

Competition between microorganisms for a single limiting resource with cell quota structure and spatial variation

James P. Grover · Sze-Bi Hsu · Feng-Bin Wang

Received: 26 August 2010 / Revised: 19 April 2011
© Springer-Verlag 2011

Abstract Microbial populations compete for nutrient resources, and the simplest mathematical models of competition neglect differences in the nutrient content of individuals. The simplest models also assume a spatially uniform habitat. Here both of these assumptions are relaxed. Nutrient content of individuals is assumed proportional to cell size, which varies for populations that reproduce by division, and the habitat is taken to be an unstirred chemostat where organisms and nutrients move by simple diffusion. In a spatially uniform habitat, the size-structured model predicts competitive exclusion, such that only the species with lowest break-even concentration persists. In the unstirred chemostat, coexistence of two competitors is possible, if one has a lower break-even concentration and the other can grow more rapidly. In all habitats, the calculation of competitive outcomes depends on a principal eigenvalue that summarizes relationships among cell growth, cell division, and cell size.

S.-B. Hsu and F.-B. Wang's research partially supported by National Council of Science, Republic of China.

J. P. Grover
Department of Biology and Program in Environmental and Earth Sciences,
University of Texas at Arlington, P.O. Box 19498, Arlington, USA
e-mail: grover@uta.edu

S.-B. Hsu
Department of Mathematics and National Center for Theoretical Science,
National Tsing Hua University, Hsinchu 300, Taiwan, ROC
e-mail: sbhsu@math.nthu.edu.tw

F.-B. Wang (✉)
Department of Mathematics, National Tsing Hua University, Hsinchu 300, Taiwan, ROC
e-mail: d917203@oz.nthu.edu.tw

Keywords Chemostat · Competitive exclusion · Coexistence · Quota · Spatial habitat

Mathematics Subject Classification (2010) 35K55 · 37C65 · 92D25

1 Introduction

Competition between species for resources is a fundamental ecological process (Grover 1997; Tilman 1982). Any mathematical model that explicitly addresses both resource and population dynamics must specify how much resource is consumed in the production of one new individual. The simplest competition models neglect differences between individuals, using one ordinary differential equation to govern the dynamics of each species. These population dynamics are coupled to dynamics of one or more resources by assuming a constant quota of nutrient per individual, or equivalently, a constant yield of individuals from consumption of a unit of resource (Grover 1997). Alternatively, quotas may vary. Rapid population growth often requires a larger quota than slow growth (Droop 1983). Assuming that all individuals have the same quota at any instant, the dynamics of quota for a species can be described by an ordinary differential equation, leading to variable-internal-stores models (Grover 1991; Hsu and Hsu 2008; Hsu et al. 2010; Smith and Waltman 1994). When quotas differ among individuals at any instant, the distribution of quotas among each species' population, and the dynamic changes of population size and quota distribution must be addressed with a structured population model (Diekmann and Metz 1986).

Classical models of competition also often assume a simple, well-mixed habitat, such as the chemostat culture system, in which a nutrient resource is supplied via an inflow, and a balancing outflow removes nutrient and organisms (Smith and Waltman 1995). The chemostat is a highly idealized portrayal of an aquatic habitat such as a lake or pond. Alternatively and more realistically, the habitat may be poorly mixed, and have spatial gradients of resource availability. In such cases the distributions of the resource and of each species' population over space must be addressed. One simple, spatially distributed habitat is the unstirred chemostat, in which inflow of resource occurs at one point and outflow at another, with diffusive transport of nutrient and organisms between these points (Hsu and Waltman 1993).

Many simple models with a single growth-limiting resource in a well-mixed habitat make a simple prediction about competitive dynamics: the species with the lowest break-even concentration for the nutrient resource will win (Grover 1997; Hsu et al. 1977). Generically, each competing species requires a different nutrient concentration to support reproduction that balances its mortality rate; the one with the lowest such break-even requirement ultimately consumes so much that other species cannot persist in the long term. With only a single limiting resource in a well mixed habitat, two or more species cannot coexist, a result known as the Competitive Exclusion Principle (Grover 1997). This conclusion arises for models with constant quota (Hsu et al. 1977) as well as for variable-internal-stores models (Hsu and Hsu 2008; Smith and Waltman 1994).

For competition models with constant quota, outcomes of competition in a spatially variable habitat can differ from those in an otherwise equivalent well mixed habitat. Notably, it is often possible for two species to coexist on a single limiting resource, when one species has a lower break-even concentration and the other has a higher maximal rate of population growth, a result that depends quantitatively on parameters describing the species. This result arises in the unstirred chemostat (Hsu et al. 1977, 1994; Hsu and Waltman 1993), and also in habitats with advective as well as diffusive transport (Baxley and Robinson 1998; Grover et al. 2009).

The dynamics of competition with both variable quotas and a spatially variable habitat have received very little attention. Partial differential equations that describe the distributions of quotas among populations must be combined with those describing spatial transport, potentially leading to very complex models. An approximation that avoids some of the potential complexity is to assume that at any location, all individuals have the same quota, as if there were instantaneous redistribution of resources among individuals at the same place. This assumption leads to a set of partial differential equations for distributions over space without explicitly representing the distributions of quotas in populations (Hsu et al. 2010). For a model of competition in the unstirred chemostat based on this approach, coexistence of two species on one resource is again possible for competitors with appropriate parameter values. The consequences of relaxing the assumption of equal quotas for individuals at a given location remain unclear. Computational models that avoid this assumption have been constructed (Grover 2009), and while coexistence of two competitors on one resource is not common in such models it can occur.

Here, we take a step towards understanding competition when both spatial and quota variation occur. We present a model for both the distributions of quotas in populations and the distributions of populations and the resource over space. The setting is the unstirred chemostat, and a particularly simple form of quota variation is postulated—the quota of resource for an individual is proportional to its size, and individuals reproduce by simple division into two equally-sized daughters. Quota increases as individuals grow, which is coupled to resource consumption, and as individuals get larger they become more likely to divide. Such a model applies best to microorganisms reproducing by simple binary cell division, and to nutrient resources that compose a large fraction of the microbial cell. Carbon, which bacteria obtain from dissolved sugars or other organic compounds, is an example of such a nutrient. Another might be silicon for diatoms, which composes the cell wall and is thus strongly related to cell size. By treating quota as proportional to cell size, we build on previous work addressing size-structured populations, extending it to competition in a spatially variable habitat.

Models for populations structured by age or size are often based on the McKendrick–Von Foerster equation (Sinko and Streifer 1967). Though many properties of such models are well known, very few studies have addressed either spatially varying habitats or competition between species. Some single-species, age-structured models in a spatially varying habitat can be reduced to partial differential equations representing distributions in space alone (Gurtin and Maccamy 1981), and for such models the semigroup generated by the age-structure model in the spatially variable habitat has properties similar to the semigroup generated in a spatially uniform habitat (Chan and Guo 1989, 1994). Models of competition with size structure have been

examined in spatially uniform settings. With the assumption of a negligible juvenile period prior to reproduction, Cushing (1989, 1990) reduced a size-structured model of two competing species and one limiting resource to a system of ordinary differential equations which demonstrated competitive exclusion. His model is most appropriate for application to small, invertebrate animals.

To our knowledge, no previous study has examined a size-structured model of competition for a resource in a spatially variable habitat. Here, we do so using a model somewhat different from that of Cushing (1989, 1990), appropriate for microorganisms reproducing by fission into two daughter cells, similar to prior single-species models for a spatially uniform habitat (Diekmann et al. 1984; Diekmann and Metz 1986). The quotas of the nutrient resource for each species are assumed to be proportional to their size. We are able to show that in an unstirred chemostat setting, with diffusion of populations and nutrient, the quota-structured model predicts qualitatively similar results to previous unstructured models (Hsu et al. 1994; Hsu and Waltman 1993). Namely, coexistence of two competitors is possible for some parameter values, with outcomes of persistence and coexistence related to principal eigenvalue problems.

The organization of the paper is as follows. In Sect. 2, we study a competition model for a single limiting resource with quota structure in the well-mixed habitat. A population operator (with division) was studied by the authors (Diekmann et al. 1984; Heijmans 1985) in L^1 space (or C space). By appealing to the asymptotic behavior of the semigroup associated with this operator, the size-structure model in a uniform habitat can be reduced to the classical one in Hsu (1978) and the so-called Competitive Exclusion Principle is proved. In Sect. 3, we further study a model with quota structure in the variable habitat, that is, we add a spatial diffusion term into our model. In contrast to the operator without diffusion, we identify the generator and determine its spectral properties in the Hilbert space. Furthermore, the structure of the semigroup for the population with diffusion is essentially determined by those of the semigroup for the population without diffusion. The property of the asymptotic behavior of this semigroup (with diffusion) reduces the model with quota structure in the unstirred chemostat to the one in Hsu and Waltman (1993) and then we can show that coexistence is possible.

2 Competition of n microorganisms for a single limiting resource with quota structure

2.1 Preliminaries: a population operator in L^1 space

In this section, we review the following equation (Diekmann et al. 1984; Diekmann and Metz 1986; Heijmans 1985):

$$\frac{\partial n(t, q)}{\partial t} + \frac{\partial(g(q)n(t, q))}{\partial q} = -\mu(q)n(t, q) - b(q)n(t, q) + 4b(2q)n(t, 2q). \quad (2.1)$$

Here t denotes time, q stands for the size of an individual cell. n is the population density function, that is, $\int_{q_1}^{q_2} n(t, q) dq$ represents the number of cells with size between

q_1 and q_2 at time t . The functions $\mu(q)$, $b(q)$ and $g(q)$ are the rates at which cells of size q die, divide and grow, respectively. The second term at the left hand side (The first term at the right hand side) denotes changes due to the growth (death or dilution) of cells. The last two terms describe the reproduction process. The factor 4 in the birth term may be strange to the readers. We refer the Appendix in [Diekmann et al. \(1984\)](#) for a derivation of equation (2.1).

We assume that an individual cannot divide before reaching a minimal size $q_{\min} > 0$. Consequently, cells with size less than $\frac{1}{2}q_{\min}$ can not exist, which is expressed by the boundary condition

$$n\left(t, \frac{1}{2}q_{\min}\right) = 0. \tag{2.2}$$

Furthermore, we assume that cells have to divide before reaching a maximal size which is denoted by q_{\max} . Thus we have to impose the following condition on b :

$$\int_{q_{\min}}^{q_{\max}} b(q) dq = \infty.$$

Throughout this paper, we impose the following assumptions on g , μ and b :

- (H_g) g is a continuous, strictly positive function on $[\frac{1}{2}q_{\min}, q_{\max}]$.
- (H _{μ}) μ is a non-negative, integrable function on $[\frac{1}{2}q_{\min}, q_{\max}]$.
- (H_b) $b(q) = 0$ on $[\frac{1}{2}q_{\min}, q_{\min}]$ and $b(q) > 0$ on (q_{\min}, q_{\max}) ,
 b is integrable on $[q_{\min}, q_{\max} - \epsilon]$ for all $\epsilon > 0$ and
 $\lim_{\epsilon \downarrow 0} \int_{q_{\min}}^{q_{\max} - \epsilon} b(q) dq = \infty$.

We shall assume that the initial condition n^0 is

$$n(0, q) = n^0(q). \tag{2.3}$$

Let $E(q) = \exp(-\int_{q_{\min}/2}^q \frac{\mu(\eta)+b(\eta)}{g(\eta)} d\eta)$. Then the transformation

$$m(t, q) = \frac{g(q)}{E(q)} n(t, q) \tag{2.4}$$

leads the system (2.1), (2.2) and (2.3) into the following evolution equation (see, e.g., [Diekmann et al. 1984](#) and [Diekmann and Metz 1986](#), p. 48):

$$\begin{cases} \frac{\partial m(t, q)}{\partial t} = -g(q) \frac{\partial m(t, q)}{\partial q} + k(q)m(t, 2q), \\ m(t, \frac{1}{2}q_{\min}) = 0, \\ m(0, q) = m^0(q), \end{cases} \tag{2.5}$$

where

$$k(q) = \begin{cases} 4 \frac{g(q)}{E(q)} \frac{E(2q)}{g(2q)} b(2q), & \text{for } \frac{1}{2}q_{\min} \leq q \leq \frac{1}{2}q_{\max}, \\ 0, & \text{for } q > \frac{1}{2}q_{\max}, \end{cases} \tag{2.6}$$

and $m^0(q) = \frac{g(q)}{E(q)}n^0(q)$. It is clear that $E(q_{\max}) = 0$. From (2.4), it follows that $n(t, q)$ has to go to zero as $q \uparrow q_{\max}$ (see, e.g., Diekmann and Metz 1986, p. 49). That is, $n(t, q_{\max}) = 0$ holds automatically.

