Theoretical model of interactions between particle-associated and free-living bacteria to predict functional composition and succession in bacterial communities

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ABSTRACT: We examined the interactions between 3 hypothesized functional groups of heterotrophic bacteria: POC specialists, which use only particulate organic carbon (POC); free-living DOC specialists, which use only dissolved organic carbon (DOC); and generalists, which use POC when particle-associated and DOC when free-living. We focused on (1) competitive interactions for the use of POC and DOC, and (2) commensal interactions, whereby DOC is supplied by the enzymatic hydrolysis of POC by particle-associated cells. Using a simple model, we found that the quantity and quality of POC and DOC, and the balance between the rate of POC hydrolysis and the release of DOC determine the coexistence between generalists and the specialists in the bacterial community. Surprisingly, a high level of POC hydrolysis, which is an apparently commensal process of generalists, was found to exclude free-living DOC specialists from the community. These factors also determine the community dynamics during a shift in the supply of POC, as may occur during a phytoplankton bloom. This model predicts 3 possible patterns for the order of succession in the community composition, and 2 distinct directions in which the distribution of production within the free-living community could change. These diverse patterns would affect both the biogeochemical processes and the community dynamics at higher trophic levels.

KEY WORDS: Generalists · Competition · Commensalism · Hydrolysis · Bacterial production

INTRODUCTION

Particles and ambient water represent 2 distinct, extremely different habitats for bacteria in aquatic environments. Particle-associated and free-living bacteria often exhibit different physiological traits, as indicated by differences in production and growth (Unanue et al. 1992, Friedrich et al. 1999), ectoenzymatic activity (Karner & Herndl 1992, Smith et al. 1992, Riemann et al. 2000), and kinetics of substrate uptake (Ayo et al. 2001). These observations support the hypothesis that some bacterial groups adapt to nutrient-rich, particulate microhabitats ('particle specialists'; Riemann et al. 2000), whereas other groups adapt to nutrient-poor, ambient water ('free-living specialists').

Furthermore, it has been thought that these groups do not interact with each other in terms of nutrient availability and usage, because they use distinct energy sources, i.e. particulate organic carbon (POC) versus dissolved organic carbon (DOC). Recently, the application of new molecular methods has indicated that particle-associated and free-living bacteria belong to distinct phylogenetic groups (DeLong et al. 1993, Acinas et al. 1997, Crump et al. 1999), supporting the above hypothesis.

Other lines of evidence, however, indicate that particle-associated and free-living communities sometimes show common features in terms of phylogenetic composition (Hollibaugh et al. 2000, Riemann & Winding 2001) and metabolic functions (Worm et al. 2001).

This suggests the existence of 'generalists' that migrate between the particulate and water phases, using both POC and DOC as organic resources. Riemann & Winding (2001) examined denaturing gradient gel electrophoresis (DGGE) profiles of bacterial communities during a diatom bloom. They found that several bands (species) were common to both the particle-associated and free-living fractions, even during a pre-bloom period in which low abundance of particle-associated bacteria suggested a low concentration of labile and available particles. It follows that these species use DOC during the pre-bloom period, whereas they use both DOC and POC after the bloom. This observation strongly suggests the existence of generalists. Riemann & Winding (2001) also found that a number of major bands in the free-living fraction disappeared as the number of particles and particle-associated bacteria increased. This disappearance of some phylogenic types of free-living bacteria may be due to competitive exclusion in the ambient water. Furthermore, Kirchman (2002) has hypothesized that species in the *Cytophaga-Flavobacteria* cluster are possible members of such a generalist group (but see Fandino et al. 2001); members of this cluster are abundant in both particle-associated and free-living communities, and are able to use the high molecular mass fraction of dissolved organic matter (DOM) (Cottrell & Kirchman 2000). If generalists do exist, they appear in both the particle-associated and free-living communities, and compete with other particle-associated and free-living bacteria for POC and DOC.

Studies of hydrolytic processes on particles do not support the hypothesis that particle-associated and free-living bacteria do not interact with each other for POC and DOC. Because hydrolytic activity on particle surfaces is high, but the rate of consumption of hydrolysate by particle-associated cells is often low ('uncoupled' hydrolysis), DOM is supplied from particles to the surrounding water (Smith et al. 1992, Grossart & Simon 1998, Schweitzer et al. 2001, Grossart et al. 2003), resulting in increased production of the free-living assemblage (Friedrich et al. 1999, Grossart et al. 2003). In other words, there are commensal interactions, i.e. positive influences of particle-associated cells on free-living cells.

Therefore, hydrolytic processes and the existence of generalists are important factors determining the interactions between the particle-associated and free-living communities. In other words, these 2 factors largely influence the composition and production distribution within both communities. However, the existence of generalists and their physiological traits remain poorly documented. It is also difficult to experimentally control parameters related to hydrolysis. Therefore, at present, theoretical approaches are useful for examining the potential roles of generalists and hydrolysis on the interactions among particle-associated and free-living bacteria, and for predicting the outcome in the community dynamics.

In this study, we used a simple theoretical model to analyze the dynamics of 3 hypothetical groups of bacteria in aquatic environments: POC specialists, DOC specialists, and generalists. We defined these groups based on the source of energy used by each group. POC (or DOC) specialists use only POC (or DOC), whereas the generalists use both POC and DOC. Simplifying assumptions were made to clarify the environmental conditions under which different groups of bacteria with different resource-use strategies would dominate in aquatic bacterial communities. We examined the predicted community dynamics during a shift in the supply of POC and DOC, such as may occur during a phytoplankton bloom. We found that various patterns were predicted for both the order of succession in the community composition and the changes in the distribution of production among functionally different groups. In particular, we demonstrate that the following parameters, which reflect the nature and quality of POC and DOC, influence these patterns through the behavior of generalists: (1) bacterial growth efficiency (BGE) using POC and DOC, (2) intensity of hydrolysis, and (3) DOC release rate from hydrolyzed POC.

METHODS

Model description. *Definition of variables:* A flow diagram of the model is shown in Fig. 1. We assumed 2 fractions as carbon sources: POC (C_P), and DOC (C_D). In addition, we defined 3 bacterial strategies for the use of energy sources: DOC specialists (D), occurring only in the free-living fraction and consuming only DOC; POC specialists (P), occurring in both the free-living and particle-associated fractions; and generalists (G), occurring in both the free-living and particle-associated fractions. By definition, POC specialists consume only POC; their cells multiply on particle surfaces and release their daughter cells to the surrounding water (Jacobsen & Azam 1984, Friedrich et al. 1999, Kiørboe et al. 2002). These newly produced, free-living cells either quickly find and colonize fresh particles (Kiørboe et al. 2002) without consuming DOC or remain dormant in a 'seed-bank' role (Pernthaler et al. 1998) until they find new particles. We assumed that the particle-associated cells of generalists consume only POC, whereas the free-living cells consume only DOC. The limitation of bacterial growth by inorganic nutrients (Kirchman 2000) is not considered in this model system.

