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Biophysical Chemistry 104 (2003) 501–508

Biophysical Chemistry

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The cooperative binding of large ligands to a one-dimensional lattice: the steric hindrance effect

Takuhiro Nishio[a], Toshio Shimizu[b,*], Jan C.T. Kwak[c], Akira Minakata[a]

[a]*Department of Physics, Hamamatsu University School of Medicine, Hamamatsu 431-3192, Japan*
[b]*Department of Electronic and Information System Engineering, Faculty of Science and Technology, Hirosaki University, Hirosaki 036-8561, Japan*
[c]*Department of Chemistry, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J3*

Received 26 November 2002; received in revised form 3 February 2003; accepted 10 February 2003

Abstract

The cooperative binding of monomeric ligands to a long lattice of a linear polymer with complete or partial steric hindrance is treated using a matrix method. Results and typical calculations of the model are represented. Non-saturated cooperative binding as well as two-step (biphasic) binding isotherms can be interpreted by the steric hindrance model. This is applicable to the analysis of the binding of surfactants to polymer. The usefulness and the limitation also are discussed.

Keywords: Cooperative binding of ligands; Lattice of linear polymer; Binding isotherm; Steric hindrance; Matrix method

1. Introduction

The description of the binding process of small molecules or ions to a linear array of binding sites is of long standing interest in biophysics and in colloid and polymer science. In these applications, the linear array is a polymer, natural or synthetic, with equivalent binding sites spaced at short regular distances along the length of the polymer. The ligand may be a small molecule, but also a larger molecule.

The binding of small molecules by a polymeric molecule containing a large number of binding sites is normally described by a binding isotherm, where the number of bound molecules is plotted as a function of the equilibrium concentration of unbound (free) small molecules. Of particular interest is the case where this binding isotherm is cooperative, i.e. where the presence of an occupied binding site on the polymer favors binding of a small molecule to a neighboring, unoccupied site. Such situations may be found for instance in the binding of surfactants to linear polymer and in the non-specific ligand binding to the polymeric protein or DNA.

An early statistical description of such a system is due to Schwarz, who used a linear Ising model

*Corresponding author. Tel.: +81-172-393638; fax: +81-172-393638.
E-mail address: slsimi@aries.si.hirosaki-u.ac.jp (T. Shimizu).

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doi:10.1016/S0301-4622(03)00039-5

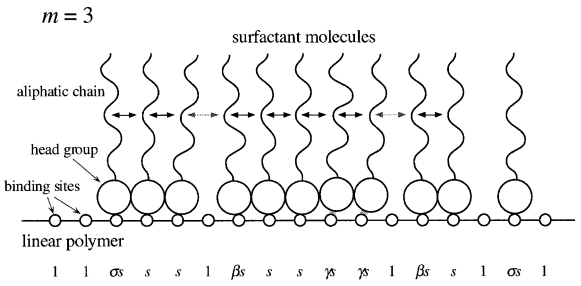

Fig. 1. Schematic representation of the binding of surfactant molecules to the linear polymer lattice with steric hindrance. The head group of the surfactant is slightly larger than the distance between binding sites on the polymer. Attractive interactions, indicated by arrows between aliphatic chains cause the cooperative binding. Weak interactions are indicated by shaded arrows. At the bottom of figure, the statistical weight of binding state is added for each surfactant molecule.

procedure to describe the binding isotherms of cationic dyes to anionic polypeptides [1–3]. Theoretical approach progressed for the analysis of the oligomer–polymer associations [4]. McGhee and von Hippel introduced the complication of ligands which are considerably larger than the linear distance between two binding sites, leading to what they call binding site 'overlap' [5]. Satake and Yang were the first to apply a methodology similar to the one by Schwarz to the binding of surfactants by synthetic polymers [6].

Although these past treatments have covered the case of overlap where a binding ligand occupied two or more discrete binding sites, actual situations will be more complex at the microscopic level. For the case of a linear array of binding sites, in particular, it is likely that the ligand will not occupy or block exactly one, two, or more sites, but a non-integer number of sites. If the ligand size is slightly larger than the linear distance between neighboring sites, the next site can still be occupied, but after a certain number of consecutively occupied sites the next binding site is completely or partially 'blocked'. Thus, the next site must be remained unoccupied, or its binding ability must be weakened.

