialists. A model for this interaction could take the following form, a generalization of (8a) and (8b) (with death incorporated into the net birth terms r_A, r_B, etc.):

$$
\begin{aligned}
&\partial A/\partial t = r_A(\alpha)A + \mu\nabla^2 A - \chi_A \nabla\cdot(A\nabla\alpha)\,,\\
&\partial B/\partial t = r_B(\beta)B + \mu\nabla^2 B - \chi_B \nabla\cdot(B\nabla\beta)\,,\\
&\partial C/\partial t = [r_{C1}(\alpha) + r_{C2}(\beta)]C + \mu\nabla^2 C - \chi_{CA}\nabla\cdot(C\nabla\alpha) - \chi_{CB}\nabla\cdot(C\nabla\beta),\\
&\partial\alpha/\partial t = -Y_A^{-1} r_A(\alpha)A - Y_{C1}^{-1} r_{C1}(\alpha)C + D_\alpha\nabla^2\alpha + S_\alpha(x,t),\\
&\partial\beta/\partial t = -Y_B^{-1} r_B(\beta)B - Y_{C2}^{-1} r_{C2}(\beta)C + D_\beta\nabla^2\beta + S_\beta(x,t).\\
&r_A(\alpha) > r_{C1}(\alpha),\ r_B(\beta) > r_{C2}(\beta),\ \chi_A > \chi_{CA},\ \chi_B > \chi_{CB}\,,\\
&Y_A > Y_{C1},\ Y_B > Y_{C2}\,.
\end{aligned}
\tag{11}
$$

I suspect that coexistence will be possible, at least for nutrient source terms $S_\alpha(x,t)$ and $S_\beta(x,t)$ which provide localized pulses of nutrient at points that are randomly distributed in space and time. I have started an investigation of a compartmental version of (11) but have as yet no results to report.

If indeed taxes play a subtle role in community organization, then one can anticipate corresponding subtle effects of pollutants that clog the sensory apparatus. A start on examining sublethal effects of pollutants has been made for example by Chet and Mitchell (1976) in an experimental study of chemotaxis, and by Segel and Ducklow (1982) in a theoretical examination of some aspects of coral ecology.

Overview

In pulling together the strands of this discourse, I would like to stress reasons for paying more attention to cellular ecology, by which I mean not only "traditional" microbial ecology but also the ecology of cells in higher organisms. The importance of this field is enormous, dealing as it does with myriads of living organisms that have profound influences on the biosphere in general, and on human development and disease in particular. With the advent of genetic engineering futuristic applications such as "biomining" (Brierly 1982) become possible, and require knowledge of population interactions. There are common threads, such as the phenomenological chemotaxis equation (5), that link the community behavior of bacteria, slime mold amoebae and blood cells. Perhaps most important to professional ecologists is the fact that microrganisms - particularly bacteria - offer relatively simple opportunities to formulate general principles in ways that are amenable to experimental test.

The study of bacterial chemotaxis seems to offer an unmatched opportunity for an integrated approach to understanding the interaction of genetics, physiology, and ecology. Molecular biologists are intensively studying the detailed mechanisms of bacterial chemotaxis in an attempt to unravel in full detail at least one process of sensory transduction. As anticipated by Adler (1966) when he started the study, existing detailed knowledge of bacterial genetics and the ease of inducing mutations in microorganisms have been indispensable tools. Impressive progress has been made in the understanding of the flagellar motor and of the receptor, but much remains to be done, especially on the connections between the receptor and the motor. Still, for the ecologist and the student of evolutionary theory, concentration on the effects of bacterial chemotaxis offers the enormous advantage of dealing with an environmental response for which details such as "cost", number of genes involved, and mutation frequency are becoming better and better understood.

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