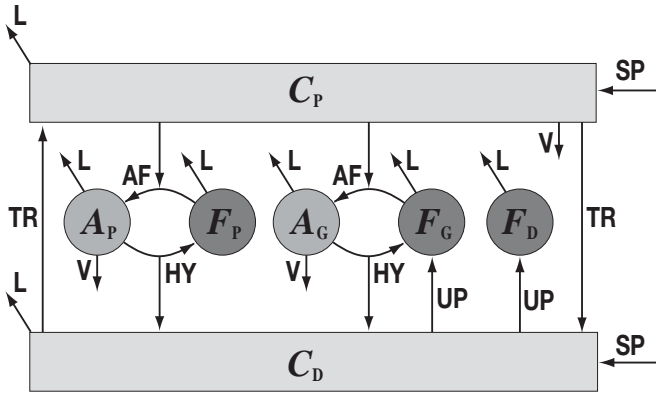We defined 'aggregates' (A_P and A_G) as particles colonized by POC specialists or generalists, respectively.

Fig. 1. Model flow diagram. C_P: POC, C_D: DOC, A_P: aggregates inhabited by POC specialists, F_P: free-living POC specialist cells, A_G: aggregates inhabited by generalists, F_G: free-living generalist cells, F_D: free-living DOC specialist cells, AF: aggregate formation, HY: hydrolysis processes, UP: uptake of DOC, L: loss processes, V: vertical sinking, TR: transformation between POC and DOC, and SP: supply of organic carbon. Recycling processes are not represented for simplicity

In other words, an aggregate consists of POC combined with the particle-associated fraction of POC specialists or generalists. We set F_D, F_P, F_G as free-living cells of DOC specialists, POC specialists, and generalists, respectively. Note that the units for POC and DOC are carbon concentration (mgC l^{-1}) and the units for F_D, F_P, F_G, A_P, and A_G are densities of cells or aggregates (l^{-1}). Among these 7 components, we considered 3 main processes: (1) colonization of particles by free-living POC specialist and generalist cells, (2) hydrolysis of POC and subsequent processes, (3) consumption of DOC by free-living generalists and DOC specialists. We constructed a simple box model that describes the interactions and dynamics among these 7 compartments.

Colonization of particles by free-living cells: We ignored heterogeneity among particles and assumed that every particle contains the same amount of carbon. The concentration of particles can then be calculated by dividing the POC concentration by the carbon content, i.e. C_P/α (see Table 2 for definitions of variables and parameters). We assumed that either POC specialists or generalists, but not both, colonize each particle; thus, we considered competition between POC specialists and generalists for particles to colonize, and did not consider competition within one aggregate. For the free-living cells, we assumed that the rate of colonization of particles, i.e. the loss rate of free-living cells due to colonization, is in proportion to the concentration of particles and the density of their free-living cells. That is, we set the rate per cell to $a_P(C_P/\alpha)$ (d^{-1}) and $a_G(C_P/\alpha)$ (d^{-1}), respectively. We assumed that sequential colonization stops and particles become an 'aggregate' after n free-living cells colonize 1 particle. We assumed a fixed number of colonizers per particle

(n), independent of bacterial density in the surrounding water. The rate of aggregate formation was $a_P(C_P/\alpha)F_P/n$ and $a_G(C_P/\alpha)F_G/n$ for POC specialists and generalists, respectively. The carbon content of bacteria per cell was β; therefore, the carbon content per aggregate was $\alpha + n\beta$ under this assumption.

Hydrolysis of POC and subsequent processes: For simplicity, we did not consider the population dynamics of bacteria on each aggregate, but took into account only the dynamics of the density of aggregates. We assumed that n bacterial cells colonize each particle and consume it by hydrolysis at rate h (i.e. the loss rate of aggregate [d^{-1}]). Of the hydrolyzed carbon, the fraction f_F (the 'uptake ratio') is consumed by the colonizing bacteria for reproduction, and the fraction f_D (the 'release ratio') is released to the surrounding water as DOC. Released DOC enters the DOC pool (C_D), where it can be consumed by free-living cells of both generalists and DOC specialists. The remainder of the particulate carbon is converted to non-labile forms, so it follows that $0 < f_F + f_D < 1$ always holds. When each aggregate is completely consumed, the original colonizing cells and the newly reproduced cells are released to the surrounding water and enter the compartment of the free-living fraction of POC specialists (F_P) and generalists (F_G). The number of newly reproduced cells can be calculated as $e_P\alpha f_F/\beta$, where e_P is the growth efficiency of bacteria using POC. The unassimilated fraction of carbon $(1 - e_P)\alpha f_F$ is converted to CO_2 by bacterial respiration. Thus, the total number of cells released per aggregate is $n + e_P\alpha f_F/\beta$.

Consumption of DOC: We assumed that the specific growth rates of free-living generalist and DOC-specialist cells were $u_G C_P$ and $u_D C_P$ per cell (d^{-1}), respectively. Therefore, we can calculate the uptake rates of DOC by free-living generalists and DOC specialists as $e_D^{-1}u_G C_D\beta F_G$ and $e_D^{-1}u_D C_D\beta F_D$, respectively, where e_D is the growth efficiency of bacteria using DOC. Unassimilated carbon is converted to CO_2 by respiration. Note that free-living POC specialist cells do not take up DOC.