The statistical treatment of these cases is presented in this paper. Similar approach with matrix method had been developed for treating the loop-formation in nucleic acids [7]. The typical results will show that our model of non-matching sizes of binding site and ligand leads to asymmetric binding isotherms closely following the isotherms observed in experimental studies [8–14]. By the model, we can consider a few types of the interactions between the ligands on the polymer lattice.

2. Theory

2.1. The binding model

We consider a linear lattice consisting of regularly spaced equivalent binding sites of large number N. The distance (or spacing) between adjoining binding sites is considered to be smaller to a certain degree than the size of the ligands. When a certain number (m) of consecutive binding sites are occupied with ligands in the cooperative manner, it happens that one neighboring binding site is completely or partially blocked due to the steric crowding effect of bound ligands.

There are at least three parameters involved in this binding model with complete steric hindrance: the maximum number of binding sites occupied constructively, m; the statistical weight of an occupied state of the binding site relative to the unoccupied state, σs; the relative statistical weight of an occupied state next to the occupied site, s, where σ is called the cooperative parameter. At this point a simple case of steric hindrance can be introduced. If we assume that a relative weak nearest-neighbor interaction exists between bound ligands separated from each other by an unoccupied binding site, and introducing the parameter β, $\sigma \le \beta \le 1$, the relative statistical weight of an occupied state next to an excluded site after consecutive ($\ge m$) binding sites is defined as βs. When $\beta = 1$, there is full nearest-neighbor interaction between the ligands across an unoccupied site. When $\beta = \sigma$, there is no nearest-neighbor interaction across an unoccupied site.

In addition, in order to consider incomplete steric hindrance, we introduce a parameter γ, $0 \le \gamma \le 1$, to describe this effect. The relative statistical weight of an occupied state of the (partially) excluded binding site is defined as γs. When

$\gamma=0$, there is complete steric hindrance. When $\gamma=1$, there is no steric hindrance.

Fig. 1 schematically represents this model in the case of $m=3$ with partial steric hindrance for surfactant molecules bound to a linear polymer lattice.

2.2. Procedure for obtaining the saturation function

In general, for a chain of N equivalent units, the partition function, Z, is written as a product of matrices. For the problem that we are considering here, the partition function is expressed as:

$$Z=\mathrm{tr}\mathbf{W}_m^N \tag{1}$$

where $\mathbf{W}_m$ is the $(m+2)\times(m+2)$ matrix of statistical weights and m is the maximum number of constructively occupied sites in the presence of the excluded effect due to the steric hindrance of bound ligands on neighboring sites. Here, the chain is assumed to make a circle. The partition function in Eq. (1) is expressed with the eigenvalues of the matrix $\mathbf{W}_m$ under the periodic boundary condition, as follows;

$$Z=\lambda_1^N+\lambda_2^N+\lambda_3^N+\cdots+\lambda_{m+1}^N+\lambda_{m+2}^N \tag{2}$$

where λ_1, λ_2, etc., and λ_{m+2} are the eigenvalues of the matrix $\mathbf{W}_m$. If the chain has open ends, end effect must be incorporated. In either case, for the long chain where N is considered large enough to eliminate boundary effects, Z is given in good approximation by the maximum eigenvalue, λ_1, as,

$$Z\approx\lambda_1^N \tag{3}$$

The eigenvalues of $\mathbf{W}_m$ are obtained by solving the characteristic equation. An alternative method to obtain the secular equation also was known [15].

The partition function can be used directly to compute the fraction, θ, of sites occupied by a ligand, i.e.

$$\theta=\frac{1}{N}\frac{\partial\ln Z}{\partial\ln s} \tag{4}$$

where s is the statistical weight of occupied site when the preceding binding site is already occupied by a ligand. And, s is defined as:

$$s=\frac{K}{\sigma}C_\mathrm{f} \tag{5}$$

where K is intrinsic binding constant, σ is cooperative parameter, and C_f is free ligand concentration.