Let $X = \{\psi \in C[\frac{1}{2}q_{\min}, q_{\max}] : \psi(\frac{1}{2}q_{\min}) = 0\}$ provided with the supremum norm. We will look for a solution $t \mapsto m(t, \cdot)$ of (2.5) which takes values in the Banach space X . We rewrite (2.5) as the abstract Cauchy problem

$$\begin{cases} \frac{dm}{dt} = Am, \\ m(0) = m^0, \end{cases}$$

where A is an un-bounded operator defined by

$$(A\psi)(q) = \begin{cases} -g(q)\psi'(q) + k(q)\psi(2q), & \text{for } \frac{q_{\min}}{2} \leq q \leq \frac{q_{\max}}{2}, \\ -g(q)\psi'(q), & \text{for } \frac{q_{\max}}{2} < q \leq q_{\max}, \end{cases}$$

with a domain

$$D(A) = \left\{ \psi \in X : \psi \text{ is } C^1 \text{ on } \left[\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max} \right) \cup \left(\frac{1}{2}q_{\max}, q_{\max} \right]; \text{ the limits } \lim_{q \uparrow \frac{1}{2}q_{\max}} [-g(q)\psi'(q) + k(q)\psi(2q)] \text{ and } \lim_{q \downarrow \frac{1}{2}q_{\max}} [-g(q)\psi'(q)] \text{ exist and equal each other; } -g\left(\frac{1}{2}q_{\min}\right)\psi'\left(\frac{1}{2}q_{\min}\right) + k\left(\frac{1}{2}q_{\min}\right)\psi(q_{\min}) = 0 \right\}.$$

In the following, we collect some properties related to the operator A

Lemma 2.1 (Diekmann et al. 1984; Heijmans 1985) *A is a closed, densely operator defined on X.*

Lemma 2.2 (Diekmann et al. 1984) *A is the infinitesimal generator of a C_0 semi-group $T(t)$ on X.*

Throughout the rest of this section, we make the following assumption:

$$q_{\min} > \frac{1}{2}q_{\max}, \tag{2.7}$$

which means that the smallest mother is still larger than the biggest daughter or, in other words, a cell which is just created cannot divide.

Let

$$\pi(\lambda) = 2 \int_{q_{\min}}^{q_{\max}} \frac{b(\xi)}{g(\xi)} \exp \left[- \int_{\xi/2}^{\xi} \frac{\lambda + \mu(\eta) + b(\eta)}{g(\eta)} d\eta \right] d\xi. \tag{2.8}$$

It is not hard to see that π is strictly decreasing and continuous on the real axis. Further, $\pi(-\infty) = \infty$ and $\pi(+\infty) = 0$. Thus there exists a unique real number $\hat{\lambda}_0$ satisfying

$$\pi(\hat{\lambda}_0) = 1.$$

Lemma 2.3 (Theorem 5.1 on p. 58 and Theorem 5.10 on p. 60 in [Diekmann and Metz 1986](#)) *The operator A has precisely one real eigenvalue $\hat{\lambda}_0$ which is simple. Furthermore, if $g(2q) \neq 2g(q)$ for some $q \in [\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max}]$ then $\hat{\lambda}_0$ is strictly dominant (i.e. $\hat{\lambda}_0$ is greater than the real part of the other eigenvalues of A) and it corresponds to a positive eigenvector ψ^0 .*

We are ready to state the asymptotic behavior of $T(t)$ which is defined in Lemma 2.2.

Lemma 2.4 (Theorem 9.12 on p. 67, Theorems 12.2 and 12.3 on p. 75 in [Diekmann and Metz 1986](#)) *Suppose $g(2q) \neq 2g(q)$ for some $q \in [\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max}]$. Then*

$$T(t)m^0 = \rho^0(t)[\phi^0(q) + o(1)] \text{ as } t \rightarrow \infty.$$

Here $\rho^0(t)$ is a real valued function involved in $\hat{\lambda}_0$; ϕ^0 is the stable size distribution depending on ψ^0 and the initial condition m^0 , where ψ^0 is defined in Lemma 2.3.

2.2 The model with quota structure

In this subsection, we shall focus on the system describing competition between n competitors with quota structure for grow-limiting nutrient in a chemostat, extending a one-species model given in ([Diekmann and Metz, 1986](#), Part A.I.4). Suppose that $n_i(t, q_i)$ denotes the concentration at time t with quota q_i for the i th competitor, $1 \leq i \leq n$. Let $S(t)$ denote the concentration of nutrient at time t . Then the governing equations take the forms:

$$\begin{cases} \frac{\partial n_i(t, q_i)}{\partial t} = \beta_i(S) \left\{ -\frac{\partial(g_i(q_i)n_i(t, q_i))}{\partial q_i} - b_i(q_i)n_i(t, q_i) \right. \\ \quad \left. + 4b_i(2q_i)n_i(t, 2q_i) \right\} - D_i n_i(t, q_i), \\ \frac{dS(t)}{dt} = D(S(0) - S(t)) - \sum_{i=1}^n \alpha_i \beta_i(S) \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} g_i(q_i)n_i(t, q_i)dq_i, \\ n_i(t, \frac{q_{\min,i}}{2}) = 0, \quad 1 \leq i \leq n, \\ n_i(0, q_i) = n_i^0(q_i), \quad 1 \leq i \leq n, \\ S(0) = S_0, \end{cases} \tag{2.9}$$

where D is the dilution rate; q_i and D_i are respectively the cell quota and the death rate for i th microorganism. $\beta_i(S) := \frac{\mu_{\max,i}S}{a_i + S}$ is the Monod function.

We assume that g_i satisfy

$$g_i(2q_i) \neq 2g_i(q_i) \quad \text{for some } q_i \in \left[\frac{q_{\min,i}}{2}, \frac{q_{\max,i}}{2} \right], \quad 1 \leq i \leq n. \tag{2.10}$$

Lemma 2.5 Suppose $W(t) = \sum_{i=1}^n \alpha_i \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} q_i n_i(t, q_i) dq_i$ and $Z(t) = W(t) + S(t)$ then

$$\liminf_{t \rightarrow \infty} Z(t) \geq \frac{DS^{(0)}}{D_{\max}} \quad \text{and} \quad \limsup_{t \rightarrow \infty} Z(t) \leq \frac{DS^{(0)}}{D_{\min}}, \tag{2.11}$$

where $D_{\max} = \max_{1 \leq i \leq n} \{D, D_i\}$ and $D_{\min} = \min_{1 \leq i \leq n} \{D, D_i\}$.

Proof By computation, it follows that

$$\begin{aligned} & \sum_{i=1}^n \alpha_i \beta_i(S) \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} g_i(q_i) n_i(t, q_i) dq_i - D_{\max} W \leq W'(t) \\ & \leq \sum_{i=1}^n \alpha_i \beta_i(S) \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} g_i(q_i) n_i(t, q_i) dq_i - D_{\min} W. \end{aligned}$$

Thus,

$$DS^{(0)} - D_{\max} Z \leq Z'(t) \leq DS^{(0)} - D_{\min} Z.$$

We conclude that

$$\liminf_{t \rightarrow \infty} Z(t) \geq \frac{DS^{(0)}}{D_{\max}} \quad \text{and} \quad \limsup_{t \rightarrow \infty} Z(t) \leq \frac{DS^{(0)}}{D_{\min}}.$$

□

Let $E_i(q_i) = \exp(-\int_{q_{\min,i}/2}^{q_i} \frac{b_i(\eta)}{g_i(\eta)} d\eta)$. Then the transformation

$$m_i(t, q_i) = \frac{g_i(q_i)}{E_i(q_i)} n_i(t, q_i)$$

leads the system (2.9) into the following evolution equation:

$$\begin{cases} \frac{\partial m_i(t, q_i)}{\partial t} = \beta_i(S) \{ -g_i(q_i) \frac{\partial m_i(t, q_i)}{\partial q_i} + k_i(q_i) m_i(t, 2q_i) \} - D_i m_i(t, q_i), \\ \frac{dS(t)}{dt} = D(S^{(0)} - S(t)) - \sum_{i=1}^n \alpha_i \beta_i(S) \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} E_i(q_i) m_i(t, q_i) dq_i, \\ m_i(t, \frac{q_{\min,i}}{2}) = 0, \quad 1 \leq i \leq n, \\ m_i(0, q_i) = m_i^0(q_i), \quad 1 \leq i \leq n, \\ S(0) = S_0, \end{cases} \tag{2.12}$$

where

$$k_i(q_i) = \begin{cases} 4 \frac{g_i(q_i)}{E_i(q_i)} \frac{E_i(2q_i)}{g_i(2q_i)} b_i(2q_i), & \text{for } \frac{1}{2} q_{\min,i} \leq q_i \leq \frac{1}{2} q_{\max,i}, \\ 0, & \text{for } q_i > \frac{1}{2} q_{\max,i}. \end{cases} \tag{2.13}$$

and

$$m_i^0(q_i) = \frac{g_i(q_i)}{E_i(q_i)} n_i^0(q_i).$$

Abstractly, we rewrite the equation for m_i in (2.12) as follows

$$\begin{cases} \frac{dm_i}{dt} = \beta_i(S)A_i m_i - D_i m_i, & 1 \leq i \leq n \\ m_i(0, q_i) = m_i^0(q_i), & 1 \leq i \leq n, \end{cases} \tag{2.14}$$

where

$$(A_i \psi)(q_i) = \begin{cases} -g_i(q_i)\psi'(q_i) + k_i(q_i)\psi(2q_i), & \text{for } \frac{q_{\min,i}}{2} \leq q_i \leq \frac{q_{\max,i}}{2}, \\ -g_i(q_i)\psi'(q_i), & \text{for } \frac{q_{\max,i}}{2} < q_i \leq q_{\max,i}, \end{cases}$$

with the appropriate domain. Note that the above operator A_i corresponds to the untransformed problem (2.1) if the index i is ignored and the death rates $\mu = 0$. By Lemma 2.2, we know that A_i generates a C_0 semigroup $T_i(t)$ on a space of continuous functions. From (2.10) and Lemma 2.3, it follows that the operator A_i has precisely one real eigenvalue $\hat{\lambda}_{0,i}$ which is simple. Furthermore, $\hat{\lambda}_{0,i}$ is strictly dominant and it corresponds to a positive eigenvector ψ_i^0 . We choose $\mu \equiv 0$ in (2.8) and we obtain

$$\pi_i(\lambda) = 2 \int_{q_{\min,i}}^{q_{\max,i}} \frac{b_i(\xi)}{g_i(\xi)} \exp \left[- \int_{\xi/2}^{\xi} \frac{\lambda + b_i(\eta)}{g_i(\eta)} d\eta \right] d\xi.$$

Note that $\hat{\lambda}_{0,i}$ satisfies

$$\pi_i(\hat{\lambda}_{0,i}) = 1. \tag{2.15}$$

Treating the substrate concentration S in (2.14) as a known function of time we can solve the equation for m_i :

$$m_i(t, m_i^0) = e^{-D_i t} T_i \left(\int_0^t \beta_i(S(\tau)) d\tau \right) m_i^0, \quad 1 \leq i \leq n. \tag{2.16}$$

Lemma 2.6

$$\lim_{t \rightarrow \infty} \int_0^t \beta_i(S(\tau)) d\tau = \infty, \quad \forall 1 \leq i \leq n.$$

Proof Since $\beta_i(S(\tau)) \geq 0$, the integral $\int_0^t \beta_i(S(\tau)) d\tau$ approaches a limit as $t \rightarrow \infty$, $\forall 1 \leq i \leq n$. Suppose that there exists an index i_0 such that $\lim_{t \rightarrow \infty} \int_0^t \beta_{i_0}(S(\tau))$