Loss processes and other assumptions: We assumed that bacterial mortality is caused by predation and viral lysis, and that part of the lost bacterial biomass is recycled to the POC and DOC compartments (Nagata & Kirchman 1991, 1992, Middelboe et al. 1996, Noble et al. 1999). The mortality rates per cell on aggregates and in the free-living cell compartment were defined as m_A and m_F, respectively. Thus, the rate of carbon recycling in particle-associated and free-living cells to POC is $r_P n\beta m_A$ and $r_P\beta m_F$, respectively, where r_P is the common ratio of recycling to POC. Similarly, the rate of carbon recycling to the DOC compartment following the death of particle-associated and free-living cells is $r_D n\beta m_A$ and $r_D\beta m_F$, respectively, where r_D is the com-

mon ratio of recycling to DOC. In addition, aggregates from which bacterial cells are removed return to the fresh particle compartment at the rate αm_A (mgC d^{-1}). We also considered the loss of bacterial cells on aggregates by vertical sinking, at the rate m_V. In this process, carbon from particles and particle-associated cells is completely lost from the system. We defined the loss rate of POC and DOC as m_P and m_D, respectively. Some part of the carbon loss from each compartment is due to the conversion of POC to DOC and vice versa; those respective turnover rates were defined as $m_P t_{PD}$ and $m_D t_{DP}$, respectively. The remainder of the carbon loss is eliminated from the whole system, from either the POC or DOC compartment, at rates defined as $m_P(1 - t_{PD})$ and $m_D(1 - t_{DP})$, respectively. We assumed that these processes are driven by physical (e.g. transport, mechanical decomposition, aggregation) and chemical (e.g. photochemical reactions by UV) reactions. We set the additional loss of particles by vertical sinking at the rate m_V, the same as the loss of aggregates. Finally, we assumed that POC and DOC are supplied by the autochthonous production of phytoplankton and/or allochthonous loads of suspended organic matter and dissolved organic matter at the rate s_P and s_D, respectively.

Trade-offs for competition among specialists and generalists: In this model, we focused on competition between POC specialists and generalists for particle colonization, and between DOC specialists and generalists for DOC uptake. Because generalists are able to use both POC and DOC, there must be some trade-offs between specialists and generalists, both in the real world and in the model, to facilitate their coexistence. We assumed 2 trade-offs: (1) a trade-off between POC specialists and generalists, i.e. a higher colonization rate of POC specialists than generalists ($a_P > a_G$; see Barbara & Mitchell [2003] for colonization rates in different species), and (2) a trade-off between DOC specialists and generalists, i.e. higher uptake rate in DOC specialists than generalists ($u_D > u_G$).

Mathematical analysis. Taking the processes and assumptions presented above into consideration, we developed equations relating the dynamics of the POC (C_P) and DOC (C_D) concentrations to the density of aggregates (A_P, A_G) and of free-living cells (F_P, F_D, F_G; see Tables 1 & 2). For these equations, by introducing new symbols for the convenience of calculations (Table 3), and setting the right-hand side of all equations (Eqs. 1 to 7) to zero, we calculated the POC and DOC concentrations, and the bacterial carbon concentration of each fraction (i.e. the particle-associated POC specialists and generalists, and the free-living POC specialists, DOC specialists, and generalists) under steady-state conditions. There were 7 possibilities for the bacterial composition of the system at equilibrium: no bacterial groups using the defined energy sources present (E_N), POC specialists alone (E_P), generalists alone (E_G), DOC specialists alone (E_D), and 3 states of 2 groups coexisting with different strategies (E_{GD}, E_{GP}, E_{PD}). Note that 3 groups of bacteria using different strategies cannot coexist, because only 2 resources are available in the model system (generally, the number of coexisting species at equilibrium is not larger than the number of resources; Levin 1970). For all cases, the carbon concentration in each compartment at steady states is presented in Appendix 1.

Next, for each potential equilibrium, we analytically determined the conditions for the local stability using Ruith-Harbiz criteria (see Smith & Waltman 1995). We then calculated numerically which equilibrium is locally stable, depending on the parameters. We showed numerically that only 1 of the 7 possible steady states is stable for any given set of parameters. This analysis permitted us to describe the composition of the bacterial community that would result, depending on the values of the parameters. In particular, we focused on the following parameters that reflect the nature and quality of POC and DOC: (1) BGE using POC and DOC, (2) intensity of hydrolysis, and (3) DOC release ratio from hydrolyzed POC.

Table 1. Model equations

$$\mathrm{d}A_P / \mathrm{d}t = (a_P / n)(C_P / \alpha)F_P - hA_P - (m_A + m_V)A_P \tag{1}$$

$$\mathrm{d}A_G / \mathrm{d}t = (a_G / n)(C_P / \alpha)F_G - hA_G - (m_A + m_V)A_G \tag{2}$$

$$\mathrm{d}F_P / \mathrm{d}t = (n + e_P \alpha f_F / \beta)hA_P - a_P(C_P / \alpha)F_P - m_F F_P \tag{3}$$

$$\mathrm{d}F_G / \mathrm{d}t = (n + e_P \alpha f_F / \beta)hA_G - a_G(C_P / \alpha)F_G + u_G C_D F_G - m_F F_G \tag{4}$$

$$\mathrm{d}F_D / \mathrm{d}t = u_D C_D F_D - m_F F_D \tag{5}$$

$$\mathrm{d}C_P / \mathrm{d}t = s_P - (\alpha / n)(C_P / \alpha)(a_P F_P + a_G F_G) - (m_P + m_V)C_P + t_{DP}m_D C_D + (\alpha + r_P n\beta)m_A(A_P + A_G) + r_P m_F \beta(F_P + F_G + F_D) \tag{6}$$

$$\mathrm{d}C_D / \mathrm{d}t = s_D + \alpha f_D h(A_P + A_G) + t_{PD}m_P C_P - m_D C_D - e_D^{-1}u_G C_D(\beta F_G) - e_D^{-1}u_D C_D(\beta F_D) + r_D m_F \beta(F_P + F_G + F_D) + r_D m_A n\beta(A_P + A_G) \tag{7}$$

Table 2. Definitions of variables and parameters used in the model. Default values are based on literature data and values denoted by asterisk are hypothesized values

Symbol	Definition	Unit	Default value
Variables			
A_X	Abundance of aggregate (X = P, G)	particles l^{-1}	
F_X	Abundance of free-living cells (X = P, G, D)	cells l^{-1}	
C_P	Concentration of POC	mg l^{-1}	
C_D	Concentration of DOC	mg l^{-1}	
Parameters			
a_X	Colonization rate to particles (X = P, G)	particle^{-1} d^{-1}	
u_G	Specific growth rate of free-living generalists	d^{-1}/(mgC l^{-1})	0.2[a]
u_D	Specific growth rate of free-living DOC specialists	d^{-1}/(mgC l^{-1})	0.3[a]
h	Hydrolysis rate of POC	d^{-1}	0.5[b]
m_A	Specific loss rate of particle-associated cell	d^{-1}	0.2[c,d]
m_F	Specific loss rate of free-living cell	d^{-1}	0.2[c,d]
m_P	Specific loss rate of POC	d^{-1}	0.1*
m_D	Specific loss rate of DOC	d^{-1}	0.1*
m_V	Specific loss rate of aggregates and POC by vertical sinking	d^{-1}	0.1*
f_F	Fraction of hydrolyzed POC consumed by bacteria	–	0.3*
f_D	Fraction of hydrolyzed POC released as DOC	–	0.3*
e_P	Growth efficiency on particle	–	0.2[e]
e_D	Growth efficiency in ambient water	–	0.2[e]
t_{PD}	Conversion ratio of POC to DOC	–	0.1*
t_{DP}	Conversion ratio of DOC to POC	–	0.1*
r_P	Recycled ratio of bacterial biomass to POC	–	0.1*
r_D	Recycled ratio of bacterial biomass to DOC	–	0.1*
α	Carbon content per particle	mgC particle^{-1}	
β	Carbon content of bacteria	mgC cell^{-1}	
n	Number of bacterial cells per particle	–	
s_P	Supply rate of POC	mgC l^{-1} d^{-1}	0.4[f]
s_D	Supply rate of DOC	mgC l^{-1} d^{-1}	0.1[f]

