

*Size-Structured Population Models of Daphnia with
Several Algae Resources and Unification by Characteristic
Equations*

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Chapter 1 in [3], contains an introduction to the research work on size-structured models of Daphnia species and I refer readers to that book. I also note that therein I considered three different models for Daphnia species. Among them two are of partial differential equations types, and one is of an integral equation type. These models are coupled with an ordinary differential equation that describes the change in the algae concentration together with the effects of Daphnia species feeding on the algae concentration. By considering the steady states and characteristic equations, I showed that these three types of models can be unified, in the sense that they share the same steady states and a unique characteristic equation. In addition, I obtained an explicit formula for their unique characteristic equation.

In this paper, I would like to extend my previous results by considering several algae resources for the Daphnia species instead of one, and also generalize the vital rates i.e., the birth, death and growth rates, in addition to the feeding rates therein by incorporating the total population size for each Daphnia species, and prove that the same unification holds, viz, the generalization does not alter the unification of the models. I also note that the unification holds for the two partial differential equations types, but the integral equation type model, for example, see [1], lacks a complete set of equations to determine the characteristic equation for this general case.

However, the unification holds for the three types of models in the case when the vital rates and the feeding rates do not depend on any of the population sizes of the Daphnia species. In addition, I obtain an explicit formula for determining the unique characteristic equation, which generalizes the one given in the above mentioned book.

In [4], a size-structured population dynamics model for a single Daphnia species with two algae resources is considered, and conditions for the stability of the steady states are obtained. Furthermore, a generalization to the case when several resources are available is proposed, but not analyzed.

The model that I shall consider is formulated via partial differential equations for $n \geq 1$ Daphnia species population and $m \geq 1$ algae species as sources of food for the Daphnia species population. The model is also related to models described and analyzed in [3] and the references therein, for example, [2], [5], and is given by

$$\left\{ \begin{array}{l} \frac{\partial p_i(\tau, t)}{\partial t} + \frac{\partial p_i(\tau, t)}{\partial \tau} + \mu_i(a_i(\tau, t), \vec{F}(t), \vec{P}(t))p_i(\tau, t) = 0, \quad a_i(\tau, t) > 0, \quad \tau > 0, \quad 1 \leq i \leq n, \\ p_i(0, t) = \int_0^\infty \beta_i(a_i(\tau, t), \vec{F}(t), \vec{P}(t))p_i(\tau, t)d\tau, \quad t \geq 0, \\ \frac{\partial a_i(\tau, t)}{\partial \tau} + \frac{\partial a_i(\tau, t)}{\partial t} = V_i(a_i(\tau, t), \vec{F}(t), \vec{P}(t)), \quad a_i(\tau, t) > 0, \quad \tau > 0, \\ a_i(0, t) = 0, \quad t \geq 0, \\ \frac{dF_j(t)}{dt} = \phi_j(F_j(t)) - \sum_{i=1}^n \int_0^\infty I_{ji}(a_i(\tau, t), \vec{F}(t), \vec{P}(t))p_i(\tau, t)d\tau, \quad t > 0, \\ F_j(0) = F_{j0}, \quad 1 \leq j \leq m, \quad \vec{F}(t) = (F_1(t), F_2(t), \dots, F_m(t)), \quad t \geq 0, \\ P_i(t) = \int_0^\infty p_i(\tau, t)d\tau, \quad t \geq 0, \quad 1 \leq i \leq n, \quad \vec{P}(t) = (P_1(t), P_2(t), \dots, P_n(t)), \quad t \geq 0. \end{array} \right. \quad (1)$$

The steady states of our model, given by the system (1), must satisfy the following:

$$p_{i\infty}(\tau) = p_{i\infty}(0)\pi_i^*(\tau), \quad \pi_i^*(\tau) = e^{-\int_0^\tau \mu_i(a_i(\sigma), \vec{F}_\infty, \vec{P}_\infty) d\sigma}, \quad 1 \leq i \leq n, \quad (2)$$

$$p_{i\infty}(0) = \int_0^\infty \beta_i(a_i(\tau), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau) d\tau, \quad \vec{F}_\infty = (F_{1\infty}, F_{2\infty}, \dots, F_{m\infty}), \quad (3)$$

$$\phi_j(F_{j\infty}) = \sum_{i=1}^n \int_0^\infty I_{ji}(a_i(\tau), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau) d\tau, \quad 1 \leq j \leq m, \quad 1 \leq i \leq n, \quad (4)$$

$$a_i'(\tau) = V_i(a_i(\tau), \vec{F}_\infty, \vec{P}_\infty), \quad \tau > 0, \quad 1 \leq i \leq n, \quad a_i(0) = 0, \quad \vec{P}_\infty = (P_{1\infty}, P_{2\infty}, \dots, P_{n\infty}). \quad (5)$$

I note that the characteristic equation of the model, given by the system (1), can be obtained via methods similar to that given in [3], Chapter 1, and therefore, I omit the details. I also note that the characteristic equation of the related partial differential equation model, which can be found in [3], Chapter 1, can be obtained similarly. The proof that the two characteristic equations are identical is elegant, and I will clarify below.