Using Eq. (4), we finally have the expression as:

$$\theta=\frac{1}{N}\frac{\partial\ln\lambda_1^N}{\partial\ln s}=\frac{s}{\lambda_1}\frac{\partial\lambda_1}{\partial s} \tag{6}$$

The fractions of the binding state, ν_σ, ν_β and ν_γ, of which the statistical weights of binding are σs, βs and γs, respectively, are evaluated similarly, as:

$$\nu_\sigma=\frac{\sigma}{\lambda_1}\frac{\partial\lambda_1}{\partial\sigma} \tag{7}$$

$$\nu_\beta=\frac{\beta}{\lambda_1}\frac{\partial\lambda_1}{\partial\beta} \tag{8}$$

$$\nu_\gamma=\frac{\gamma}{\lambda_1}\frac{\partial\lambda_1}{\partial\gamma} \tag{9}$$

In the cases of $m\geq2$, the remaining fraction ν_s, of which statistical weight is s, is calculated as:

$$\nu_s=\theta-(\nu_\sigma+\nu_\beta+\nu_\gamma) \tag{10}$$

2.3. The partition function for large ligand binding to linear binding site lattice

The simplest case of this problem is that a ligand binds with excluding one site, that is, the maximum number of consecutive occupied sites, m, is limited to 1. Three sites in total must be correlated in this case. We derive the partition function for this case and then show how it can be generalized for any exclusion effect and for any number of correlated sites.

Let 's' be the bound state for the *i*-th site and 'u' the unbound state. If site *i* is in the s state, then site $i+1$ is (partially) blocked. The statistical weight of the binding to the site is γs. If site $i-1$ is in the s state and site *i* is in the u state, a ligand can bind to the next site $i+1$ with relatively weak interaction to the ligand bound at site $i-1$ (βs). If site $i-1$ and *i* are both in the u state, the binding to site $i+1$ is suppressed in the cooperative manner (σs). The statistical weight matrix of the present model is given as

	$i+1$	s	u	s	u
$i-1$	i	s	s	u	u
s	s	γs	1	0	0
s	u	0	0	βs	1
u	s	γs	1	0	0
u	u	0	0	σs	1

(11a)

	$i+1$	u	s	u
$i-1$	i	s	s∪u	u
s	u	0	βs	1,
s∪u	s	1	γs	0
u	u	0	σs	1

(11b)

where ∪ represents a combination of states. The eigenvalues of this matrix $\mathbf{W}_1$ are obtained by solving the following characteristic equation:

$$\lambda^3-(1+\gamma s)\lambda^2+(\gamma-\beta)s\lambda+(\beta-\sigma)s=0 \tag{12}$$

The fraction of occupied sites is given as:

$$\theta=\frac{s}{\lambda_1}\frac{\partial\lambda_1}{\partial s}=\frac{s}{\lambda_1}\frac{\gamma\lambda_1^2-(\gamma-\beta)\lambda_1-(\beta-\sigma)}{3\lambda_1^2-2(1+\gamma s)\lambda_1+(\gamma-\beta)s}$$
$$=s\frac{\gamma\lambda_1^2-(\gamma-\beta)\lambda_1-(\beta-\sigma)}{(1+\gamma s)\lambda_1^2-2(\gamma-\beta)s\lambda_1-3(\beta-\sigma)s} \tag{13}$$

Each fraction of binding state is given as:

$$\nu_\sigma=\frac{\sigma s}{(1+\gamma s)\lambda_1^2-2(\gamma-\beta)s\lambda_1-3(\beta-\sigma)s} \tag{14}$$

$$\nu_\beta=\frac{\beta(s\lambda_1-s)}{(1+\gamma s)\lambda_1^2-2(\gamma-\beta)s\lambda_1-3(\beta-\sigma)s} \tag{15}$$

$$\nu_\gamma=\frac{\gamma(s\lambda_1^2-s\lambda_1)}{(1+\gamma s)\lambda_1^2-2(\gamma-\beta)s\lambda_1-3(\beta-\sigma)s} \tag{16}$$