[a]Ducklow (2000), [b]Grossart & Simon (1998), [c]Strom (2000), [d]Grossart et al. (2003), [e]del Giorgio & Cole (2000), [f]Williams (2000)

Table 3. Model simplifications. Default values are hypothetical

New symbol	Definition	Unit	Default value
P	C_P	mgC l^{-1}	–
D	C_D	mgC l^{-1}	–
A_x	$\beta n A_x$ (X = P, G)	mgC l^{-1}	–
F_x	βF_x (X = P, G, D)	mgC l^{-1}	–
k	$\alpha \beta^{-1} n^{-1}$		100
a'_P	$a_P \beta^{-1} n^{-1}$		2.5
a'_G	$a_G \beta^{-1} n^{-1}$		1.0

Furthermore, we examined the dependence of community composition at equilibrium on POC and DOC, which are among the most important factors influencing the composition of the bacterial community (Riemann et al. 2000, Riemann & Winding 2001, Selje & Simon 2003). This permitted us to predict successional changes along the spatio-temporal variations in the supplies of POC and DOC, for example, under conditions of heterogeneous distribution of organic carbon in estuarine ecosystems, or with changes in carbon distributions during a phytoplankton bloom. In addition to changes in community composition, we also examined

changes in the distribution of production of each bacterial group with changes in the supply rate of POC. Production rate was calculated by the concentrations of carbon and the density of bacteria at equilibrium. These analyses are based on the assumption that the composition and production are changing with the steady states of the system, during relatively slow changes in POC and DOC supply. This assumption is partly justified by the observation that the changes in the phylogenetic composition occurred rapidly, on a scale of 1 to 2 d, during phytoplankton blooms (Pinhassi et al. 1999, Riemann et al. 2000, Fandino et al. 2001).

RESULTS

Community composition at steady states and community succession

A distinct community composition emerged, depending on various parameters reflecting the quality and quantity of carbon (Fig. 2). There were 5 patterns in composition, depending on the growth efficiency of

bacteria (del Giorgio & Cole 2000) using POC and DOC (Fig. 2a: D, P, G, GD, GP). Note that no bacteria could maintain populations in region N, where the quality of carbon was too low. This figure shows that high BGE for POC leads to the dominance of POC users (POC specialists and generalists; Regions P and GP), whereas high BGE for DOC results in the dominance of DOC users (DOC specialists and generalists; Regions D and GD). Fig. 2a also shows that generalists are members of a community with a broad range of BGE values, but that a monoculture of generalists is realized over a smaller range (Region G in Fig. 2a), while coexistence with other specialists is realized over larger ranges (Regions GD and GP).

We next examined the effect of POC hydrolysis, which also reflects the quality of POC. Fig. 2b shows the dependence of the bacterial community composition on the rate of POC hydrolysis (h) and the rate of POC supply (s_P). Theoretically, increases in the rate of hydrolysis would have both positive and negative influences on DOC specialists: the supply of DOC released from aggregates increases with the rate of hydrolysis, enhancing the growth of DOC specialists

(the positive effect), but at the same time, increased hydrolysis leads to increased production of free-living generalists, resulting in more intense competition for DOC between free-living cells of DOC specialists and generalists (the negative effect). Therefore, the net effect on DOC specialists is intuitively unclear. This model revealed that it was negative (Fig. 2b); when the rate of hydrolysis is very high (Regions G and GP), DOC specialists are progressively excluded. In contrast, when the rate of hydrolysis is low (Region D), which reflects the low quality of particles, DOC specialists, which take up DOC more rapidly than generalists, have a better strategy than generalists that use both DOC and POC, resulting in the competitive exclusion of generalists. Therefore, the coexistence between DOC specialists and generalists is realized only at intermediate levels of the hydrolysis rate (Region GD).

Furthermore, Fig. 2c shows that a different community composition emerges, even when the total hydrolysis rate (h) is constant, depending on the variable partitioning of hydrolyzed POC, i.e. the fraction of the hydrolyzed carbon taken up by particle-associated cells (uptake ratio: f_F) and the fraction released to the surrounding water as DOC (DOC release ratio: f_D). In particular, the uptake ratio by particle-associated cells strongly influences community composition. The increase in the uptake ratio leads to the exclusion of DOC specialists because of increased competition for DOC by increased production of free-living generalists. In contrast, the release ratio to DOC has less of an influence on composition. An increased DOC release ratio does not exclude generalists, because increased DOC supply is used by both DOC specialists and generalist free-living cells, and does not change the competitive relationship between them.