$d\tau < \infty$. Then $S(t) \rightarrow 0$ as $t \rightarrow \infty$. Since $\beta_i(S) = \frac{\mu_{\max,i}S}{a_i+S}$, it follows that $\beta_i(S) = \beta_{i_0}(S) \frac{\mu_{\max,i}}{\mu_{\max,i_0}} \frac{a_{i_0}+S}{a_i+S}$ and

$$\tilde{L}\beta_{i_0}(S) \leq \beta_i(S) \leq \bar{L}\beta_{i_0}(S),$$

where $\tilde{L} = \frac{\mu_{\max,i}}{\mu_{\max,i_0}} \min\{1, \frac{a_{i_0}}{a_i}\}$ and $\bar{L} = \frac{\mu_{\max,i}}{\mu_{\max,i_0}} \max\{1, \frac{a_{i_0}}{a_i}\}$. Observing the above inequality, we conclude that $\lim_{t \rightarrow \infty} \int_0^t \beta_i(S(\tau))d\tau < \infty \forall 1 \leq i \leq n$. From (2.16), it follows that $m_i(t, m_i^0) \rightarrow 0$ as $t \rightarrow \infty$, and hence, $n_i(t, n_i^0) \rightarrow 0$ as $t \rightarrow \infty$, thus $W(t) \rightarrow 0$ as $t \rightarrow \infty$. Therefore $W(t) + S(t) \rightarrow 0$ as $t \rightarrow \infty$. It contradicts (2.11) and this contradiction complete our proof. \square

Combining (2.16), Lemma 2.4 and Lemma 2.6, it follows that

$$m_i(t, m_i^0) = \rho_i(t)\{\phi_i^0(q_i) + o(1)\} \text{ as } t \rightarrow \infty, \tag{2.17}$$

where ϕ_i^0 is the stable size distribution and $\rho_i(t)$ is a real valued function. Substituting (2.17) into the equation for m_i and S , respectively, it follows that

$$\begin{cases} \frac{d\rho_i(t)}{dt} = \hat{\lambda}_{0,i}(\beta_i(S) - d_i)\rho_i, & 1 \leq i \leq n, \\ \frac{dS(t)}{dt} = D(S^{(0)} - S(t)) - \sum_{i=1}^n \alpha_{i,0}\beta_i(S)\rho_i(t), \end{cases} \tag{2.18}$$

where

$$d_i = \frac{D_i}{\hat{\lambda}_{0,i}}, \tag{2.19}$$

and $\alpha_{i,0} = \alpha_i \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} E_i(q_i)\phi_i^0(q_i)dq_i$.

We note that Hsu (1978) constructed a Lyapunov function to prove that the Competitive Exclusion Principle holds for the system (2.18). More precisely, the species with the lowest break-even concentration will win the competition. Define the break-even concentration for species i ,

$$S_i^* = \frac{a_i d_i}{\mu_{\max,i} - d_i}, \tag{2.20}$$

where it is assumed that $\mu_{\max,i} > d_i$ if S_i^* is to be defined. Exactly as in Smith and Waltman (1995, Chapter 1), if $\mu_{\max,i} \leq d_i$ or if $S_i^* > S^{(0)}$ then $\lim_{t \rightarrow \infty} \rho_i(t) = 0$; in this case, system (2.18) will be reduced to a lower-dimensional dynamical system, that is, one with fewer competitors. Thus we only consider species with $\mu_{\max,i} > d_i$. Following Hsu (1978, Theorem 3.3), we have the main results related to (2.18):

Theorem 2.1 *Suppose that $0 < S_1^* < S_2^* \leq S_3^* \leq \dots \leq S_n^*$ and $S_1^* < S^{(0)}$. Then*

$$\begin{cases} \lim_{t \rightarrow \infty} \rho_1(t) = D \frac{S^{(0)} - S_1^*}{d_1 \alpha_{1,0}}, \\ \lim_{t \rightarrow \infty} \rho_i(t) = 0, & 2 \leq i \leq n. \end{cases}$$

It is worth noting that Lemma 2.4 implies ϕ_i^0 depends on the initial data $m_i^0(q_i)$, and hence, $\alpha_{i,0}$ depends on the initial data $m_i^0(q_i)$, $\forall 1 \leq i \leq n$. From Theorem 2.1, it follows that the density and size distribution of the winner’s population depends on the initial size distribution. However, the break-even concentration S_i^* is independent of the initial size distribution (see (2.20)). We shall explain this observation biologically in the third paragraph of the discussion section.

In the following, we shall give some biological interpretations related to the system (2.9) and (2.18). From Theorem 2.1, (2.19) and (2.20), it follows that the competitive outcomes depend on the parameters $\mu_{\max,i}$, a_i and $d_i := \frac{D_i}{\hat{\lambda}_{0,i}}$. From (2.15), $\hat{\lambda}_{0,i}$ will depend on the rates of growth g_i and fission b_i .

Remark 2.1 From (2.19) and (2.20), it follows that S_i^* will be smaller provided that $\hat{\lambda}_{0,i}$ is larger. In other words, a larger $\hat{\lambda}_{0,i}$ will help species i to win the competition.

Remark 2.2 In the following, we shall show that the model with quota structure may reverse the outcome of competition for the classical model without quota structure under appropriate assumptions. The classical model without quota structure takes the form Hsu (1978):

$$\begin{cases} \frac{d\rho_i(t)}{dt} = (\frac{\mu_{\max,i}S}{a_i+S} - D_i)\rho_i, & 1 \leq i \leq n, \\ \frac{dS(t)}{dt} = D(S(0) - S(t)) - \sum_{i=1}^n \alpha_i \frac{\mu_{\max,i}S}{a_i+S} \rho_i(t). \end{cases} \tag{2.21}$$

For the system (2.21), we define the break-even concentration for species i ,

$$S_i^{**} = \frac{a_i D_i}{\mu_{\max,i} - D_i}, \quad 1 \leq i \leq n.$$

For convenience, we consider the case that $n = 2$ and assume that

$$\frac{\mu_{\max,2}}{D_2} > \frac{\mu_{\max,1}}{D_1} > 1, \quad 0 < a_2 - a_1 < a_2 \frac{\mu_{\max,1}}{D_1} - a_1 \frac{\mu_{\max,2}}{D_2}. \tag{2.22}$$

From (2.22), it follows that

$$S_1^{**} < S_2^{**}, \tag{2.23}$$

and

$$\frac{D_2}{\mu_{\max,2}} < \frac{D_1}{\mu_{\max,1}} < \frac{a_2 - a_1}{a_2 \frac{\mu_{\max,1}}{D_1} - a_1 \frac{\mu_{\max,2}}{D_2}} < 1. \tag{2.24}$$

Suppose that each species in the system (2.9) shares the same size structure, that is,

$$\hat{\lambda}_{0,i} := \hat{\lambda}_0, \quad i = 1, 2. \tag{2.25}$$

By (2.20), (2.24) and (2.25), it follows that

$$S_1^* > S_2^*, \tag{2.26}$$

provided that $\hat{\lambda}_0$ satisfies

$$\frac{D_1}{\mu_{\max,1}} < \hat{\lambda}_0 < \frac{a_2 - a_1}{a_2 \frac{\mu_{\max,1}}{D_1} - a_1 \frac{\mu_{\max,2}}{D_2}}. \tag{2.27}$$

From (2.23), (2.26) and the discussions above, we conclude that the model (2.9) with quota structure may reverse the outcome of competition for the classical model (2.21) under the assumptions (2.22), (2.25) and (2.27). Although the model with quota structure superficially resembles the classical model, this result illustrates an important difference. The latter assumes that population growth is simply proportional to the nutrient consumption function $\beta_i(S)$; thus the break-even concentration can be calculated directly from its parameters. In the model with quota structure, population growth depends also on the demographic processes of cell growth, reproduction, and death. The principal eigenvalue $\hat{\lambda}_{0,i}$ summarizes the influence of these processes and thus it appears in the calculation for the break even concentration, and influences the outcome of competition.

3 The competition model with quota structure and diffusion

3.1 A population operator in L^2 space

In this section, we reconsider the equation (2.5) in the Hilbert space $L^2(\frac{q_{\min}}{2}, q_{\max})$, that is,

$$\begin{cases} \frac{\partial m(t,q)}{\partial t} = \mathbf{A}m(t, q), \\ m(t, \frac{1}{2}q_{\min}) = 0, \\ m(0, q) = m^0(q), \end{cases}$$

where \mathbf{A} is the following population operator defined in the $L^2(\frac{q_{\min}}{2}, q_{\max})$ space:

$$\mathbf{A}\phi(q) = \begin{cases} -g(q) \frac{d\phi(q)}{dq} + k(q)\phi(2q), & \text{for } \frac{q_{\min}}{2} \leq q \leq \frac{q_{\max}}{2}, \\ -g(q) \frac{d\phi(q)}{dq}, & \text{for } \frac{q_{\max}}{2} < q \leq q_{\max}, \end{cases} \tag{3.1}$$

with a domain $D(\mathbf{A}) = \{\phi(q) \mid \phi, \mathbf{A}\phi \in L^2(\frac{q_{\min}}{2}, q_{\max}), \phi(\frac{q_{\min}}{2}) = 0\}$. Further, $k(q)$ is defined in (2.6), that is, $k(q) = 0, \forall q > \frac{1}{2}q_{\max}$.

For $\lambda \in \mathbb{C}$, we first construct $R(\lambda, \mathbf{A}) := (\lambda I - \mathbf{A})^{-1}$, the resolvent of \mathbf{A} . The abstract inhomogeneous equation

$$(\lambda I - \mathbf{A})\phi = f, \quad \forall f \in L^2\left(\frac{q_{\min}}{2}, q_{\max}\right),$$

implies

$$\begin{cases} g(q)\phi'(q) + \lambda\phi(q) = f(q), & \frac{q_{\max}}{2} \leq q \leq q_{\max}, \\ g(q)\phi'(q) + \lambda\phi(q) = f(q) + k(q)\phi(2q), & \frac{q_{\min}}{2} \leq q \leq \frac{q_{\max}}{2}, \\ \phi\left(\frac{q_{\min}}{2}\right) = 0. \end{cases} \quad (3.2)$$

Throughout the rest of this section, we suppose that the assumption (2.7) holds. By the similar arguments as in Diekmann and Metz (1986, pp. 56–61), we solve the first equation of (3.2) to obtain

$$\phi(q) = C e^{\lambda(G(q_{\max}/2) - G(q))} + \int_{\frac{q_{\min}}{2}}^q e^{\lambda(G(\xi) - G(q))} \frac{f(\xi)}{g(\xi)} d\xi, \quad \text{for } \frac{q_{\max}}{2} \leq q \leq q_{\max}, \quad (3.3)$$

where the constant C will be determined and G is defined by

$$G(q) = \int_{\frac{q_{\min}}{2}}^q \frac{d\xi}{g(\xi)}. \quad (3.4)$$

By (2.7) and (3.3), it follows that the right hand side of the second equation in (3.2) can be expressed as known functions and the unknown constant C . From the facts above, we deduce that

$$\begin{aligned} \phi(q) = \int_{\frac{q_{\min}}{2}}^q e^{\lambda(G(\xi) - G(q))} & \left[C e^{\lambda(G(q_{\max}/2) - G(2\xi))} k(\xi) + f(\xi) \right. \\ & \left. + k(\xi) \int_{\frac{q_{\max}}{2}}^{2\xi} e^{\lambda(G(\eta) - G(2\xi))} \frac{f(\eta)}{g(\eta)} d\eta \right] \frac{d\xi}{g(\xi)}, \quad \text{for } \frac{q_{\min}}{2} \leq q \leq \frac{q_{\max}}{2}. \end{aligned} \quad (3.5)$$

By calculations, it is easy to see

$$\lim_{q \downarrow \frac{q_{\max}}{2}} \phi(q) = C \quad \text{and} \quad \lim_{q \uparrow \frac{q_{\max}}{2}} \phi(q) = \pi(\lambda)C + \zeta(\lambda, f),$$

where

$$\pi(\lambda) = \int_{\frac{q_{\min}}{2}}^{\frac{q_{\max}}{2}} e^{\lambda(G(\xi)-G(2\xi))} \frac{k(\xi)}{g(\xi)} d\xi, \tag{3.6}$$

$$\zeta(\lambda, f) = \int_{\frac{q_{\min}}{2}}^{\frac{q_{\max}}{2}} e^{\lambda(G(\xi)-G(q_{\max}/2))} \left[f(\xi) + k(\xi) \int_{\frac{q_{\min}}{2}}^{2\xi} e^{\lambda(G(\eta)-G(2\xi))} \frac{f(\eta)}{g(\eta)} d\eta \right] \frac{d\xi}{g(\xi)}. \tag{3.7}$$

It remains to choose appropriate constants C such that $\phi(q)$ is continuous at $q = \frac{q_{\max}}{2}$, that is, C should obey the property:

$$(1 - \pi(\lambda))C = \zeta(\lambda, f).$$

If $\pi(\lambda) \neq 1$, the constant C is given by

$$C = (1 - \pi(\lambda))^{-1} \zeta(\lambda, f).$$

Next, consider the case where $\pi(\lambda) = 1$. If we choose $f \equiv 0$, the function ϕ defined in (3.3) and (3.5) is an element of $D(\mathbf{A})$ such that $(\lambda I - \mathbf{A})\phi = 0$, for arbitrary complex number C . This implies $\lambda \in \sigma_p(\mathbf{A})$, where $\sigma_p(\mathbf{A})$ is the point spectral set of \mathbf{A} .

