

We have a set of  $s$  species, for each species  $i \in \{1, 2, \dots, s\}$ , and each  $w > w_{e,i}$ , the abundance  $N_i(w)$  satisfies the McKendrick-von Foerster equation

$$\frac{\partial N_i(w)}{\partial t} = -\frac{\partial[N_i(w)g_i(w)]}{\partial w} - \mu_i(w)N_i(w) \quad (1)$$

(steady state solution is  $N_i(w) \propto \frac{1}{g_i(w)} \exp\left(-\int_{w_{e,i}}^w \frac{\mu(w')}{g(w')} dw'\right)$ ), also, reproduction is modeled by the boundary condition

$$g_i(w_{e,i})N_i(w_{e,i}) = \frac{\epsilon_i}{2w_{e,i}} \int_0^\infty N_i(w)E_{r,i}(w)\psi(w).dw. \quad (2)$$

Here

$$g_i(w) = g_i[N](w) = \begin{cases} (1 - \psi_i(w)) E_{g,i}[N](w) & \text{if } E_{g,i}[N](w) > 0 \\ 0 & \text{otherwise.} \end{cases} \quad (3)$$

denotes the growth rate of a weight  $w$  member of species  $i$  when the system is in state  $N$ . Here

$$E_g[N](w) = \alpha_i h_i w^n \left( \frac{E_{e,i}[N](w)}{E_{e,i}[N](w) + h_i w^n} \right) - k_{s,i} w^p - k_i w. \quad (4)$$

denotes the energy available for growth and reproduction, and  $hw^n$  is the maximum food intake rate of a weight  $w$  individual. The total energy intake  $f(w)hw^n$ , however we suppose energy is only assimilated with an efficiency  $\alpha$  and a weight  $w$  individual must spend energy  $kw^p$  in order to satisfy its metabolic needs or else it will be subject to potential starvation. Often we assume  $n = p$  and  $k = 0$ . Here

$$E_{e,i}[N](w) = \gamma_i w^q \int_0^\infty w' \phi_i \left( \frac{w'}{w} \right) \left( N_R(w') + \sum_{j=1}^s \theta_{ij} N_j(w') \right) dw' \quad (5)$$

denotes the energy encountered and

$$\phi_i \left( \frac{w'}{w} \right) = \exp \left[ - \left( \ln \left( \frac{\beta_i w'}{w} \right) \right)^2 / (2\sigma_i^2) \right] \quad (6)$$

represents the preference that a predator of weight  $w$  has for a prey of weight  $w'$ .

The mortality rate is given by

$$\mu_i(w) = \mu_{b,i}(w) + \mu_{F,i}(w) + \mu_{p,i}(w) \quad (7)$$

where the predation mortality rate is

$$\mu_p(w) = \int_0^\infty \sum_j \left( \frac{hw'^n}{E_e(w')} \right) \left( \frac{E_{e,i}[N](w)}{E_{e,i}[N](w) + h_i w^n} \right) N_j(w', t) \phi_i \left( \frac{w}{w'} \right) \gamma w'^q dw' \quad (8)$$

A state  $N$  is a specification of  $N_i(w) \in \mathbb{R}$  for each  $i \in \{1, \dots, s\}$ , and each  $w > 0$ . This is said to be a steady state if  $\frac{\partial N_i(w)}{\partial t} = 0$ , for each  $i \in \{1, \dots, s\}$ , and each  $w > 0$ .

## Transplant Principle

We can construct an equilibria where  $g_i(w) = P_i(w)(1 - \psi_i(w))$ , and  $P_i(w) = \bar{h}_i w^n$ , and  $\mu_i(w) = \mu_0 w^{n-1}$ . Any abundance multipliers, dodgy background and resource setup

We should also consider the case where  $P_i(w) = \sum_k a_{i,k} w^{\alpha_k}$  and  $\mu_i(w) = \sum_k b_{i,k} w^{\beta_k}$

because we can solve the MvF exactly for such growth and death rates, I presume, and it should be possible to reconstruct size spectra so that (for certain parameter choices at least), we can consider

\*I'm wondering if it might be possible to get the analytic form of a steady state  $N$  such that such that aggregate abundance equals the sum of two powers (so  $\sum_i N_i(w) = \kappa_1 w^{-\lambda_1} + \kappa_2 w^{-\lambda_2}$ , which consists of a combination of two stable community.R style assemblages of background species which use different parameters to each other. If we have the case where growth and death are given by sums of powers, we could solve the MvF in this case, and if we have two background assemblages which vary over continua of characteristic size then perhaps we can combine them to produce the above size spectrum, the associated death and growth rates would also be described by sums of powers, and we can solve the MvF in such a case, and we will have two different solution shapes, but since each is associated with a continua of characteritic sizes, and can set the abundances so that the integral over the abundances of the two assemblages is the sum of the two power laws. This seems to be possible if we make the exponents,  $n, p, q$  species specific. Indeed it would be good to explore generalizations of the single homogeneous steady state construction procedure in this regard, of adding extra collections of background species, associated with different exponents, so that the aggregation of abundance over all species equals a sum of power laws.