Finally, we examined the dependence of the community composition on the rates of supply of POC and DOC in order to predict successional patterns when there is a shift in the organic carbon supply rate (Fig. 2d). We made the simplifying assumption that the rate of supply of POC (s_P) increases during phytoplankton blooms, while the rate of supply of DOC (s_D) remains fixed. The results show 3 successional patterns with an increasing POC supply rate, depending on the supply rate of DOC. When the DOC supply rate is not limiting (dashed arrow [1] in Fig. 2d), the basic order of succession is (1) DOC specialists only (Region D), (2) the emergence of generalists and their coexistence with DOC specialists (Region GD), (3) the disappearance of DOC specialists (Region G), and (4) the emergence of POC specialists and their coexistence with generalists (Region GP). When the rate of supply of DOC is limiting, DOC specialists cannot maintain their population and 2 patterns of succession
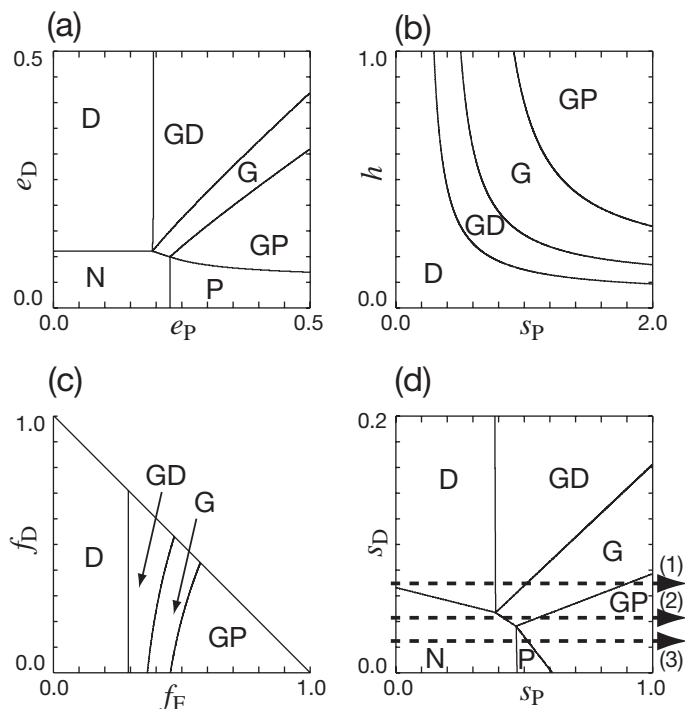

Fig. 2. Composition of the bacterial community as a consequence of variations in key parameters. The composition of species is denoted as follows: N: extinction of all 3 groups, D: dominance of DOC specialists, P: dominance of POC specialists, G: dominance of generalists, GD: coexistence of generalists and DOC specialists, GP: coexistence of generalists and POC specialists. Dashed arrows in (d) represent temporal changes in POC supply rate. Parameters were set as default values from Tables 1 & 2
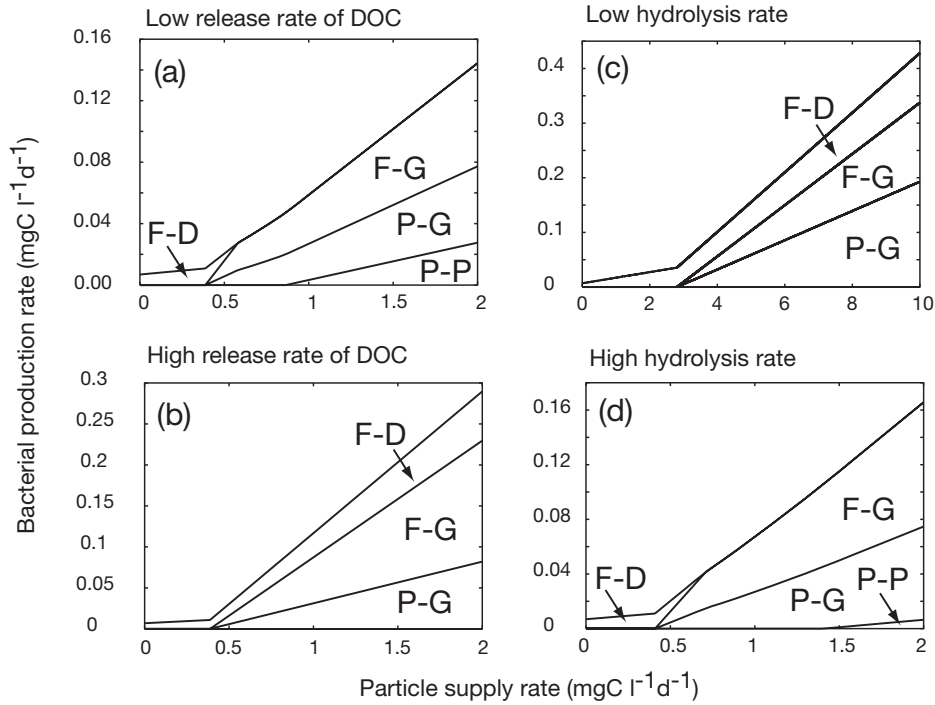
Fig. 3. Changes in the distribution of bacterial production with increasing POC supply, showing the production of the groups using each strategy. F-D: production of free-living DOC specialists, F-G: production of the free-living fraction of generalists, P-P: production of the particle-associated fraction of POC specialists. Parameter values: (a) $f_F = 0.3$, $f_D = 0.2$, (b) $f_F = 0.3$, $f_D = 0.7$, (c) $h = 0.08$, (d) $h = 0.45$. Other parameters were set as default values from Tables 1 & 2

develop. When the DOC supply rate is intermediate (dashed arrow [2] in Fig. 2d), generalists emerge earlier than POC specialists. However, when the DOC supply rate is very low (dashed arrow [3] in Fig. 2d), POC specialists emerge earlier than generalists. Similarly, the order of succession with increasing rates of supply of DOC depends on the rate of supply of POC. Furthermore, even in the more realistic case, in which both POC and DOC supplies change during the bloom, we can predict the successional order if the temporal patterns of POC and DOC supply are known.

Effects of particle abundance on the distribution of bacterial production

Next, we examined the effects of particle abundance on the distribution of bacterial production, i.e. the production rate of each bacterial group. We can qualitatively predict the changes in bacterial production that occur in response to spatio-temporal variations in the POC supply rate. The effects of DOC abundance on the structure of bacterial production are relatively simple and, therefore, are not shown here.

The production of particle-associated cells is expected to increase with increasing POC supply rates,

and this proved to be true in the model (Fig. 3). Similarly, the total production of the free-living fraction (F-D + F-G, Fig. 3) was shown to always increase with increasing POC supply rates, regardless of the values set for the other parameters (Fig. 3). This is probably because increases in POC lead to increases in the DOC released from aggregates, resulting in the increased production of free-living cells, regardless of whether the DOC is used by generalist or by DOC specialist cells.

However, increasing the rate of POC supply changes the distribution of production in the free-living fraction of the community in different ways, depending on other factors (Fig. 3). For example, the production of DOC specialists (F-D) decreases with increasing POC supply when the fraction of hydrolysate released to the water (f_D) is low (Fig. 3a), whereas the production of DOC specialists increases when the DOC release rate is high (Fig. 3b). In contrast, the production of DOC specialists (F-D) increases with increasing POC supply when the rate of hydrolysis (h) is low (Fig. 3c), but decreases with increasing POC supply when the hydrolysis rate is high (Fig. 3d). In all cases, the production of generalists (F-G) increases with the POC supply.