We summarize the discussions above:

Lemma 3.1 *Suppose that the assumption (2.7) holds. Let $\rho(\mathbf{A})$ and $\sigma_p(\mathbf{A})$ represent the resolvent set and point spectral set of \mathbf{A} , respectively.*

- (i) *If $\pi(\lambda) \neq 1$, then $\lambda \in \rho(\mathbf{A})$ and the corresponding resolvent $R(\lambda, \mathbf{A})$ can be expressed as*

$$(R(\lambda, \mathbf{A})f)(q) = (1 - \pi(\lambda))^{-1} \zeta(\lambda, f)\Psi(\lambda, q) + Q(\lambda, f, q), \tag{3.8}$$

where

$$\Psi(\lambda, q) = \begin{cases} e^{\lambda(G(q_{\max}/2)-G(q))} & \text{for } \frac{q_{\max}}{2} \leq q \leq q_{\max}, \\ \int_{\frac{q_{\min}}{2}}^q e^{\lambda(G(\xi)-G(2\xi)-G(q)+G(q_{\max}/2))} \frac{k(\xi)}{g(\xi)} d\xi & \text{for } \frac{q_{\min}}{2} \leq q \leq \frac{q_{\max}}{2}, \end{cases} \tag{3.9}$$

and

$$Q(\lambda, f, q) = \begin{cases} \int_{\frac{q_{\max}}{2}}^q e^{\lambda(G(\xi)-G(q))} \frac{f(\xi)}{g(\xi)} d\xi, & \text{for } \frac{q_{\max}}{2} \leq q \leq q_{\max}, \\ \int_{\frac{q_{\min}}{2}}^q e^{\lambda(G(\xi)-G(q))} [f(\xi) + k(\xi) \int_{\frac{q_{\min}}{2}}^{2\xi} e^{\lambda(G(\eta)-G(2\xi))} \frac{f(\eta)}{g(\eta)} d\eta] \frac{d\xi}{g(\xi)}, & \text{for } \frac{q_{\min}}{2} \leq q \leq \frac{q_{\max}}{2}. \end{cases}$$

Furthermore, $R(\lambda, \mathbf{A})$ is a compact operator.

- (ii) $\pi(\lambda) = 1$ implies $\lambda \in \sigma_p(\mathbf{A})$. For any $\lambda \in \sigma_p(\mathbf{A})$, its geometrical multiplicity is 1 and $\Psi(\lambda, q)$ is its corresponding eigenfunction.

Thus, the spectrum of \mathbf{A} is precisely the set $\{\lambda : \pi(\lambda) = 1\}$ and \mathbf{A} has only a point spectrum (see, e.g., Diekmann and Metz 1986, p. 57).

Remark 3.1 Following Diekmann and Metz (1986, pp. 57–58), the expressions of $\pi(\lambda)$ in (2.8) and (3.6) are equivalent.

Suppose that $\hat{\lambda}_0$ is the unique real number satisfying

$$\pi(\hat{\lambda}_0) = 1.$$

Use the similar arguments as those in Diekmann and Metz (1986, Chapter II, Theorem 5.1, Theorem 5.10), we have the following results:

Lemma 3.2 *The operator \mathbf{A} has precisely one real eigenvalue $\hat{\lambda}_0$ which is simple. Furthermore, if $g(2q) \neq 2g(q)$ for some $q \in [\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max}]$ then $\hat{\lambda}_0$ is strictly dominant (i.e. $\hat{\lambda}_0$ is greater than the real part of the other eigenvalues of \mathbf{A}) and it corresponds to a positive eigenvector $\Psi(\hat{\lambda}_0, q)$, where $\Psi(\lambda, q)$ is defined in (3.9).*

For technical reasons, we impose the following additional condition on the function k , which is defined in (2.6):

(H_k) $k(\frac{q_{\max}}{2})$ is finite.

Remark 3.2 Following Diekmann and Metz (1986, pp. 31–41), we construct a function k satisfying (H_k). Let

$$\phi_b(q) = \begin{cases} \frac{1}{q_{\max} - q_{\min}} & \text{for } q_{\min} \leq q \leq q_{\max}, \\ 0, & \text{otherwise.} \end{cases}$$

Then

$$\delta(q) := \frac{\phi_b(q)}{1 - \int_{q_{\min}}^q \phi_b(\xi) d\xi} = \begin{cases} \frac{1}{q_{\max} - q} & \text{for } q_{\min} \leq q \leq q_{\max}, \\ 0, & \text{otherwise.} \end{cases}$$

Defining $b(q) := g(q)\delta(q)$ and $E(q) := \exp(-\int_{q_{\min}/2}^q \frac{b(\eta)}{g(\eta)} d\eta)$. Then it follows that

$$E(q) = \exp\left(-\int_{q_{\min}/2}^q \delta(\eta) d\eta\right) = \exp\left(-\int_{q_{\min}/2}^q \frac{1}{q_{\max} - \eta} d\eta\right),$$

that is, $E(q) = \frac{q - q_{\max}}{(q_{\min}/2) - q_{\max}}$. From (2.6), it follows that $k(q) = 4 \frac{g(q)}{E(q)} E(2q)\delta(2q) = 4 \frac{g(q)}{E(q)} \frac{1}{(q_{\max} - q_{\min}/2)}$. Thus, $k(q_{\max}/2)$ exists.

Theorem 3.1 *The operator \mathbf{A} generates a C_0 semi-group $\mathbf{T}(t)$ on $L^2(\frac{q_{\min}}{2}, q_{\max})$ under the additional condition (H_k) .*

Proof By the similar arguments as those in Song et al. (1982), we may show that the operator \mathbf{A} is closed and $D(\mathbf{A})$ is dense in $L^2(\frac{q_{\min}}{2}, q_{\max})$.

Given $\phi \in D(\mathbf{A})$, define $\langle \mathbf{A}\phi, \phi \rangle_{L^2} := \int_{q_{\min}/2}^{q_{\max}} \mathbf{A}\phi(q)\phi(q)dq$. Then

$$\begin{aligned} \langle \mathbf{A}\phi, \phi \rangle_{L^2} &= \int_{q_{\min}/2}^{q_{\max}} [-g(q)\frac{d\phi(q)}{dq} + k(q)\phi(2q)]\phi(q)dq \\ &= \int_{q_{\min}/2}^{q_{\max}} -g(q)\phi(q)d\phi(q) + \int_{q_{\min}/2}^{q_{\max}/2} k(q)\phi(2q)\phi(q)dq. \end{aligned}$$

By computations,

$$\begin{aligned} \int_{q_{\min}/2}^{q_{\max}} -g(q)\phi(q)d\phi(q) &= -\frac{1}{2} \int_{q_{\min}/2}^{q_{\max}} g(q)d(\phi(q))^2 \\ &= -\frac{1}{2} \left[g(q)(\phi(q))^2 \Big|_{q_{\min}/2}^{q_{\max}} - \int_{q_{\min}/2}^{q_{\max}} (\phi(q))^2 dg(q) \right] \\ &\leq \frac{1}{2} \int_{q_{\min}/2}^{q_{\max}} (\phi(q))^2 g'(q)dq \\ &\leq \frac{1}{2} M_1 \int_{q_{\min}/2}^{q_{\max}} (\phi(q))^2 dq = \frac{1}{2} M_1 \|\phi\|_{L^2}^2, \end{aligned}$$

where $M_1 = \max_{[q_{\min}/2, q_{\max}]} |g'(q)| < \infty$.

Let $M_2 := \max_{[q_{\min}/2, q_{\max}/2]} k(q)$. Then $M_2 < \infty$ by (H_k) . It follows that

$$\begin{aligned} \int_{q_{\min}/2}^{q_{\max}/2} k(q)\phi(2q)\phi(q)dq &\leq M_2 \int_{q_{\min}/2}^{q_{\max}/2} \phi(2q)\phi(q)dq \\ &\leq \frac{1}{2} M_2 \left[\int_{q_{\min}/2}^{q_{\max}/2} (\phi(2q))^2 dq + \int_{q_{\min}/2}^{q_{\max}/2} (\phi(q))^2 dq \right] \\ &\leq M_2 \|\phi\|_{L^2}^2. \end{aligned}$$

From the discussions above, it follows that

$$\langle \mathbf{A}\phi, \phi \rangle_{L^2} \leq \left(\frac{1}{2}M_1 + M_2 \right) \|\phi\|_{L^2}^2, \forall \phi \in D(\mathbf{A}),$$

i.e. $(\mathbf{A}, D(\mathbf{A}))$ is bounded above. By Engel and Nagel (2000, Proposition, p. 91), we complete our proof. \square

Throughout the rest of this section, we impose the following additional condition on the function g :

$$(H_{gg}) \quad g(2q) < 2g(q) \quad \text{for all } q \in \left[\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max} \right].$$

Lemma 3.3 (Diekmann and Metz 1986, p. 67, Corollary 9.7) *Suppose (H_k) and (H_{gg}) hold. Then $\mathbf{T}(t) := e^{\mathbf{A}t}$ is compact for $t \geq G(q_{\max})$, where G is defined in (3.4).*

3.2 A population operator with diffusion in L^2 space

In this subsection, we add spatial diffusion to the previous population model and identify the generator and determine its spectral properties in the Hilbert space. Roughly speaking, the structure of the semigroup for the population with diffusion is essentially determined by that of the semigroup for the population without diffusion and the Laplacian. Our governing equations are described as follows:

$$\begin{aligned} \frac{\partial n(t, q, x)}{\partial t} &= d \frac{\partial^2 n(t, q, x)}{\partial x^2} - \frac{\partial [g(q)n(t, q, x)]}{\partial q} - b(q)n(t, q, x) \\ &\quad + 4b(2q)n(t, 2q, x), \quad 0 < x < 1, \quad \frac{q_{\min}}{2} \leq q \leq q_{\max}, \quad t > 0, \end{aligned} \tag{3.10}$$

with boundary conditions

$$\begin{aligned} \frac{\partial n(t, q, 0)}{\partial x} &= 0, \quad \frac{\partial n(t, q, 1)}{\partial x} + \gamma n(t, q, 1) = 0, \quad \frac{q_{\min}}{2} < q < q_{\max}, \quad t > 0, \\ n\left(t, \frac{q_{\min}}{2}, x\right) &= 0, \quad 0 < x < 1, \end{aligned} \tag{3.11}$$

and initial conditions

$$n(0, q, x) = n^0(q, x), \tag{3.12}$$

where $n(t, q, x)$ represents the density of individuals having quota q at time t and spatial location x in $(0, 1)$. The parameter d is the diffusion coefficient and the constant γ in (3.11) represents the washout rate. The rest of the parameters are the same as those we mentioned before.

Let $E(q) = \exp(-\int_{\frac{q_{\min}}{2}}^q \frac{b(\xi)}{g(\xi)} d\xi)$ and $m(t, q, x) = \frac{g(q)n(t,q,x)}{E(q)}$. Then (3.10)–(3.12) becomes

$$\begin{aligned} \frac{\partial m(t, q, x)}{\partial t} &= d \frac{\partial^2 m(t, q, x)}{\partial x^2} - g(q) \frac{\partial m(t, q, x)}{\partial q} + k(q)m(t, 2q, x), \\ 0 < x < 1, \quad \frac{q_{\min}}{2} &\leq q \leq q_{\max}, \quad t > 0, \end{aligned} \tag{3.13}$$

with boundary conditions

$$\begin{aligned} \frac{\partial m(t, q, 0)}{\partial x} &= 0, \quad \frac{\partial m(t, q, 1)}{\partial x} + \gamma m(t, q, 1) = 0, \quad \frac{q_{\min}}{2} < q < q_{\max}, \quad t > 0, \\ m\left(t, \frac{q_{\min}}{2}, x\right) &= 0, \quad 0 < x < 1 \end{aligned} \tag{3.14}$$

and initial conditions

$$m(0, q, x) = m^0(q, x), \tag{3.15}$$

where $k(q)$ is defined in (2.6). We further assume that $k(q)$ satisfies (H_k) .