The weight matrix in Eqs. (11a) and (11b) is readily generalized to any value of $m\geq 2$. The matrices and characteristic equations for $m=2$ and 3 are shown as follows, respectively:

$$\mathbf{W}_2=\begin{bmatrix}0 & 0 & \beta s & 1\\ 1 & \gamma s & 0 & 0\\ 0 & s & 0 & 1\\ 0 & 0 & \sigma s & 1\end{bmatrix} \tag{17}$$

$$\lambda^4-(1+\gamma s)\lambda^3+(\gamma-\sigma)s\lambda^2+(\gamma\sigma-\beta)s^2\lambda+(\beta-\sigma)s^2=0 \tag{18}$$

$$\mathbf{W}_3=\begin{bmatrix}0 & 0 & 0 & \beta s & 1\\ 1 & \gamma s & 0 & 0 & 0\\ 0 & s & 0 & 0 & 1\\ 0 & 0 & s & 0 & 1\\ 0 & 0 & 0 & \sigma s & 1\end{bmatrix} \tag{19}$$

$$\lambda^5-(1+\gamma s)\lambda^4+(\gamma-\sigma)s\lambda^3+\sigma(\gamma-1)s^2\lambda^2+(\gamma\sigma-\beta)s^3\lambda+(\beta-\sigma)s^3=0 \tag{20}$$

By induction on these cases, the generalized matrix for arbitrary m can be written as:

$$\mathbf{W}_m = \begin{bmatrix} 0 & 0 & 0 & 0 & \cdots & 0 & \beta s & 1 \\ 1 & \gamma s & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & s & 0 & 0 & \cdots & 0 & 0 & 1 \\ 0 & 0 & s & 0 & \cdots & 0 & 0 & 1 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & \cdots & s & 0 & 1 \\ 0 & 0 & 0 & 0 & \cdots & 0 & \sigma s & 1 \end{bmatrix} \quad (21)$$

The eigenvalues of $\boldsymbol{W}_m$ are obtained by solving the following characteristic equation:

$$\lambda^{m+2} - (1+\gamma s)\lambda^{m+1} + (\gamma - \sigma)s\lambda^m + \sigma(\gamma - 1)[s^2\lambda^{m-1} + \cdots + s^i\lambda^{m-i+1} + \cdots + s^{m-1}\lambda^2] + (\gamma\sigma - \beta)s^m\lambda + (\beta - \sigma)s^m = 0 \quad (22)$$

Differentiating Eq. (22) with respect to s, we obtain, after some algebraic manipulations:

$$\theta = s\frac{\left\{\begin{array}{l}\gamma\lambda_1^{m+1} - (\gamma-\sigma)\lambda_1^m - \sigma(\gamma-1) \\ \quad [2s\lambda_1^{m-1} + \cdots + is^{i-1}\lambda_1^{m-i+1} + \cdots + (m-1)s^{m-2}\lambda_1^2] \\ \quad - m(\gamma\sigma - \beta)s^{m-1}\lambda_1 - m(\beta - \sigma)s^{m-1}\end{array}\right\}}{\left\{\begin{array}{l}(1+\gamma s)\lambda_1^{m+1} - 2(\gamma-\sigma)s\lambda_1^m - \sigma(\gamma-1) \\ \quad [3s^2\lambda_1^{m-1} + \cdots + (i+1)s^i\lambda_1^{m-i+1} + \cdots + ms^{m-1}\lambda_1^2] \\ \quad - (m+1)(\gamma\sigma - \beta)s^m\lambda_1 - (m+2)(\beta - \sigma)s^m\end{array}\right\}} \quad (23)$$

This is the general binding equation, which could be used to calculate the fraction of occupied sites as a function of free ligand concentration. In addition, the fractions of binding states ν_σ, ν_β, ν_γ and ν_s, are calculated using Eqs. (7)–(10), similarly to Eqs. (14)–(16).

As the ligand concentration becomes large, s also becomes large so that from Eqs. (22) and (23):

$$\lim_{s\to\infty}\left(\frac{\lambda_1}{s}\right) = \gamma \quad (24)$$

$$\lim_{s\to\infty}\theta = 1 \quad (25)$$

when $\gamma \neq 0$. If the steric hindrance effect is complete ($\gamma = 0$), then the relations

$$\lim_{s\to\infty}\left(\frac{\lambda_1}{s^{m/m+1}}\right) = \beta^{1/m+1} \quad (26)$$

$$\lim_{s\to\infty}\theta = \frac{m}{m+1} \quad (27)$$

are obtained.