Note that increasing POC supply rates always have both positive and negative effects on the production of

DOC specialists through interactions with generalists. By hydrolyzing POC, the generalists increase the supply of DOC to DOC specialists; however, the concomitant increase in the production of free-living generalist cells results in increased competition. Our model suggests that the net effect on DOC specialists shifts from negative to positive when the DOC release rate increases (compare Fig. 3a with 3b) or when the rate of hydrolysis decreases (compare Fig. 3d with 3c). Similarly, numerical calculations with equilibrium values of organic carbon and bacterial biomass demonstrated that the net effect of increased POC supply on DOC specialists shifts to positive when the BGE for DOC (e_D), recycling ratio to DOC (r_D), or mortality rate on aggregates (m_A) increase. In contrast, the net effect becomes negative when the uptake ratio of hydrolyzed POC (f_F), the BGE for POC (e_P), or carbon content per particle per bacterial carbon ($\alpha/n\beta$) increase. Moreover, some factors are neutral, i.e. the net effect of changes in the POC supply remains the same, despite changes in the ratio of recycling to POC (r_P) or in the rates of physical and chemical conversion between POC and DOC (t_{PD} and t_{DP}).

DISCUSSION

Interactions among generalists and specialists through hydrolysis

Similarities between the phylogenetic composition of particle-associated and free-living bacterial communities have recently been shown, drawing increased attention from microbial ecologists to the existence of generalists; their ecological roles, however, remain unclear. Moreover, although the hydrolysis processes on aggregates have been intensely studied in recent years, the effects on the total bacterial community, including both free-living and particle-associated fractions, remain unclear. In the present study, we defined POC specialists, DOC specialists, and generalists, and used a theoretical model to examine how interactions among bacterial groups with these 3 strategies determine the composition of the bacterial community and the distribution of secondary production by bacteria. Our model demonstrated that the outcome of interactions depends on the supply and the quality (BGE, hydrolysis rate, and DOC release ratio from aggregates) of POC and DOC. When the supply or quality of the common resource increases, generalists are able to coexist with their competitors; large supplies and high quality of DOC tend to allow coexistence with DOC specialists, and large supplies and high quality of POC tend to allow coexistence with POC specialists (Fig. 2). In contrast,

when the supply and quality of the resource used only by generalists increase, coexistence with the competitor is not favored; larger supplies and higher quality of DOC, for example, lead to the exclusion of POC specialists (Fig. 2). However, for the interactions between generalists and DOC specialists, this is not always true, because the effects of POC hydrolysis by generalists on DOC specialists are not straightforward.

The interactions between the 2 groups are commensal as well as competitive, and hydrolysis and the subsequent processes are involved in both competitive and commensal interactions. The production of new, free-living, generalist cells by using hydrolyzed POC has a negative, competitive effect on DOC specialists; thus, a high ratio of hydrolyzed POC used for production of new cells (f_F) favors the generalists. In contrast, the release of hydrolyzed POC as DOC has a positive, commensal effect on DOC specialists. Thus, when the DOC release ratio (f_D) is high, the commensal interaction prevents the exclusion of DOC specialists. This also enables the coexistence of the 2 groups, even when the supply of POC, which is used directly only by generalists, increases (Fig. 3b), implying that DOC specialists are not out-competed by generalists. Zissi & Lyberatos (2001), using a mathematical model and a chemostat experiment, obtained similar results, showing that interactions with both competitive and commensal components enable the coexistence of 2 bacteria that cannot coexist in an exclusively competitive relationship. Note that a commensal interaction also exists between generalists and POC specialists: POC specialists supply DOC to free-living generalists. However, the increased supply of DOC indirectly intensifies the competitive interactions for POC, so that the commensal interaction does not facilitate coexistence.

In addition, increases in the *total* hydrolysis rate (h) lead to increases in both the DOC release ($f_D h$; commensal) and the production of free-living generalist cells ($f_F h$; competitive). Our analysis showed that the net effect of increased hydrolysis on DOC specialists is negative and results in the exclusion of DOC specialists (Fig. 2b). Increases in the hydrolysis rate lead to increases in both resource availability (DOC) and reproduction rate (of free-living cells) for generalists (by direct uptake of hydrolysate). However, increases in the hydrolysis rate result only in increases in resource availability (DOC) for DOC specialists, without affecting their reproduction directly. The net negative effect of increased hydrolysis on DOC specialists can probably be attributed to competition between DOC specialists and increasing numbers of free-living POC-DOC generalists for the fraction of hydrolysate released as DOC.

Simplicity of our model

We made several assumptions to justify the simplification of our model formulations. (1) We assumed that aggregate formation rate was in proportion to the densities of particles and free-living bacterial cells (i.e. simple mass reaction). Although encounter rates are influenced by particle size or by swimming strategies of bacteria (Kiørboe & Jackson 2001), we did not focus on the heterogeneity in the morphologies of particles or species-specific differences in chemotoxis. Therefore, a simple encounter rate is suitable for the predictions we made. (2) A simple linear, non-saturating uptake function of DOC was assumed. The introduction of a saturating function would not change the competitive interactions among specialists and generalists at steady states. (3) Trade-offs among specialists and generalists were assumed. There are actually various types of trade-offs and differences among specialists and generalists, e.g. the differences in hydrolysis rate or in growth efficiency using POC and DOC. However, the essential point is that of the existence of trade-offs between specialists and generalists, and additional numerical calculations showed that qualitative predictions were not changed under the different types of trade-offs. (4) Another critical assumption was the first order approximation for POC and DOC loss rate due to physical or chemical processes. One of our results showed that loss processes of POC and DOC did not change the patterns of production distribution. This indirectly suggested that these processes do not critically influence the interactions among specialists and generalists, and that the assumed simple loss rate is sufficient for our theoretical investigation.

Testable predictions from this model

Consideration of the interactions among DOC specialists, generalists, and POC specialists provides testable predictions regarding (1) the successional order of functional composition, and (2) changes in the distribution of bacterial production concurrent with the spatio-temporal variation in POC supply rate.