We introduce the state $\mathbb{X} = L^2((\frac{q_{\min}}{2}, q_{\max}) \times (0, 1))$ with the usual norm and the operator $\mathbb{A} : \mathbb{X} \rightarrow \mathbb{X}$ is defined by

$$\begin{cases} \mathbb{A}\phi(q, x) = d \frac{\partial^2 \phi(q, x)}{\partial x^2} - g(q) \frac{\partial \phi(q, x)}{\partial q} + k(q)\phi(2q, x), & \forall \phi \in D(\mathbb{A}), \\ D(\mathbb{A}) = \{\phi(q, x) \mid \phi, \mathbb{A}\phi \in \mathbb{X}, \phi(\frac{q_{\min}}{2}, x) = 0, & \phi \text{ satisfies (BC)}\}, \end{cases}$$

where

$$(BC) \quad \frac{\partial \phi(q, 0)}{\partial x} = 0, \quad \frac{\partial \phi(q, 1)}{\partial x} + \gamma \phi(q, 1) = 0, \quad \frac{q_{\min}}{2} < q < q_{\max}.$$

Note that $\mathbb{A} = d \frac{\partial^2}{\partial x^2} + \mathbf{A}$.

Then the system (3.13)–(3.15) can be rewritten as follows:

$$\begin{cases} \frac{dm(t,q,x)}{dt} = \mathbb{A}m(t, q, x), \quad x \in (0, 1), \quad \frac{q_{\min}}{2} \leq q \leq q_{\max}, \quad t > 0, \\ m(0, q, x) = m^0(q, x), \quad x \in (0, 1), \quad \frac{q_{\min}}{2} \leq q \leq q_{\max}. \end{cases} \tag{3.16}$$

We denote by $(\bar{\lambda}_i, \phi_i)_{i \geq 0}$ the eigenvalue-eigenfunction pair of the following problem

$$\begin{cases} -d\phi_i''(x) = \bar{\lambda}_i \phi_i(x), \quad x \in (0, 1), \\ \phi_i'(0) = \phi_i'(1) + \gamma \phi_i(1) = 0. \end{cases}$$

Suppose $\bar{\lambda}_0$ is the principal eigenvalue corresponding to the positive eigenfunction $\phi_0(x)$ which is uniquely determined by the normalization $\max_{[0,1]} \phi_0(x) = 1$. We may assume that $0 < \bar{\lambda}_0 < \bar{\lambda}_1 \leq \bar{\lambda}_2 \leq \dots \leq \bar{\lambda}_n \rightarrow \infty$.

Recall that \mathbf{A} is defined in (3.1), the usual population operator without diffusion in $L^2(\frac{q_{\min}}{2}, q_{\max})$ space. We denote $\{\hat{\lambda}_j\}_{j \geq 0}$ to be the eigenvalues of \mathbf{A} , that is, $\{\hat{\lambda}_j\}_{j \geq 0}$ satisfy $\pi(\hat{\lambda}_j) = 1, j \geq 0$, where π is defined in (3.6). Following [Diekmann and Metz \(1986, Eq. \(5.1\) on p. 58\)](#), it is easy to see that $\hat{\lambda}_j$ satisfies

$$1 = 2 \int_{q_{\min}}^{q_{\max}} \frac{b(\xi)}{g(\xi)} \exp \left[- \int_{\xi/2}^{\xi} \frac{\hat{\lambda}_j + b(\eta)}{g(\eta)} d\eta \right] d\xi.$$

From [Lemma 3.2](#), it follows that we may assume $\hat{\lambda}_0$ is the unique real eigenvalue of \mathbf{A} . Further, $\hat{\lambda}_0$ is greater than the real part of the other eigenvalues of \mathbf{A} and it corresponds to a positive eigenvector $\psi^0 := \Psi(\hat{\lambda}_0, q)$. Thus, we may assume that

$$\hat{\lambda}_0 > \text{Re} \hat{\lambda}_1 \geq \text{Re} \hat{\lambda}_2 \geq \dots$$

Theorem 3.2 *Suppose (H_k) and (H_{gg}) hold. Then the following statements hold.*

- (i) *The operator \mathbb{A} generates a C_0 semi-group $\mathbb{T}(t)$ on \mathbb{X} ;*
- (ii) *$R(\lambda, \mathbb{A})$ is a compact operator $\forall \lambda \in \rho(\mathbb{A})$, where $R(\lambda, \mathbb{A}) := (\lambda - \mathbb{A})^{-1}$ is the resolvent of \mathbb{A} ;*
- (iii) *$\sigma(\mathbb{A}) = \sigma_p(\mathbb{A}) = \{\hat{\lambda}_i - \bar{\lambda}_i\}_{i,j=0}^\infty$, where $\sigma(\mathbb{A})$ and $\sigma_p(\mathbb{A})$ are the spectrum and the point spectrum of \mathbb{A} , respectively;*
- (iv) *The operator \mathbb{A} has a real dominant eigenvalue λ_0 , that is, λ_0 is greater than the real part of any other eigenvalue of \mathbb{A} . Furthermore, λ_0 is simple.*
- (v) *$\mathbb{T}(t)$ is compact for $t \geq G(q_{\max})$, where $G(q)$ is defined in (3.4).*

Proof Our proof is motivated by the work ([Chan and Guo 1989](#)). We first consider the following equation

$$(\lambda I - \mathbb{A})\phi = \psi, \quad \forall \psi \in \mathbb{X}. \tag{3.17}$$

We shall discuss two cases:

Case 1 $\lambda + \bar{\lambda}_i \neq \hat{\lambda}_j \quad \forall i, j \geq 0$:

Let

$$\phi_\psi(q, x) = \sum_{i=0}^\infty R(\lambda + \bar{\lambda}_i, \mathbf{A}) \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x),$$

where

$$\langle \psi(q, x), \phi_i(x) \rangle = \int_0^1 \psi(q, x) \phi_i(x) dx,$$

and $R(\lambda, \mathbf{A}) = (\lambda I - \mathbf{A})^{-1}$ is the resolvent of \mathbf{A} . Note that

$$\psi(q, x) = \sum_{i=0}^{\infty} \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x).$$

By the similar arguments as that on [Chan and Guo \(1989, pp. 165–166\)](#), it follows that $\phi_\psi(q, x) \in \mathbb{X}$ is well-defined and

$$\begin{aligned} & (\lambda I - \mathbb{A}) \sum_{i=0}^n R(\lambda + \bar{\lambda}_i, \mathbf{A}) \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x) \\ &= [((\lambda + \bar{\lambda}_i)I - \mathbf{A}) - (\bar{\lambda}_i I + d\Delta)] \sum_{i=0}^n R(\lambda + \bar{\lambda}_i, \mathbf{A}) \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x) \\ &= \sum_{i=0}^n \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x), \quad \forall n \geq 0. \end{aligned}$$

Since \mathbf{A} and Δ are closed operators, it follows that \mathbb{A} is also a closed operator in \mathbb{X} . Let $n \rightarrow \infty$ in the above equality, it follows that

$$(\lambda I - \mathbb{A})\phi_\psi(q, x) = \psi(q, x),$$

that is, $\phi_\psi(q, x)$ is a solution of (3.17). It is not hard to show that the solution of (3.17) is unique. Thus $\lambda \in \rho(\mathbb{A})$, where $\rho(\mathbb{A})$ is the resolvent set of \mathbb{A} . Furthermore,

$$R(\lambda, \mathbb{A})\psi(q, x) = \sum_{i=0}^{\infty} R(\lambda + \bar{\lambda}_i, \mathbf{A}) \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x).$$

Case 2 $\lambda + \bar{\lambda}_i = \hat{\lambda}_j$, for some $i, j \geq 0$:

Motivated by [Diekmann and Metz \(1986, p. 61, equation \(6.6\)\)](#), we define

$$\phi_i(q, x) := \Psi(\lambda + \bar{\lambda}_i, q)\phi_i(x) = \Psi(\hat{\lambda}_j, q)\phi_i(x),$$

where $\Psi(\lambda, q)$ and $G(q)$ are defined in (3.9) and (3.4), respectively. From Lemma 3.1 (ii), it follows that $(\hat{\lambda}_j I - \mathbf{A})\Psi(\hat{\lambda}_j, q) = 0$ and hence

$$(\lambda I - \mathbb{A})\phi_i(q, x) = [(\hat{\lambda}_j I - \mathbf{A}) - (\bar{\lambda}_i I + d\Delta)]\phi_i(q, x) = 0,$$

that is, $\lambda \in \sigma_p(\mathbb{A})$. Let

$$\lambda_0 = \hat{\lambda}_0 - \bar{\lambda}_0, \quad \phi_0(q, x) = \Psi(\hat{\lambda}_0, q)\phi_0(x). \tag{3.18}$$

Then λ_0 is the dominant eigenvalue of \mathbb{A} and $\phi_0(q, x)$ is the corresponding (positive) eigenfunction. Furthermore, the geometric multiplicity of λ_0 is one.

By similar arguments to those in Chan and Guo (1989, p. 167), we can prove that $R(\lambda, \mathbb{A})$ is compact on \mathbb{X} , $\forall \lambda \in \rho(\mathbb{A})$.

Given $\phi(q, x) \in D(\mathbb{A})$, define $\langle \mathbb{A}\phi, \phi \rangle_{\mathbb{X}} := \int_0^1 \int_{q_{\min}/2}^{q_{\max}} \mathbb{A}\phi(q, x)\phi(q, x)dqdx$.

Claim $\langle \mathbb{A}\phi, \phi \rangle_{\mathbb{X}} \leq M \|\phi\|_{\mathbb{X}}^2, \forall \phi(q, x) \in D(\mathbb{A})$.

Obviously, $\langle \mathbb{A}\phi, \phi \rangle_{\mathbb{X}}$ equals

$$\begin{aligned}
 & d \int_{q_{\min}/2}^{q_{\max}} \int_0^1 \frac{\partial^2 \phi(q, x)}{\partial x^2} \phi(q, x) dx dq + \int_0^1 \int_{q_{\min}/2}^{q_{\max}} \left[-g(q) \frac{d\phi(q, x)}{dq} \phi(q, x) \right] dq dx \\
 & + \int_0^1 \int_{q_{\min}/2}^{q_{\max}} [k(q)\phi(2q, x)]\phi(q, x) dq dx. \tag{3.19}
 \end{aligned}$$

The first term of (3.19) equals

$$\begin{aligned}
 & d \int_{q_{\min}/2}^{q_{\max}} \left\{ \phi(q, x) \frac{\partial \phi(q, x)}{\partial x} \Big|_{x=0}^{x=1} - \int_0^1 \left(\frac{\partial \phi(q, x)}{\partial x} \right)^2 dx \right\} dq \\
 & \leq d \int_{q_{\min}/2}^{q_{\max}} \left\{ \phi(q, x) \frac{\partial \phi(q, x)}{\partial x} \Big|_{x=1} \right\} dq \\
 & = d \int_{q_{\min}/2}^{q_{\max}} \left\{ \phi(q, 1) \frac{\partial \phi(q, 1)}{\partial x} - \phi(q, 0) \frac{\partial \phi(q, 0)}{\partial x} \right\} dq \\
 & = -\gamma d \int_{q_{\min}/2}^{q_{\max}} [\phi(q, 1)]^2 dq \leq 0.
 \end{aligned}$$

The second term of (3.19) equals

$$\begin{aligned}
 & \int_0^1 \int_{q_{\min}/2}^{q_{\max}} \left[-g(q) \frac{\partial \phi(q, x)}{\partial q} \phi(q, x) \right] dq dx \\
 & = -\frac{1}{2} \int_0^1 \int_{q_{\min}/2}^{q_{\max}} g(q) \frac{\partial (\phi(q, x))^2}{\partial q} dx dq \\
 & = -\frac{1}{2} \int_0^1 \left\{ g(q)(\phi(q, x))^2 \Big|_{q=q_{\min}/2}^{q=q_{\max}} - \int_{q_{\min}/2}^{q_{\max}} (\phi(q, x))^2 dg(q) \right\} dx
 \end{aligned}$$

$$\begin{aligned} &\leq \frac{1}{2} \int_0^1 \int_{q_{\min}/2}^{q_{\max}} (\phi(q, x))^2 g'(q) dq dx \leq \frac{1}{2} M_1 \int_0^1 \int_{q_{\min}/2}^{q_{\max}} (\phi(q, x))^2 dq dx \\ &= \frac{1}{2} M_1 \|\phi\|_{\mathbb{X}}^2, \end{aligned}$$

where $M_1 = \max_{[q_{\min}/2, q_{\max}]} |g'(q)| < \infty$.