When $m = \infty$, which means there is no steric hindrance effect at all, the characteristic equation and the fraction of occupied sites converge into:

$$\lambda^2 - (1+s)\lambda + (1-\sigma)s = 0 \quad (28)$$

$$\theta = \frac{\lambda_1 - 1}{2\lambda_1 - (1+s)} = \frac{1}{2}\left[1 - \frac{1-s}{\sqrt{(1-s)^2 + 4\sigma s}}\right] \quad (29)$$

respectively. These are exactly the same expressions as for the usual case of cooperative binding, independent of β and γ [1]. The same expressions are also obtained from Eqs. (22) and (23), with $\gamma = 1$ and $\beta = \sigma$.

In the numerical calculations, the polynomials with higher order are solved by a three-stage algorithm [16].

3. Results and discussion

3.1. Isotherms for various numbers of consecutive binding sites, m, with complete steric hindrance

First, in the case of complete steric hindrance ($\gamma = 0$), the binding isotherms were calculated at

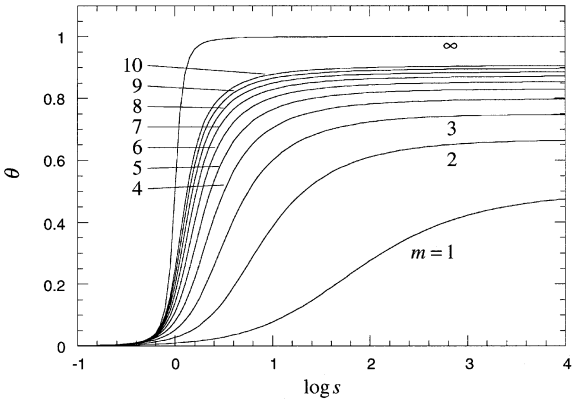

Fig. 2. The binding isotherms (log s vs. θ) of various m in the case $\gamma=0$, $\beta=\sigma=0.01$. $m=1$–10 and infinity, from bottom to top. Curve for $m=\infty$ is given by Eq. (29).

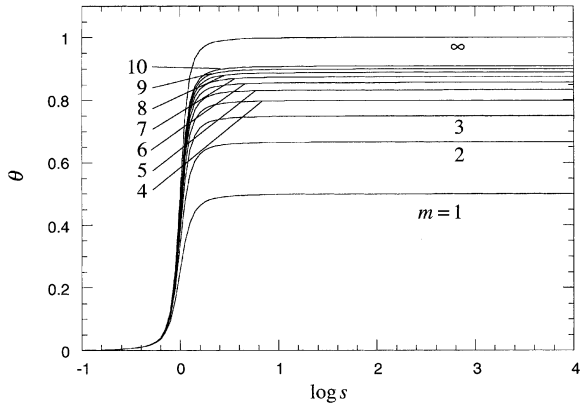

Fig. 3. The isotherms of various values of m for the case $\gamma=0$, $\beta=1$, $\sigma=0.01$. $m=1$–10 and infinity from bottom to top. Curve for $m=\infty$ is given by Eq. (29).

fixed σ by varying the number, m. Non-saturated cooperative binding can be interpreted by this model.

In Fig. 2, the isotherms for various values of m are represented by $\beta=\sigma=0.01$. The interaction between ligands is discontinued by the excluded site in these cases. As seen in the figure, there is no apparent cooperativity of binding process, when $m=1$. With increasing m, the cooperativity increases, leading to the shift of the midpoint of the binding, s at $\theta=m/2(m+1)$, toward the left (i.e. to lower ligand concentration).

Fig. 3 shows the isotherms for various values of m with $\beta=1$. In this case, the cooperativity could continue even across the excluded site, which is determined by σ. The midpoint of the binding isotherm does not shift appreciably, being placed at approximately $s=1$ (log $s=0$). Therefore, the binding isotherm shows a sharp rise followed by flat line of which the level is determined by m.