This is the first theoretical work predicting the successional order of bacterial community composition. When particle abundance increases, e.g. during a phytoplankton bloom, the successional order depends on the DOC supply rate. In the basic pattern, produced when the DOC supply rate is not limiting, the order of emergence of each group is: (1) DOC specialists, (2) generalists, and (3) POC specialists. We predicted that the emergence of POC specialists follows the emergence of generalists, which is consistent with the later emergence of 'particle specialists' in studies by

Riemann & Winding (2001) of community dynamics during an induced phytoplankton bloom. However, our model also predicted that when the DOC supply rate is very low, POC specialists emerge before generalists. In fact, because the POC and DOC supply rates change simultaneously during phytoplankton blooms, the successional order may differ from the above predictions, which are based on an assumption of a fixed DOC supply rate. However, even in that case, we can predict the successional order from the composition patterns produced by changes in the POC and DOC supply rates.

The prediction that bacterial production in both the particle-associated community and the free-living community is enhanced by increased POC supply is very intuitive. Increased supplies of DOC from the hydrolysis of aggregates supports increased production in the free-living community. In the particle-associated community, the model predicted that both POC specialists and generalists would increase production. The patterns of change in the production distribution within the free-living community are different; both generalists and DOC specialists increase production, or DOC specialists decrease production while generalists increase production. In our model, we clarified the factors that can explain these opposite effects of increased POC on production in the free-living fraction. The balance of competitive and commensal interactions between generalists and DOC specialists is important for determining the pattern of changes in production. When the quality of POC is high, as reflected by a high hydrolysis rate (h), high growth efficiency (e_P), and high carbon content of particles ($\alpha/n\beta$), the net interaction is competitive, and the production of DOC specialists will decrease with increasing particle supply. Selectively low mortality in particle-associated cells (m_A) also leads to decreases in the production of DOC specialists with increasing particle supply. In contrast, when hydrolysis is highly uncoupled with bacterial growth (high f_D and low f_F), and when the quality of DOC (e_D) is high, the net interaction is commensal, and the production of DOC specialists increases with increasing particle supply. The prediction that bacterial production in the free-living community is enhanced by increased POC supply is supported by earlier observations (Friedrich et al. 1999, Grossart et al. 2003). Furthermore, the predicted net negative effect on DOC specialists is one of the possible explanations for the observation that disappearance of some free-living species occurred during the bloom (Riemann & Winding 2001).

Chlorophyll *a* content and turbidity are often used as indices of particle abundance, which influences the interaction between particle-associated and free-living bacteria. However, it is also necessary to examine the

origin and composition of the particulate (Grossart et al. 2003) and dissolved (Crump et al. 2003) organic matter, as suggested by the prediction that the qualities of POC and DOC are important factors in determining the population dynamics of free-living bacteria. Additionally, because selective mortality rates would also mediate the interactions between particle-associated and free-living bacteria, interactions with protozoan grazers and viruses must also be taken into consideration (Jürgens & Sala 2000, Riemann et al. 2000, Artolozaga et al. 2002). We considered the production by each group separately because, if the free-living cells of DOC specialists and generalists were to be attacked by different predators or viruses, the production of each group, not the whole free-living community, would influence the higher trophic levels. Thus, different patterns of changes in production within the free-living community would lead to different changes in community structure at higher trophic levels. In addition, the question of how each fraction of bacterial production, of 3 different functional groups, influences the whole biochemical cycle in aquatic ecosystems warrants further empirical and theoretical investigation.

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Appendix 1. There are 7 equilibria in regard to bacterial composition. In this appendix, we calculated the carbon concentrations of each compartment for each equilibrium

(1) For the equilibrium where all 3 groups of bacteria are absent (E_N):

$$P_N{}^* = (s_P + t_{DP}s_D)\left[(1 - t_{PD}t_{DP})m_P + m_V\right]^{-1}$$
$$D_N{}^* = \left[(1 - t_{PD}t_{DP})m_P + m_V\right]^{-1} m_D{}^{-1}\left[t_{PD}s_P + (m_P + m_V)s_D\right]$$
$$F_{D,N}{}^* = F_{P,N}{}^* = F_{G,N}{}^* = 0$$
$$A_{P,N}{}^* = A_{G,N}{}^* = 0$$

(2) For the equilibrium where only DOC specialists exist (E_D):

$$P_D{}^* = (m_P + m_V)^{-1}(s_P + u_D{}^{-1}t_{PD}m_D m_F + r_P m_F F_{D,D}{}^*)$$
$$D_D{}^* = m_F u_D{}^{-1},$$
$$F_{D,D}{}^* = m_F{}^{-1}\left[e_D{}^{-1} - r_D - r_P t_{PD}m_P(m_P + m_V)^{-1}\right]^{-1}\left\{t_{PD}s_P m_P(m_P + m_V)^{-1} + s_D - u_D{}^{-1}m_D m_F\left[1 - t_{PD}t_{DP}m_P(m_P + m_V)^{-1}\right]\right\}$$
$$F_{P,D}{}^* = F_{G,D}{}^* = 0$$
$$P_{P,D}{}^* = P_{G,D}{}^* = 0$$

(3) For the equilibrium where only generalists exist (E_G):

$$D_G{}^* = u_G{}^{-1}\left\{k^{-1}a'_G P_G{}^*\left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F)\right] + m_F\right\}$$
$$F_{G,G}{}^* = \left\{a'_G P_G{}^*\left[1 - (h + m_A + m_V)^{-1}m_A(1 + k^{-1}r_P)\right] - m_F r_P\right\}^{-1}$$
$$\times \left(s_P - (m_P + m_V)P_G{}^* + t_{DP}m_D u_G{}^{-1}\left\{k^{-1}a'_G P_G{}^*\left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F)\right] + m_F\right\}\right)$$
$$F_{P,G}{}^* = F_{D,G}{}^* = 0$$
$$A_{G,G}{}^* = k^{-1}a'_G(h + m_A + m_V)^{-1}P_G{}^* \times F_{G,G}{}^*$$
$$A_{P,G}{}^* = 0$$

where $P_G{}^*$ is the plausible solution of the following equation:

$$\alpha x^2 + \beta x + \gamma = 0$$

where (see next page)

$$\alpha = \left\{ t_{PD} m_P - m_D a'_G (u_G k)^{-1} \left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F) \right] \right\} \times \left\{ a'_G \left[1 - (h + m_A + m_V)^{-1}(m_A + m_A r_P k^{-1}) \right] \right\}$$
$$+ \left\{ t_{DP} m_D a'_G (u_G k)^{-1} \left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F) \right] - (m_P + m_V) \right\}$$
$$\times \left\{ a'_G k^{-1} (h + m_A + m_V)^{-1}(k f_D h + r_D m_A) - a'_G (e_D k)^{-1} \left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F) \right] \right\}$$