\*We assume  $h_i = \infty, \forall i$  so that growth and death are linear, so  $g_i[N^1 + N^2](w) = g_i[N^1] + g_i[N^2](w)$  and  $\mu_i[N^1 + N^2](w) = \mu_i[N^1] + \mu_i[N^2](w)$  (do we also have to assume  $\phi_1 = \dots = \phi_s$  in order to get the death rates to act linearly.

\*It is important to distiguish two different type of steady states in multi-species hetrogenous size spectrum models. A uniform steady state is a steady state  $N$  such that for any pair of species  $i, j \in \{1, \dots, s\}$  there exists a rescaling constant  $Q_{ij}$  such that  $N_j(w) = Q_{ij} N_i(w)$ . In this case, we can find all the solutions are the same, if we then set things up so there are similar species

across many characteristic sizes, then we may be able to demonstrate that we can setup equilibria which have something

\* simplified form of transplant principal in this linear case: If  $N^1 + N^2$  and  $M^1 + M^2$  are steady states, each composed into two parts (with disjoint species sets  $sp$ ), and for each species  $i \in sp(N^1) = sp(M^1)$  we have  $g_i[N^2](w) = g_i[M^2](w)$ ,  $\mu_i[N^2](w) = \mu_i[M^2](w)$  and for each species  $j \in sp(N^2) = sp(M^2)$  we have  $g_j[N^1](w) = g_j[M^1](w)$ ,  $\mu_j[N^1](w) = \mu_j[M^1](w)$  then  $N^1 + M^2$  and  $N^2 + M^1$  are steady states

\*If there are all these extra steady states/neutralities that could be created by including extra species with different parameters, then it could be quite important to properly model the presence of rare species, which could increase their abundance in various combinations to replace a common species that goes extinct. I guess there will be cases where common species goes extinct and is replaced with a rather non-trivial combination of many other species.

\* if you have a steady state, and then you replace one species with another new species, at half the abundance which has twice the gamma, and pre-existing species have twice the theta preference, for the new species, then that will lead to another steady state.

\* under the further assumptions that  $\phi_1 = \phi_2 = \dots = \phi_s$ , and  $[N_1, N_2, \dots, N_s]$  are all proportional to one another], we can actively describe the affine set of steady states, by considering the linear algebra problem involving theta.

\*Suppose we have a size spectrum model (say for simplicity the resource dynamics are turned off), and suppose we have an unlimited feeding level (so  $h_i \rightarrow \infty, \forall i$ ), and also suppose  $k_i = k_{s,i} = 0$ , and suppose each species has the same feeding kernel function (i.e.,  $\beta_1 = \dots = \beta_s$  and  $\sigma_1 = \dots = \sigma_s$ ), so  $\phi_1 = \dots = \phi_s = \phi$ . It follows that

$$\mu_{p,i}[N](w) = \int_0^\infty \phi\left(\frac{w}{w'}\right) w'^q \left( \sum_j \gamma_j \theta_{ji} N_j(w', t) \right) dw' \quad (9)$$

and

$$g_i[N](w) = (1 - \psi_i(w)) \alpha_i w^q \int_0^\infty \phi\left(\frac{w'}{w}\right) w' \left( \gamma_i \left( N_R(w') + \sum_j \theta_{ij} N_j(w') \right) \right) dw'. \quad (10)$$

are the expressions for the predation mortality, and growth rates in such a system. Suppose  $N$  is a steady state of such a system, and suppose  $N'$  is another system state, with the abundances of different species rescaled, so for each species  $i$  there exists a multiplier  $A_i$  such that species  $i$  has abundance  $N'_i(w) = A_i N_i(w)$ , for each  $w$ , in the new system state. Now, if this new system state  $N'$  is such that

$$\sum_{j=1}^s \gamma_j \theta_{ji} N_j(w', t) = \sum_{j=1}^s \gamma_j \theta_{ji} A_j N_j(w', t) = \sum_{j=1}^s \gamma_j \theta_{ji} N'_j(w', t) \quad (11)$$

and

$$\gamma_i \left( N_R(w') + \sum_{j=1}^s \theta_{ij} N_j(w') \right) = \gamma_i \left( N'_R(w') + \sum_{j=1}^s \theta_{ij} A_j N_j(w') \right) = \gamma_i \left( N'_R(w') + \sum_{j=1}^s \theta_{ij} N'_j(w') \right) \quad (12)$$

for each species  $i$  and weight  $w$  then this new state  $N'$  will also be a steady state of our system.

Note, above we may turn off the plankton dynamics, or simply assume  $N'_R(w') = N_R(w')$ .