Firstly, we note that both characteristic equations are of the form $\det A = 0$, where A is an $(2n + m)$ -square matrix. Secondly, the characteristic equation for the related partial differential equations model, can be proved to be the same, by realizing that, after some obvious reductions in the associated matrix:

$$V_{iP_N}(0, \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(0), \quad 1 \leq i, N \leq n, \quad V_{iF_k}(0, \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(0), \quad 1 \leq i \leq n, \quad 1 \leq k \leq m.$$

Furthermore, these terms are not present in the matrix for the system (1). Consequently, we can conclude that the two matrices have the same determinant, and accordingly, the two models have the same characteristic equation.

Of course, it is easy to see that the three models share the same steady states via methods similar to those given in [3], Chapter 1, for the special case when $m = 1$, viz, when there is only one type of algae resource.

In order to facilitate my further exposition, I disregard the subscript "i" for "a", and define the following:

$$\begin{aligned}
k_{12}^{iF_k}(\tau) &= \int_0^\infty \int_\sigma^{\tau+\sigma} \beta_i(a(\tau+\sigma), \vec{F}_\infty, \vec{P}_\infty) \frac{\pi_i^*(\tau+\sigma)}{\pi_i^*(s)} \mu_{ia}(a(s), \vec{F}_\infty, \vec{P}_\infty) \times \\
&e \int_\sigma^s V_{ia}(a(b), \vec{F}_\infty, \vec{P}_\infty) db \\
&V_{iF_k}(a(\sigma), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(s) ds d\sigma + \\
&\int_0^\infty \beta_i(a(\tau+\sigma), \vec{F}_\infty, \vec{P}_\infty) \frac{\pi_i^*(\tau+\sigma)}{\pi_i^*(\sigma)} \mu_{iF_k}(a(\sigma), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\sigma) d\sigma - \\
&\int_0^\infty \beta_{ia}(a(\tau+\sigma), \vec{F}_\infty, \vec{P}_\infty) e \int_\sigma^{\tau+\sigma} V_{ia}(a(b), \vec{F}_\infty, \vec{P}_\infty) db \\
&V_{iF_k}(a(\sigma), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau+\sigma) d\sigma, \\
k_{22}^{jiF_k}(\tau) &= \int_0^\infty \int_\sigma^{\tau+\sigma} I_{ji}(a(\tau+\sigma), \vec{F}_\infty, \vec{P}_\infty) \frac{\pi_i^*(\tau+\sigma)}{\pi_i^*(s)} \mu_{ia}(a(s), \vec{F}_\infty, \vec{P}_\infty) \times \\
&e \int_\sigma^s V_{ia}(a(b), \vec{F}_\infty, \vec{P}_\infty) db \\
&V_{iF_k}(a(\sigma), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(s) ds d\sigma +
\end{aligned}$$

$$\int_0^\infty I_{ji}(a(\tau + \sigma), \vec{F}_\infty, \vec{P}_\infty) \frac{\pi_i^*(\tau + \sigma)}{\pi_i^*(\sigma)} \mu_{iF_k}(a(\sigma), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\sigma) d\sigma -$$

$$\int_0^\infty I_{jia}(a(\tau + \sigma), \vec{F}_\infty, \vec{P}_\infty) e^{\int_\sigma^{\tau+\sigma} V_{ia}(a(b), \vec{F}_\infty, \vec{P}_\infty) db} V_{iF_k}(a(\sigma), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau + \sigma) d\sigma,$$

$$k_{21}^{ji}(\tau) = I_{ji}(a(\tau), \vec{F}_\infty, \vec{P}_\infty) \pi_i^*(\tau),$$

$$\Theta_{jk}^{F_k} = \begin{cases} \left[\sum_{i=1}^n \int_0^\infty I_{jiF_k}(a(\tau), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau) d\tau \right] - \phi_j'(F_{j\infty}), & k = j, \\ \sum_{i=1}^n \int_0^\infty I_{jiF_k}(a(\tau), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau) d\tau, & k \neq j, \end{cases}$$

$$c_{ik}^{F_k} = \int_0^\infty \beta_{iF_k}(a(\tau), \vec{F}_\infty, \vec{P}_\infty) p_{i\infty}(\tau) d\tau, \quad 1 \leq i \leq n, \quad 1 \leq k \leq m,$$

$$\mathfrak{F}_i(\xi) = 1 - \mathcal{L}\{k_{11}^i(\tau)\}(\xi), \quad 1 \leq i \leq n,$$

$$k_{11}^i(\tau) = \beta_i(a(\tau), \vec{F}_\infty, \vec{P}_\infty) \pi_i^*(\tau), \quad 1 \leq i \leq n.$$