Fig. 4 shows the dependence of the isotherm for $m=2$ on the parameter β at fixed σ ($=0.01$) with complete steric hindrance ($\gamma=0$). With increasing β (from $\beta=\sigma$ to 1), the cooperativity increases and the midpoint of the binding isotherm is shifted to lower concentration.

3.2. Binding with partial steric hindrance

A 'two-step' binding isotherm can be represented by this model, when the steric hindrance effect is incomplete ($0<\gamma<1$).

In Fig. 5, the dependence of the isotherm on γ is represented for $m=2$ and $\beta=\sigma=0.01$. With increasing γ, the binding of the second step is strengthened. For values of γ larger than σ the cooperativity of the first step also increases. Furthermore, when the value γ is sufficiently larger than β, the binding isotherm appears monophasic,

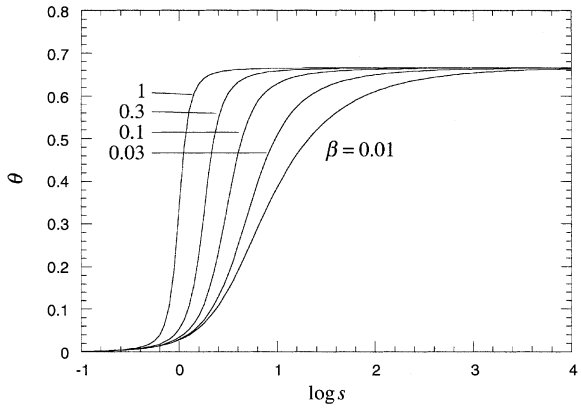

Fig. 4. The dependence of the isotherm on β for the case $m=2$, $\gamma=0$, $\sigma=0.01$. $\beta=1$, 0.3, 0.1, 0.03 and 0.01, from left to right.

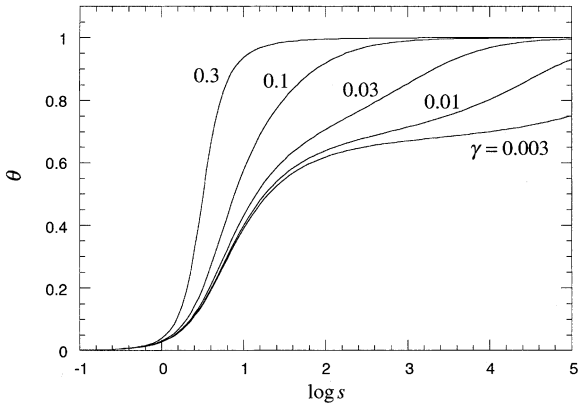

Fig. 5. The dependence of the binding isotherm on γ for $m=2$, $\sigma=\beta=0.01$. $\gamma=0.3$, 0.1, 0.03, 0.01 and 0.003, from top to bottom.

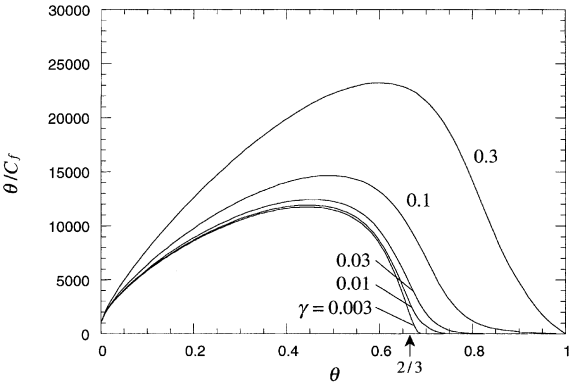

Fig. 7. Scatchard plot of data in Fig. 6 when $K=1000$. The free ligand concentration C_f is obtained by the relation $C_f=\sigma s/K$. A point of $\theta=m/(m+1)=2/3$ is indicated by an arrow in the abscissa.

and the inflection point shifts to lower values of s. Fig. 6 shows the dependence on γ for $m=2$, $\beta=0.1$ and $\sigma=0.01$. Also in this case, the binding cooperativity of the first step slightly increases with increasing γ. Scatchard plots of the data in Fig. 6 are shown in Fig. 7, in the case that K is given as 1000. Extensive cooperativity is represented in the range of $\theta<m/m+1$. The value m must be assumed only in the low γ case using the plot of single experimental data set. In Fig. 8, the change of each fraction of binding state with s from the data in Fig. 6 is represented at $\gamma=0.1$.