Using the fact that $\phi(2q, \cdot) \equiv 0 \forall q > q_{\max}/2$, it follows that the third term of (3.19) equals

$$\int_0^1 \int_{q_{\min}/2}^{q_{\max}/2} [k(q)\phi(2q, x)]\phi(q, x) dq dx.$$

Let $M_2 := \max_{[q_{\min}/2, q_{\max}/2]} k(q)$. Then $M_2 < \infty$ by (H_k) . It follows that

$$\begin{aligned} &\int_0^1 \int_{q_{\min}/2}^{q_{\max}/2} k(q)\phi(2q, x)\phi(q, x) dq \leq M_2 \int_0^1 \int_{q_{\min}/2}^{q_{\max}/2} \phi(2q, x)\phi(q, x) dq dx \\ &\leq \frac{1}{2} M_2 \left\{ \int_0^1 \int_{q_{\min}/2}^{q_{\max}/2} (\phi(2q, x))^2 dq dx + \int_0^1 \int_{q_{\min}/2}^{q_{\max}/2} (\phi(q, x))^2 dq dx \right\} \leq M_2 \|\phi\|_{\mathbb{X}}^2. \end{aligned}$$

From the discussions above, it follows that

$$\langle \mathbb{A}\phi, \phi \rangle_{\mathbb{X}} \leq \left(\frac{1}{2} M_1 + M_2 \right) \|\phi\|_{\mathbb{X}}^2, \forall \phi \in D(\mathbb{A}),$$

i.e. $(\mathbb{A}, D(\mathbb{A}))$ is bounded above on the Hilbert space \mathbb{X} . Thus, (i)–(iv) are valid by Engel and Nagel (2000, Proposition, p. 91).

Finally, we are ready to prove (v). Let $e^{\mathbb{A}t}$ be the semi-group generated by \mathbb{A} . From Lemma 3.3, it follows that $e^{\mathbb{A}t}$ is compact for $t \geq G(q_{\max})$. By the similar arguments as that on Chan and Guo (1989, pp. 169–170), we can prove that

$$\mathbb{T}(t)\psi(q, x) = \sum_{i=0}^{\infty} e^{\mathbb{A}t} e^{-\bar{\lambda}_i t} \langle \psi(q, x), \phi_i(x) \rangle \phi_i(x), \quad \forall \psi(q, x) \in \mathbb{X},$$

and $\mathbb{T}(t)$ is an compact operator on \mathbb{X} , for $t \geq G(q_{\max})$. □

From the proof of Theorem 3.2, it follows that

$$\begin{aligned} \mathbb{R}(\lambda, \mathbb{A})f(q, x) &= \mathbb{R}(\lambda + \bar{\lambda}_0, \mathbb{A})\langle f(q, x), \phi_0(x) \rangle \phi_0(x) \\ &\quad + \sum_{i=1}^{\infty} \mathbb{R}(\lambda + \bar{\lambda}_i, \mathbb{A})\langle f(q, x), \phi_i(x) \rangle \phi_i(x), \end{aligned}$$

where $f(q, x) \in \mathbb{X}$ and $R(\lambda, \mathbf{A})$ is defined in (3.8). Recall that $\lambda_0 := \hat{\lambda}_0 - \bar{\lambda}_0$ which is defined in (3.18). By similar arguments as those in Diekmann and Metz (1986, p. 61), it is not hard to see that the residue of $\lambda \mapsto R(\lambda, \mathbf{A})f(q, x)$ in $\lambda = \lambda_0$ is given by

$$\begin{aligned} & \lim_{\lambda \rightarrow \lambda_0} [(\lambda - \lambda_0)R(\lambda, \mathbf{A})f(q, x)] \\ &= \lim_{\lambda \rightarrow \lambda_0} \{(\lambda - \lambda_0)[R(\lambda + \bar{\lambda}_0, \mathbf{A})\langle f(q, x), \phi_0(x) \rangle \phi_0(x)]\} \\ &= \lim_{\lambda \rightarrow \lambda_0} \left\{ \frac{\lambda - \lambda_0}{1 - \pi(\lambda + \bar{\lambda}_0)} [\zeta(\lambda + \bar{\lambda}_0, \mathbf{f})\Psi(\lambda + \bar{\lambda}_0, q)\phi_0(x)] \right\} \\ &= \frac{1}{-\pi'(\hat{\lambda}_0)} [\zeta(\hat{\lambda}_0, \mathbf{f})\Psi(\hat{\lambda}_0, q)\phi_0(x)], \end{aligned}$$

where $\mathbf{f}(q) = \langle f(q, x), \phi_0(x) \rangle$. Therefore, the projection \mathbb{P} onto $\mathcal{N}(\lambda_0 I - \mathbf{A})$ along $\mathcal{R}(\lambda_0 I - \mathbf{A})$ is given by

$$\mathbb{P}f(q, x) = \frac{\zeta(\hat{\lambda}_0, \mathbf{f})}{-\pi'(\hat{\lambda}_0)} \Psi(\hat{\lambda}_0, q)\phi_0(x).$$

For any $m^0(q, x) \in \mathbb{X}$, it easy to see that

$$\mathbb{T}(t)m^0(q, x) = \mathbb{T}(t)[\mathbb{P}m^0(q, x) + (I - \mathbb{P})m^0(q, x)].$$

Following the similar arguments in Diekmann and Metz (1986, p. 67), it is not hard to see that

$$\mathbb{T}(t)m^0(q, x) = e^{\lambda_0 t} \left[\frac{\zeta(\hat{\lambda}_0, \mathbf{m}^0)}{-\pi'(\hat{\lambda}_0)} \Psi(\hat{\lambda}_0, q)\phi_0(x) + O(e^{-\epsilon t}) \right], \quad \text{as } t \rightarrow \infty,$$

where

$$\mathbf{m}^0(q) = \langle m^0(q, x), \phi_0(x) \rangle. \tag{3.20}$$

We summarize our main results concerned with the asymptotic behavior of the solution for (3.16).

Theorem 3.3 *Suppose the notations π, ζ, Ψ and \mathbf{m}^0 are defined in (3.6), (3.7), (3.9) and (3.20) respectively. Let $\mathbb{T}(t) := e^{(d\Delta)t} e^{\mathbf{A}t}$ be the C_0 semi-group generated by $\mathbf{A} := d \frac{\partial^2}{\partial x^2} + \mathbf{A}$ on \mathbb{X} , where $e^{(d\Delta)t}$ and $e^{\mathbf{A}t}$ are the semi-groups generated by $d\Delta := d \frac{\partial^2}{\partial x^2}$ and \mathbf{A} respectively. Then the following statements hold.*

- (i) *For $m^0(q, x) \in \mathbb{X}$, there exists a unique solution $m(t, q, x)$ to equation (3.16), which is given by*

$$m(t, q, x) = \mathbb{T}(t)m^0(q, x) \in C((0, \infty), \mathbb{X});$$

- (ii) If $m^0(q, x) \in D(\mathbb{A})$, then $m(t, q, x) = \mathbb{T}(t)m^0(q, x) \in C^1((0, \infty), \mathbb{X})$;
- (iii) $m(t, q, x) := e^{(d\Delta)t} e^{\mathbb{A}t} m^0(q, x)$ has the following asymptotic expression

$$e^{(d\Delta)t} e^{\mathbb{A}t} m^0(q, x) = e^{-\bar{\lambda}_0 t} e^{\hat{\lambda}_0 t} [C\Psi(\hat{\lambda}_0, q)\phi_0(x) + O(e^{-\epsilon t})], \text{ as } t \rightarrow \infty,$$

where $C = \frac{\zeta(\hat{\lambda}_0, m^0)}{-\pi'(\hat{\lambda}_0)}$ and ϵ is a small positive number.

3.3 The model with quota structure and diffusion

In this subsection, we study a size-structured model of competition for a resource in a spatially variable habitat. The motivations of the formulations were discussed in the introduction. The governing equations take the form:

$$\begin{cases} \frac{\partial S(t,x)}{\partial t} = d \frac{\partial^2 S}{\partial x^2} - \sum_{i=1}^2 \alpha_i \beta_i(S) \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} g_i(q_i) n_i(t, q_i, x) dq_i, \\ \frac{\partial n_i(t,q_i,x)}{\partial t} = d \frac{\partial^2 n_i}{\partial x^2} + \beta_i(S) \left\{ -\frac{\partial [g_i(q_i) n_i(t,q_i,x)]}{\partial q_i} - b_i(q_i) n_i(t, q_i, x) \right. \\ \left. + 4b_i(2q_i) n_i(t, 2q_i, x) \right\}, \quad i = 1, 2, \end{cases} \quad (3.21)$$

with boundary conditions

$$\begin{cases} \frac{\partial S(t,0)}{\partial x} = -S^{(0)}, \quad \frac{\partial S(t,1)}{\partial x} + \gamma S(t, 1) = 0, \\ \frac{\partial n_i(t,q_i,0)}{\partial x} = 0, \quad \frac{\partial n_i(t,q_i,1)}{\partial x} + \gamma n_i(t, q_i, 1) = 0, \quad \frac{q_{\min,i}}{2} < q_i < q_{\max,i}, \quad t > 0, \\ n_i(t, \frac{q_{\min,i}}{2}, x) = 0, \quad 1 \leq i \leq 2, \end{cases} \quad (3.22)$$

and initial conditions

$$\begin{cases} S(0, x) = S^0(x), \\ n_i(0, q_i, x) = n_i^0(q_i, x), \quad 1 \leq i \leq 2, \end{cases} \quad (3.23)$$

where $n_i(t, q_i, x)$ represents the density of i th individuals having quota q_i at time t and spatial location x in $(0, 1)$. The parameter d is the diffusion coefficient and the constant γ in (3.22) represents the washout rate. $S(t, x)$ denotes the density of the nutrient at time t and position $x \in (0, 1)$. $S^{(0)}$ is the input concentration of the nutrient. The rest of the parameters are the same as those we defined before.

Lemma 3.4 Let $W(t, x) = \sum_{i=1}^2 \alpha_i \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} q_i n_i(t, q_i, x) dq_i$ and $Z(t, x) = W(t, x) + S(t, x)$. Then $Z(x, t)$ satisfies

$$\lim_{t \rightarrow \infty} Z(x, t) = z(x) \quad \text{uniformly in } x \in [0, 1], \quad (3.24)$$

where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$.

Proof By direct computation, $Z(t, x)$ satisfies the following equation:

$$\begin{cases} \frac{\partial Z(t,x)}{\partial t} = d \frac{\partial^2 Z}{\partial x^2}, & x \in (0, 1), \quad t > 0, \\ \frac{\partial Z(t,0)}{\partial x} = -S(0), \quad \frac{\partial Z(t,1)}{\partial x} + \gamma Z(t, 1) = 0. \end{cases} \tag{3.25}$$

Then one can use the standard argument as in [Hsu and Waltman \(1993\)](#) to conclude that $\lim_{t \rightarrow \infty} Z(x, t) = z(x)$ uniformly in $x \in [0, 1]$. \square

Let

$$E_i(q_i) = \exp \left(- \int_{\frac{q_{\min,i}}{2}}^{q_i} \frac{b_i(\xi)}{g_i(\xi)} d\xi \right) \quad \text{and} \quad m_i(t, q_i, x) = \frac{g_i(q_i)n_i(t, q_i, x)}{E_i(q_i)}.$$

Then (3.21)–(3.23) become

$$\begin{cases} \frac{\partial S(t,x)}{\partial t} = d \frac{\partial^2 S}{\partial x^2} - \sum_{i=1}^2 \alpha_i \beta_i(S) \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} E_i(q_i) m_i(t, q_i, x) dq_i, \\ \frac{\partial m_i(t, q_i, x)}{\partial t} = d \frac{\partial^2 m_i}{\partial x^2} + \beta_i(S) \{ -g_i(q_i) \frac{\partial m_i(t, q_i, x)}{\partial q_i} + k_i(q_i) m_i(t, 2q_i, x) \}, \quad i = 1, 2, \end{cases} \tag{3.26}$$

with boundary conditions

$$\begin{cases} \frac{\partial S(t,0)}{\partial x} = -S(0), \quad \frac{\partial S(t,1)}{\partial x} + \gamma S(t, 1) = 0, \\ \frac{\partial m_i(t, q_i, 0)}{\partial x} = 0, \quad \frac{\partial m_i(t, q_i, 1)}{\partial x} + \gamma m_i(t, q_i, 1) = 0, \quad \frac{q_{\min,i}}{2} < q_i < q_{\max,i}, \quad t > 0, \\ m_i(t, \frac{q_{\min,i}}{2}, x) = 0, \quad 1 \leq i \leq 2, \end{cases} \tag{3.27}$$

and initial conditions

$$\begin{cases} S(0, x) = S^0(x), \\ m_i(0, q_i, x) = m_i^0(q_i, x), \quad 1 \leq i \leq 2, \end{cases} \tag{3.28}$$

where $k_i(q_i)$ is defined in (2.13) and $m_i^0(q_i, x) = g_i(q_i)n_i^0(q_i, x)/E_i(q_i)$, $i = 1, 2$.