The special case when the vital and feeding rates do not depend on the individual population sizes of Daphnia species P_i , $1 \leq i \leq n$, then I can show that the three types of models share the same characteristic equation via directly computing the characteristic equation for the third type models, of the integral equation type, see for example, [3] and [1], and also realize that it is the same as the characteristic equation of the system (1).

I also note that for the above mentioned special case, and, in addition, when $m = 1$, I obtain the same case that is studied in [3], Chapter 1, where I obtained that the characteristic equation therein is given by the following formula:

$$\left[\prod_{i=1}^n \mathfrak{F}_i(\xi) \right] \Phi_1(\xi) = 0, \quad (6)$$

where $\Phi_1(\xi)$ is given by

$$\Phi_1(\xi) = \xi + \Theta_{11}^{F_1} - \sum_{i=1}^n \mathcal{L}\{k_{22}^{1iF_1}(\tau)\}(\xi) + \sum_{i=1}^n \frac{[c_{i1}^{F_1} - \mathcal{L}\{k_{12}^{iF_1}(\tau)\}(\xi)] \mathcal{L}\{k_{21}^{1i}(\tau)\}(\xi)}{\mathfrak{F}_i(\xi)}, \quad (7)$$

\mathcal{L} denotes the Laplace transform, and $\prod_{i=1}^n \mathfrak{F}_i(\xi) = \mathfrak{F}_1(\xi)\mathfrak{F}_2(\xi)\dots\mathfrak{F}_n(\xi)$.

Furthermore, I can generalize the characteristic equation, given by equation (6), and obtain

$$\prod_{i=1}^n \mathfrak{F}_i(\xi) \prod_{j=1}^m \Phi_j(\xi) = 0, \quad n = 1, 2, 3, \dots, \quad m = 1, 2, 3, \dots, \quad (8)$$

where $\Phi_j(\xi)$, $2 \leq j \leq m$, is given by

$$\Phi_j(\xi) = \mathfrak{B}_{jj}(\xi) - \sum_{i=1}^n \frac{\mathfrak{D}_{ij}(\xi) \mathcal{L}\{k_{21}^{ji}(\tau)\}(\xi)}{\mathfrak{F}_i(\xi)} - \quad (9)$$

$$\sum_{i=1}^{m-1} \frac{1}{\Phi_i(\xi)} \left[\mathfrak{B}_{ji}(\xi) - \sum_{k=1}^n \frac{\mathfrak{D}_{ki}(\xi) \mathcal{L}\{k_{21}^{jk}(\tau)\}(\xi)}{\mathfrak{F}_k(\xi)} \right] \left[\mathfrak{B}_{ij}(\xi) - \sum_{k=1}^n \frac{\mathfrak{D}_{kj}(\xi) \mathcal{L}\{k_{21}^{ik}(\tau)\}(\xi)}{\mathfrak{F}_k(\xi)} \right], \quad 2 \leq j \leq m,$$

and $\mathfrak{D}_{ik}(\xi)$, $\mathfrak{B}_{jk}(\xi)$, $\mathfrak{F}_{ki}(\xi)$, $1 \leq j, k \leq m$, $1 \leq i \leq n$, are given, respectively, by the following formulas:

$$\mathfrak{D}_{ik}(\xi) = \mathcal{L}\{k_{12}^{ikF_k}(\tau)\}(\xi) - c_{ik}^{F_k}, \quad 1 \leq i \leq n, \quad 1 \leq k \leq m, \quad (10)$$

$$\mathfrak{B}_{jk}(\xi) = \delta_{jk}\xi + \Theta_{jk}^{F_k} - \sum_{i=1}^n \mathcal{L}\{k_{22}^{jiF_k}(\tau)\}(\xi), \quad 1 \leq j, k \leq m, \quad (11)$$

$$\mathfrak{S}_{ki}(\xi) = \mathcal{L}\{k_{21}^{ki}(\tau)\}(\xi), \quad 1 \leq k \leq m, \quad 1 \leq i \leq n, \quad (12)$$

where $\delta_{jk} = 1$, if $j = k$, and zero otherwise.

I note that the formula given by equation (9) can be utilized in order to prove that the three types of models have the unique characteristic equation (8).

References

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