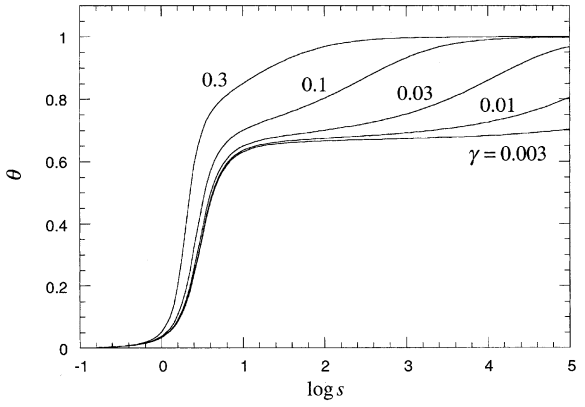

Fig. 6. The dependence of the isotherm on γ for $m=2$, $\sigma=0.01$, $\beta=0.1$. $\gamma=0.3$, 0.1, 0.03, 0.01 and 0.003, from top to bottom.

With increasing s, the fractions ν_s and ν_β increase abruptly with the first binding step of θ, and then decrease gradually, while the fraction ν_σ disappears very quickly after appearing in earlier stage of the binding. When the second binding step appears, the fraction of weak binding, ν_γ, becomes dominant due to the molecular crowding effect. Finally, the fraction ν_γ becomes unity with saturation of binding.

4. Concluding remarks

The problem of the cooperative binding of monomeric (large) ligands to a long one-dimen-

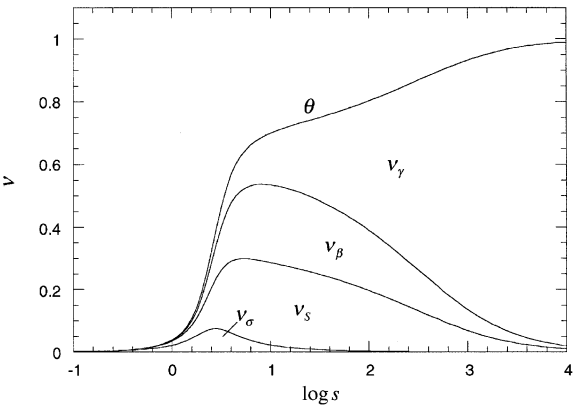

Fig. 8. Fraction change of binding state (summation plot) from Fig. 6 at $\gamma=0.1$. θ is expressed as the sum of four fractions.

sional lattice of polymer with (partial) steric hindrance is solved using the matrix method. The present model and its formulation must be applicable to the analysis of various experimental studies, for example, analysis of the ligand binding to the filamentous (polymeric) protein. Another applicability is in the binding of surfactants to polymer molecule as represented in Fig. 1. Non-saturated binding and two-step binding isotherms are often observed in this type of system [8–14]. These phenomena can be interpreted by the present model.

There are obvious limitations to the model presented in this paper. First, the polymer may undergo conformational change upon binding of small molecules, which is not considered here. As another point, in the case of ionic surfactant binding to a linear polyelectrolyte, the consideration of the long-range electrostatic force may be necessary. Counterion condensation should be taken into account, when the charge density of the polyion is higher than a critical value. Even in these cases, however, steric hindrance will influence the binding state. Fitting experimental binding isotherms on the basis of the present model must be useful in characterizing the binding properties. In particular, we have shown that the commonly observed 'two-step' binding isotherm for surfactants binding to linear polymers would appear in the presence of a steric hindrance effect even if different binding sites are absent. Further studies are required in order to analyze the many available experimental data with this model. A trial of data fitting is now in preparation.

Acknowledgments

The calculations in this study were carried out using the workstation in the information processing center of the Hamamatsu University School of Medicine.

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