Abstractly, we rewrite the equation of m_i in (3.26)–(3.28) as follows:

$$\begin{cases} \frac{dm_i(t, q_i, x)}{dt} = d \frac{\partial^2 m_i}{\partial x^2} + \beta_i(S) \mathbf{A}_i m_i, & x \in (0, 1), \quad \frac{q_{\min,i}}{2} \leq q_i \leq q_{\max,i}, \quad t > 0, \quad i = 1, 2, \\ m_i(0, q_i, x) = m_i^0(q_i, x), & x \in (0, 1), \quad \frac{q_{\min,i}}{2} \leq q_i \leq q_{\max,i}, \end{cases}$$

where \mathbf{A}_i satisfies

$$\begin{cases} \mathbf{A}_i \phi(q_i) = -g_i(q_i) \frac{d\phi(q_i)}{dq_i} + k_i(q_i) \phi(2q_i), \quad \forall \phi \in D(\mathbf{A}_i), \\ D(\mathbf{A}_i) = \{ \phi(q_i) \mid \phi, \mathbf{A}_i \phi \in L^2(\frac{q_{\min,i}}{2}, q_{\max,i}), \phi(\frac{q_{\min,i}}{2}) = 0 \}. \end{cases}$$

Treating the substrate concentration S as a known function of time we can solve the equation for m_i by

$$m_i(t, q_i, x) = e^{(d\Delta)t} e^{\mathbf{A}_i t} \int_0^t \beta_i(S(\tau, x)) d\tau m_i^0(q_i, x), \quad \forall x \in [0, 1], \quad i = 1, 2, \quad (3.29)$$

where $e^{(d\Delta)t}$ and $e^{\mathbf{A}_i t}$ are the semi-groups generated by $d\Delta := d \frac{\partial^2}{\partial x^2}$ and \mathbf{A}_i respectively.

By (3.24) and similar arguments as those in the proof of Lemma 2.6, the following result holds:

Lemma 3.5

$$\lim_{t \rightarrow \infty} \int_0^t \beta_i(S(\tau, x)) d\tau = \infty, \quad \forall x \in [0, 1], \quad i = 1, 2.$$

Let $G_i(q_i) = \int_{\frac{q_{\min,i}}{2}}^{q_i} \frac{d\xi}{g_i(\xi)}$, $\forall 1 \leq i \leq 2$. Suppose π_i, ζ_i and Ψ_i are respectively defined in (3.6), (3.7) and (3.9) where we replace the notations q_{\min}, q_{\max}, G, k and g by $q_{\min,i}, q_{\max,i}, G_i, k_i$ and g_i respectively, $\forall 1 \leq i \leq 2$. From Lemma 3.2, we may assume $\hat{\lambda}_{0,i}$ is the unique real eigenvalue of \mathbf{A}_i and $\hat{\lambda}_{0,i}$ corresponds to a positive eigenvector $\Psi_i(\hat{\lambda}_{0,i}, q_i)$.

From Theorem 3.3(iii), (3.29) and Lemma 3.5, it follows that

$$m_i(t, q_i, x) = e^{-\hat{\lambda}_{0,i} t} e^{\hat{\lambda}_{0,i} \int_0^t \beta_i(S(\tau)) d\tau} [C_i \Psi_i(\hat{\lambda}_{0,i}, q_i) \phi_0(x) + O(e^{-\epsilon t})] \text{ as } t \rightarrow \infty, \quad 1 \leq i \leq 2,$$

where $C_i = \frac{\zeta_i(\hat{\lambda}_{0,i}, \mathbf{m}_i^0)}{-\pi_i'(\hat{\lambda}_{0,i})}$ and $\mathbf{m}_i^0(q_i) = (m_i^0(q_i, x), \phi_0(x))$. That is,

$$m_i(t, q_i, x) = \rho_i(t, x) [\Pi_i(\hat{\lambda}_{0,i}, q_i) + o(1)] \text{ as } t \rightarrow \infty, \quad 1 \leq i \leq 2, \quad (3.30)$$

where $\rho_i(t, x)$ is a real valued function depending on t and x ; $\Pi_i(\hat{\lambda}_{0,i}, q_i) := C_i \Psi_i(\hat{\lambda}_{0,i}, q_i)$. Substituting (3.30) into the equation for m_i and S , respectively, it follows that

$$\begin{cases} \frac{\partial \rho_i(t, x)}{\partial t} = d \frac{\partial^2 \rho_i}{\partial x^2} + \hat{\lambda}_{0,i} \beta_i(S) \rho_i(t, x), & t > 0, \quad x \in (0, 1), \quad 1 \leq i \leq 2, \\ \frac{\partial S(t, x)}{\partial t} = d \frac{\partial^2 S(t, x)}{\partial x^2} - \sum_{i=1}^2 \alpha_{i,0} \beta_i(S) \rho_i(t, x), & t > 0, \quad x \in (0, 1), \\ \frac{\partial S(t, 0)}{\partial x} = -S^{(0)}, \quad \frac{\partial S(t, 1)}{\partial x} + \gamma S(t, 1) = 0, \\ \frac{\partial \rho_i(t, 0)}{\partial x} = 0, \quad \frac{\partial \rho_i(t, 1)}{\partial x} + \gamma \rho_i(t, 1) = 0, & i = 1, 2, \end{cases} \quad (3.31)$$

where $\alpha_{i,0} = \alpha_i \int_{\frac{q_{\min,i}}{2}}^{q_{\max,i}} E_i(q_i) \Pi_i(\hat{\lambda}_{0,i}, q_i) dq_i$.

Note that the system (3.31) has been discussed in Hsu et al. (1994) and Hsu and Waltman (1993). Introducing the new variable

$$\Theta(t, x) = S(t, x) + \sum_{i=1}^2 \frac{\alpha_{i,0}}{\hat{\lambda}_{0,i}} \rho_i(t, x)$$

into (3.31), it is not hard to see that $\Theta(t, x)$ satisfies (3.25). Thus $\lim_{t \rightarrow \infty} \Theta(x, t) = z(x)$ uniformly in $x \in [0, 1]$, where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$. Following Hsu et al. (1994) and Hsu and Waltman (1993), we conclude that the limiting system of (3.31) is as follows:

$$\begin{cases} \frac{\partial \rho_1}{\partial t} = d \frac{\partial^2 \rho_1}{\partial x^2} + \hat{\lambda}_{0,1} \beta_1(z(x) - \frac{\alpha_{1,0}}{\hat{\lambda}_{0,1}} \rho_1 - \frac{\alpha_{2,0}}{\hat{\lambda}_{0,2}} \rho_2) \rho_1, & t > 0, x \in (0, 1), \\ \frac{\partial \rho_2}{\partial t} = d \frac{\partial^2 \rho_2}{\partial x^2} + \hat{\lambda}_{0,2} \beta_2(z(x) - \frac{\alpha_{1,0}}{\hat{\lambda}_{0,1}} \rho_1 - \frac{\alpha_{2,0}}{\hat{\lambda}_{0,2}} \rho_2) \rho_2, & t > 0, x \in (0, 1), \\ \frac{\partial \rho_i(t,0)}{\partial x} = 0, \quad \frac{\partial \rho_i(t,1)}{\partial x} + \gamma \rho_i(t, 1) = 0, & i = 1, 2. \end{cases} \quad (3.32)$$

It is easy to see that the system (3.32) is a competition model and one can use the theory of monotone dynamical system to analyze it (see, e.g., Hsu et al. 1994; Hsu and Waltman 1993). Recall that $\beta_i(S) = \frac{\mu_{\max,i} S}{a_i + S}$, $i = 1, 2$. Let $\eta_i, i = 1, 2$, be the principal eigenvalue of the problem

$$\begin{cases} d \Phi_i''(x) + \eta_i \frac{z(x)}{a_i + z(x)} \Phi_i(x) = 0, & x \in (0, 1), \\ \Phi_i'(0) = \Phi_i'(1) + \gamma \Phi_i(1) = 0, & i = 1, 2, \end{cases}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization $\max_{[0,1]} \Phi_i(x) = 1$. The following results related to the system (3.31) can be found in (Hsu and Waltman, 1993, Theorem 3.6)

Theorem 3.4 Let $\hat{\mu}_{\max,i} = \hat{\lambda}_{0,i} \mu_{\max,i}, i = 1, 2$.

- (i) If $\hat{\mu}_{\max,i} < \eta_i, i = 1, 2$, then $\lim_{t \rightarrow \infty} S(x, t) = z(x)$ and $\lim_{t \rightarrow \infty} \rho_i(x, t) = 0$ uniformly in $x \in [0, 1], i = 1, 2$, where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$,
- (ii) If $\hat{\mu}_{\max,1} > \eta_1$ and $\hat{\mu}_{\max,2} < \eta_2$, then

$$\begin{cases} \lim_{t \rightarrow \infty} S(x, t) = z(x) - \frac{\alpha_{1,0}}{\hat{\lambda}_{0,1}} \rho_1^*(x), \\ \lim_{t \rightarrow \infty} \rho_1(x, t) = \rho_1^*(x), \text{ uniformly in } x \in [0, 1], \\ \lim_{t \rightarrow \infty} \rho_2(x, t) = 0, \end{cases} \quad (3.33)$$

- (iii) If $\hat{\mu}_{\max,1} < \eta_1$ and $\hat{\mu}_{\max,2} > \eta_2$, then

$$\begin{cases} \lim_{t \rightarrow \infty} S(x, t) = z(x) - \frac{\alpha_{2,0}}{\hat{\lambda}_{0,2}} \rho_2^*(x), \\ \lim_{t \rightarrow \infty} \rho_1(x, t) = 0, \text{ uniformly in } x \in [0, 1], \\ \lim_{t \rightarrow \infty} \rho_2(x, t) = \rho_2^*(x). \end{cases} \quad (3.34)$$

Here, $\rho_i^*(x)$ is the unique positive steady state of

$$\begin{cases} \frac{\partial \rho_i}{\partial t} = d \frac{\partial^2 \rho_i}{\partial x^2} + \hat{\lambda}_{0,i} \beta_i(z(x) - \frac{\alpha_{i,0}}{\hat{\lambda}_{0,i}} \rho_i) \rho_i, & t > 0, x \in (0, 1), \\ \frac{\partial \rho_i(t, 0)}{\partial x} = 0, \quad \frac{\partial \rho_i(t, 1)}{\partial x} + \gamma \rho_i(t, 1) = 0, & i = 1, 2. \end{cases}$$

The authors [Hsu and Waltman \(1993, Theorem 3.7\)](#) also discuss some competitive exclusion results for the system (3.31):

Theorem 3.5 *Suppose that $\hat{\mu}_{\max,i} > \eta_i$, where $\hat{\mu}_{\max,i} = \hat{\lambda}_{0,i} \mu_{\max,i}$, $i = 1, 2$. (i.e. each competitor would survive alone in the chemostat without competition):*