$$\beta = \left\{ t_{PD} m_P - m_D a'_G (u_G k)^{-1} \left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F) \right] \right\}(-r_P m_F) + \left\{ a'_G \left[1 - (h + m_A + m_V)^{-1} m_A (1 + k^{-1} r_P) \right] \right\}(s_D - m_D m_F u_G^{-1})$$
$$+ \left\{ t_{DP} m_D a'_G (u_G k)^{-1} \left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F) \right] - (m_P + m_V) \right\} \times \left[(r_D - e_D^{-1}) m_F \right] + \left\{ a'_G k^{-1} (h + m_A + m_V)^{-1}(k f_D h + r_D m_A) \right.$$
$$\left. - a'_G (e_D k)^{-1} \left[1 - h(h + m_A + m_V)^{-1}(1 + ke_P f_F) \right] \right\} \times (s_P + t_{DP} m_D m_F u_G^{-1})$$

$$\gamma = m_F (-e_D^{-1} + r_D)(s_P + u_G^{-1} t_{DP} m_D m_F) - r_P m_F (s_D - u_G^{-1} m_D m_F)$$

(4) For the equilibrium where only POC specialists exist (E_P):

$$P_P^* = a'_P^{-1} k m_F \left[h(h + m_A + m_V)^{-1}(1 + ke_P f_F) - 1 \right]$$

$$D_P^* = m_D^{-1} \left\{ a'_P P_P^* \left[1 - (h + m_A + m_V)^{-1} m_A (1 + k^{-1} r_P) \right] - r_P m_F - t_{DP} \left[(h + m_A + m_V)^{-1} a'_P (f_D h + k^{-1} r_D m_A) P_P^* + r_D m_F \right] \right\}^{-1}$$
$$\times \left(\left[(h + m_A + m_V)^{-1} a'_P (f_D h + k^{-1} r_D m_A) P_P^* + r_D m_F \right] \left[s_P - (m_P + m_V) P_P^* \right] \right.$$
$$\left. + (s_D + t_{PD} m_P P_P^*) \left\{ a'_P P_P^* \left[1 - m_A (h + m_A + m_V)^{-1}(1 + k^{-1} r_P) \right] - r_P m_F \right\} \right])$$

$$F_{P,P}^* = \left\{ a'_P P_P^* \left[1 - (h + m_A + m_V)^{-1}(1 + k^{-1} r_P) m_A \right] - r_P m_F \right\}^{-1} \times \left[s_P - (m_P + m_V) P_P^* + t_{DP} m_D D_P^* \right]$$

$$F_{D,P}^* = F_{G,P}^* = 0$$

$$A_{P,P}^* = k^{-1} a'_P (h + m_A + m_V)^{-1} P_P^* \times F_{P,P}^*$$

$$A_{G,P}^* = 0$$

(5) For the equilibrium where DOC specialists and POC specialists coexist (E_{XD}) (X = G):

$$P_{XD}^* = a'_X^{-1} k m_F \left[(h + m_A + m_V)^{-1} h(1 + ke_P f_F) - 1 \right]^{-1} (1 - u_D^{-1} u_X)$$

$$D_{XD}^* = u_D^{-1} m_F$$

$$F_{D,XD}^* = m_F^{-1} (e_D^{-1} - r_D)^{-1} \left\{ s_D + t_{PD} m_P P_{XD}^* - m_D D_{XD}^* + \left[a'_X (f_D h + k^{-1} r_D m_A)(h + m_A + m_V)^{-1} P_{XD}^* - u_X D_{XD}^* + r_D m_F \right] F_{X,XD}^* \right\}$$

$$F_{X,XD}^* = \left\{ a'_X \left[1 - (h + m_A + m_V)^{-1} m_A (1 + k^{-1} r_P) \right] P_{XD}^* - r_P m_F - r_P (e_D^{-1} - r_D)^{-1} \left[a'_X (h + m_A + m_V)^{-1}(f_D h + k^{-1} r_D m_A) P_{XD}^* - u_X D_{XD}^* + r_D m_F \right] \right\}^{-1}$$
$$\times \left[s_P - (m_P + m_A) P_{XD}^* + t_{DP} m_D D_{XD}^* + r_P (e_D^{-1} - r_D)^{-1}(s_D + t_{PD} m_P P_{XD}^* - m_D D_{XD}^*) \right]$$

$$A_{X,XD}^* = k^{-1} a'_X (h + m_A + m_V)^{-1} P_{XD}^* \times F_{X,XD}^*$$

(6) For the equilibrium where DOC specialists and POC specialists coexist (E_{XD}) (X = P):

we can calculate the equilibrium using the same equations as those for E_{GD} (Eq. 5), noting that we set $u_P = 0$.

(7) For the equilibrium where generalists and POC specialists coexist (E_{GP}):

$$P_{GP}^* = a'_P^{-1} k m_F \left[(h + m_A + m_V)^{-1} h(1 + ke_P f_F) - 1 \right]^{-1}$$

$$D_{GP}^* = u_G^{-1} \left\{ a'_G k^{-1} \left[1 - (h + m_A + m_V)^{-1} h(1 + ke_P f_F) \right] P_{GP}^* + m_F \right\}$$

$$F_{D,GP}^* = 0$$

$$\begin{pmatrix} F_{P,GP}^* \\ F_{G,GP}^* \end{pmatrix} = (AD - BC)^{-1} \begin{pmatrix} D & -B \\ -C & A \end{pmatrix} \begin{pmatrix} X \\ Y \end{pmatrix}$$

where

$$A = a'_P \left[1 - (h + m_A + m_V)^{-1}(1 + k^{-1} r_P) m_A \right] P_{GP}^* - r_P m_F$$

$$B = a'_G \left[1 - (h + m_A + m_V)^{-1}(1 + k^{-1} r_P) m_A \right] P_{GP}^* - r_P m_F$$

$$C = a'_P (f_D h + k^{-1} r_D m_A) P_{GP}^* + r_D m_F$$

$$D = a'_G (f_D h + k^{-1} r_D m_A) P_{GP}^* + r_D m_F - u_G D_{GP}^*$$

$$X = s_P - (m_P + m_V) P_{GP}^* + t_{DP} m_D D_{GP}^*$$

$$Y = -s_D - t_{PD} m_P P_{GP}^* + m_D D_{GP}^*$$

$$A_{P,GP}^* = k^{-1} a'_P (h + m_A + m_V)^{-1} P_{GP}^* \times F_{P,GP}^*$$

$$A_{G,GP}^* = k^{-1} a'_G (h + m_A + m_V)^{-1} P_{GP}^* \times F_{G,GP}^*$$