- (i) *If $(\hat{\mu}_{\max,2} \leq \hat{\mu}_{\max,1}, \frac{\hat{\mu}_{\max,2}}{\hat{\mu}_{\max,1}} < \frac{a_2}{a_1})$ or $(\hat{\mu}_{\max,2} > \hat{\mu}_{\max,1}, \frac{\hat{\mu}_{\max,2}}{\hat{\mu}_{\max,1}} < \frac{a_2}{a_1}, 0 < z(x) < \frac{\hat{\mu}_{\max,1} a_2 - \hat{\mu}_{\max,2} a_1}{\hat{\mu}_{\max,2} - \hat{\mu}_{\max,1}})$ then (3.33) holds;*
- (ii) *If $(\hat{\mu}_{\max,1} \leq \hat{\mu}_{\max,2}, \frac{\hat{\mu}_{\max,1}}{\hat{\mu}_{\max,2}} < \frac{a_1}{a_2})$ or $(\hat{\mu}_{\max,1} > \hat{\mu}_{\max,2}, \frac{\hat{\mu}_{\max,1}}{\hat{\mu}_{\max,2}} < \frac{a_1}{a_2}, 0 < z(x) < \frac{\hat{\mu}_{\max,2} a_1 - \hat{\mu}_{\max,1} a_2}{\hat{\mu}_{\max,1} - \hat{\mu}_{\max,2}})$ then (3.34) holds.*

In order to discuss the coexistence for the system (3.31), we denote Λ_1 to be the principal eigenvalues of the problems

$$\begin{cases} d\Psi_1''(x) + \Lambda_1 \frac{z(x) - \frac{\alpha_{2,0}}{\hat{\lambda}_{0,2}} \rho_2^*(x)}{a_1 + z(x) - \frac{\alpha_{2,0}}{\hat{\lambda}_{0,2}} \rho_2^*(x)} \Psi_1(x) = 0, & x \in (0, 1), \\ \Psi_1'(0) = \Psi_1'(1) + \gamma \Psi_1(1) = 0, \end{cases} \tag{3.35}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization $\max_{[0,1]} \Psi_1(x) = 1$. Similarly, we denote Λ_2 to be the principal eigenvalues of the problems

$$\begin{cases} d\Psi_2''(x) + \Lambda_2 \frac{z(x) - \frac{\alpha_{1,0}}{\hat{\lambda}_{0,1}} \rho_1^*(x)}{a_2 + z(x) - \frac{\alpha_{1,0}}{\hat{\lambda}_{0,1}} \rho_1^*(x)} \Psi_2(x) = 0, & x \in (0, 1), \\ \Psi_2'(0) = \Psi_2'(1) + \gamma \Psi_2(1) = 0, \end{cases} \tag{3.36}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization $\max_{[0,1]} \Psi_2(x) = 1$.

By the standard properties of the principal eigenvalues, it is easy to see that $\Lambda_i > \eta_i$, $i = 1, 2$. The following results concern the coexistence of the limiting system (3.32):

Theorem 3.6 ([Hsu et al. 1994; Hsu and Waltman 1993](#)) *Let $\hat{\mu}_{\max,i} = \hat{\lambda}_{0,i} \mu_{\max,i}$, $i = 1, 2$. Suppose that $\hat{\mu}_{\max,i} > \Lambda_i$ (it implies that $\hat{\mu}_{\max,i} > \eta_i$), $i = 1, 2$. Then the system (3.32) is uniformly persistent. Thus, the system (3.32) has at least one positive steady-state solution.*

By similar arguments to those in [Wang \(2010, Section 3.2\)](#), we can further lift the coexistence of the limiting system (3.32) to the full system (3.31) by the concept of “chain transitive sets” (see, e.g., [Zhao 2003](#)). Thus, we have the following results:

Theorem 3.7 *Let $\hat{\mu}_{\max,i} := \hat{\lambda}_{0,i}\mu_{\max,i} > \Lambda_i, i = 1, 2$. Then the system (3.31) is uniformly persistent and it has at least one positive steady-state solution.*

We note that the simulations in [So and Waltman \(1989\)](#) indicates that coexistence occurs in a very narrow parameter region. Recall that $\hat{\mu}_{\max,i} = \hat{\lambda}_{0,i}\mu_{\max,i}$, where $\hat{\lambda}_{0,i}$ depends on the rates of growth g_i and fission b_i and $\mu_{\max,i}$ is the maximal growth rate of i -th microorganism. In other words, the outcomes of the system (3.21)–(3.23) will be affected by the dependence of growth and reproduction on quota.

Remark 3.3 If $\hat{\lambda}_{0,i}$ is larger, it follows that Λ_i is smaller (by (3.35) and (3.36)) and $\hat{\mu}_{\max,i}$ is larger. From Theorem 3.7, we conclude that a system with larger $\hat{\lambda}_{0,i}, i = 1, 2$, will facilitate the coexistence of species.

4 Discussion

This study examined models combining competition for a resource between size-structured populations and spatially structured habitats. To our knowledge, no prior study has examined this combination. We have demonstrated that outcomes are similar to competition models for spatially structured habitats that lack population size-structure ([Hsu et al. 1994](#); [Hsu and Waltman 1993](#)). Coexistence of two competitors is possible, depending on parameter values, and both persistence of one population and coexistence of two are related to principal eigenvalue problems similar to those arising in other spatial models ([Baxley and Robinson 1998](#); [Grover et al. 2009](#); [Hsu et al. 1994](#); [Hsu and Waltman 1993](#)).

In addition, we have shown that the classical result of competitive exclusion applies when size-structured species compete for a single resource in a spatially uniform habitat—one species wins which has the lowest break-even concentration for the nutrient. This result was also seen in a somewhat different size-structured competition model ([Cushing 1989, 1990](#)). However, size structure complicates the calculation of the break-even concentration. A calculation based on the S^{**} parameters of the classical model without size structure can be incorrect ([Remark 2.2](#)). With size structure, the correct prediction of competitive outcomes requires the principal eigenvalue that summarizes the relationships among cell growth, cell division, and cell size.

Size structure introduces another complication in the understanding of competitive outcomes—dependence on the initial size distribution. In the model of size structure in a well-mixed chemostat, system (2.9), the break-even concentration is independent of the initial size distribution, so also is the identity of the competitive winner. But the density and size distribution of the winner's population does depend on the initial size distribution. The situation is more complex for the model of size structure and diffusion in space, system (3.21). Competitive outcomes are again related to invasibility of semi-trivial equilibria where one species is a resident at equilibrium and the other is an invader at low density. Successful invasion depends on the spatial distribution of available nutrient that is created by the resident species at equilibrium. That is, the break-even nutrient concentration that governs invasibility in a well-mixed chemostat is replaced by the break-even spatial distribution of the nutrient. This nutrient distribution depends on the initial cell size distribution of the resident species. Thus

competitive outcomes depend on this initial condition. There is a practical implication for invasion experiments conducted by letting the resident species establish in monoculture, and then introducing the invader. If replicate monocultures of the resident are initiated with different cell size distributions, the competitive outcomes for these replicates might differ.

Although coexistence of two size-structured species competing for one resource is possible, we conjecture that the range of parameter values permitting coexistence is narrow, as was found for competition in the unstirred chemostat without size structure (Hsu et al. 1994; Hsu and Waltman 1993; So and Waltman 1989). In other spatially varying habitats, coexistence of competitors is possible, but arises only for a narrow range of parameters (Baxley and Robinson 1998; Grover et al. 2009).

The model analyzed here assumes that nutrient quota is proportional to cell size. While this is true for some nutrients, other nutrients vary independently of cell size and may be more strongly related to growth rate (Droop 1983). In such cases, an approximate model for spatially variable habitats had very similar results to those presented here (Hsu et al. 2010). A computational model for this situation again suggested coexistence would arise only for a restricted range of parameter values (Grover 2009). In deriving the results presented here, it was necessary to assume that the minimal quota exceeded half the maximal quota ($q_{\min} > \frac{1}{2}q_{\max}$), limiting the total range of quota variation to a factor of 4 at most. For nutrients composing a large fraction of cell mass, and thus with quotas likely to vary in proportion to cell size, this assumption is not restrictive since the size range of cells reproducing by binary fission is similarly limited. For nutrients whose quotas vary more widely, alternative models will be required (Grover 2009; Hsu et al. 2010).

With other parameters fixed, coexistence in the model analyzed here is related to the maximal growth rates of competitors ($\hat{\mu}_{\max,i}$). As used here, this parameter has a subtly different meaning from the parameter denoted $\mu_{\max,i}$ in unstructured models for microbial competition. In unstructured models, $\mu_{\max,i}$ is the maximal rate at which a population grows in numbers when resource availability is infinite, and it is simply proportional to the maximal rate of nutrient consumption. In the structured model presented here, $\mu_{\max,i}$ is the maximal rate at which an individual acquires nutrient when resource availability is infinite. The rate at which the population grows in numbers also depends on the functions governing cell division in relation to size, $b_i(q)$, and cell growth in relation to size, $g_i(q)$. The eigenvalue problems governing persistence and coexistence incorporate these dependencies, essentially stating that at steady state each mother cell of size q must on average produce exactly one daughter surviving to this size (Diekmann et al. 1984).

Acknowledgments We are very grateful to two anonymous referees for careful reading and helpful suggestions which led to improvements of our original manuscript. This work was partially done when the first author visited National Center of Theoretical Science in December, 2008. We thank Prof. S. Levin for helpful suggestions during this visit.

References

Baxley JV, Robinson SB (1998) Coexistence in the unstirred chemostat. *Appl Math Comput* 89:41–65

- Cushing JM (1989) A competition model for size-structured species. *SIAM J Appl Math* 49:838–858
- Cushing JM (1990) Some competition models for size-structured populations. *Rocky Mt J Math* 20: 879–897
- Chan WL, Guo BZ (1989) On the semigroup of age-dependent population dynamics with spatial diffusion. *Manuscr Math* 66:161–181
- Chan WL, Guo BZ (1994) On the semigroup for age-dependent population dynamics with spatial diffusion. *J Math Anal Appl* 184:190–199
- Droop MR (1983) 25 years of algal growth kinetics: a personal view. *Bot Mar* 26:99–112
- Diekmann O, Metz JAJ (1986) The dynamics of physiologically structured populations. *Lecture notes in biomath*, vol 68. Springer, New York
- Diekmann O, Heijmans HJAM, Thieme HR (1984) On the stability of the cell size distribution. *J Math Biol* 19(2):227–248
- Engel KJ, Nagel R (2000) One-parameter semigroups for linear evolution equations. Springer, New York
- Grover JP (1991) Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. *Am Nat* 138:811–835
- Grover JP (1997) Resource competition. Chapman and Hall, London
- Grover JP (2009) Is storage an adaptation to spatial variation in resource availability? *Am Nat* 173:E44–E61
- Grover JP, Hsu SB, Wang FB (2009) Competition and coexistence in flowing habitats with a hydraulic storage zone. *Math Biosci* 222:42–52
- Gurtin ME, MacCamy RC (1981) Diffusion models for age-structured populations. *Math Biosci* 54:49–59
- Heijmans HJAM (1985) An eigenvalue problem related to cell growth. *J Math Anal Appl* 111(1):253–280
- Hsu SB (1978) Limiting behavior for competing species. *SIAM J Appl Math* 34:760–763
- Hsu SB, Hsu TH (2008) Competitive exclusion of microbial species for a single-limited resource with internal storage. *SIAM J Appl Math* 68:1600–1617
- Hsu SB, Waltman P (1993) On a system of reaction-diffusion equations arising from competition in an unstirred chemostat. *SIAM J Appl Math* 53:1026–1044
- Hsu SB, Hubbell S, Waltman P (1977) Mathematical theory for single nutrient competition in continuous cultures of microorganisms. *SIAM J Appl Math* 32:366–383
- Hsu SB, Smith HL, Waltman P (1994) Dynamics of competition in the unstirred chemostat. *Can Appl Math Q* 2(4):461–483
- Hsu SB, Jiang J, Wang FB (2010) On a system of reaction-diffusion equations arising from competition with internal storage in an unstirred chemostat. *J Differ Equ* 248:2470–2496
- Sinko JW, Streifer W (1967) A new model for age-size structure of a population. *Ecology* 48:910–918
- Smith HL, Waltman PE (1994) Competition for a single limiting resource in continuous culture: the variable-yield model. *SIAM J Appl Math* 34:1113–1131
- Smith HL, Waltman PE (1995) The theory of the chemostat. Cambridge University Press, Cambridge
- So JWH, Waltman P (1989) A nonlinear boundary value problem arising from competition in the chemostat. *Appl Math Comput* 32:169–183
- Song J, Yu JY, Wang XZ, Hu SJ, Zhao ZX, Liu JQ, Feng DX, Zhu GT (1982) Spectral properties of population operator and asymptotic behaviour of population semigroup. *Acta Math Sci* 2(2):139–148
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton
- Wang FB (2010) A system of partial differential equations modeling the competition for two complementary resources in flowing habitats. *J Differ Equ* 249:2866–2888
- Zhao X-Q (2003) Dynamical systems in population biology. Springer, New York