\* A corollary of the above, is that, for such a size spectrum system S, where the growth rate and death rates are purely governed by the form of the functions  $a_i[N](w) := \sum_{j=1}^s \gamma_j \theta_{ji} N_j(w', t)$  and  $b_i[N](w) := \gamma_i \left( N_R(w') + \sum_{j=1}^s \theta_{ij} N_j(w') \right)$ , is that we have a set of  $k$  steady states  $N^1, \dots, N^k$  of the type of system described above, then any new state  $N^*$  formed by an affine combination of these steady states (in the sense that  $\exists \lambda_1, \dots, \lambda_k : N^* = \sum_{e=1}^k \lambda_e N^e$  and  $\sum_e \lambda_e = 1$ ) must be also be a steady state. To see this note that our linearity, and the fact that  $N^*$  is an affine combination implies  $a_i[N^1](w) = \dots = a_i[N^k](w) = a_i[N^*](w)$  and  $b_i[N^1](w) = \dots = b_i[N^k](w) = b_i[N^*](w)$ ,  $\forall w$  and so  $g_i[N^1](w) = \dots = g_i[N^k](w) = g_i[N^*](w)$  and  $\mu_i[N^1](w) = \dots = \mu_i[N^k](w) = \mu_i[N^*](w)$ ,

and so each of the states  $N^1, \dots, N^k$  have the same death and growth rates, and, so they all correspond to steady states of the simplified MvF system SS where death and growth are held fixed at these rates.  $N^*$  is a linear combination of the steady states  $N^1, \dots, N^k$  and so  $N^*$  is another steady state of the simplified system SS (because any linear combination of steady states if SS is a steady state of SS), but also, when reconsidering state  $N^*$  within the full system S (i.e., the proper system where  $g$  and  $\mu$  are given by integrals over abundance), we still have that  $\mu[N^*] = \mu[N^1] = \dots = \mu[N^k]$  and  $g[N^*] = g[N^1] = \dots = g[N^k]$  and so  $N^*$  will also be a steady state of S. To summarise: If feeding level is unlimited, and feeding kernels are the same for each species then the set of steady states  $N$  which have a particular form of the functions  $\sum_{j=1}^s \gamma_j \theta_{ji} N_j(w', t)$  and  $\gamma_i \left( N_R(w') + \sum_{j=1}^s \theta_{ij} N_j(w') \right)$  form an affine set of steady states,

\* homogeneous case as a special case of the above

\* Let N be a steady state of an unlimited feeding rate size spectrum model within which the form of each growth rate is just governed by the form of  $N_R(w) + \sum_{i=1}^s N_i(w)$ , now if growth rates and mortality rates can be linearly recombined, we can prove that any redistribution of abundances produces another steady state of the same system. In the scale free model, a similar phenomenon occurs, but this time the solutions have the same shape but are shifted.

\* special system where all species are identical, apart from that we can have arbitrary theta values

\* Transplants using tricks with alpha, gamma, theta and A\_i

\* demonstrate why we saw a bunch of steady states in our work on steady states by converting the code

\* We say a size spectrum model has unlimited intake if  $h_i = \infty, \forall i$

\* We say an unlimited intake size spectrum model in state  $N$  has ‘power law sum aggregate abundance’ if  $\exists \lambda_1, \dots, \lambda_k, \exists \kappa_1, \dots, \kappa_k, \exists B_1, \dots, B_s$  such that  $N_R(w) + \sum_j \theta_{ij} N_j(w) = B_i \sum_{e=1}^k \kappa_e w^{-\lambda_e}$ , and  $\exists D_1, \dots, D_s, \exists \mu_{0,1}, \dots, \mu_{0,k}, \exists n_1, \dots, n_k$  such that  $\mu_i(w) = \mu_{p,i}[N](w) + \mu_{b,i}(w) = D_i \sum_{e=1}^k \mu_{0,e} w^{n_e-1}$

\* An unlimited intake size spectrum model in state  $N$  has ‘species-scaled power law aggregate abundance’ if it has power law sum aggregate abundance with  $k = 1$ . In this case  $\exists \kappa^{(1)}, \dots, \kappa^{(s)}, \exists \mu_0^{(1)}, \dots, \mu_0^{(s)}$  : such that  $N_R(w) + \sum_j \theta_{ij} N_j(w) = \kappa^{(i)} w^{-\lambda}$  and  $\mu_{p,i}[N](w) + \mu_{b,i}(w) = \mu_0^{(i)} w^{n-1}$ .

\* An unlimited intake size spectrum model in state  $N$  has ‘power law aggregate abundance’ if it has ‘species-scaled power law aggregate abundance’ with  $\kappa^{(1)} = \dots = \kappa^{(s)} = \kappa, \mu_0^{(1)} = \dots = \mu_0^{(s)} = \mu_0$ .

\* A spectrum model is [gamma,theta,alpha,feeding-kernel,..etc.] homogeneous, if every species has the same parameter/function [gamma,theta,alpha,feeding-kernel,..etc.]

\* A state  $N$  is ‘single shaped’ if  $\forall i, j \exists Q_{i,j} : Q_{i,j} N_i(w) = N_j(w), \forall j$

\* If the intake is unlimited, and the feeding-kernels are homogeneous, then the set of steady states that can be converted between by altering the steady state in such a way that the death and growth rates of individuals can be preserved, corresponds to an affine set (the same I observed with R.L.).

\* The above can be generalized to allow different species to be associated with different death rates, and therefore to have different solutions, but one can still describe the affine structure of the steady states, but now it corresponds to a ‘species-scaled power law aggregate abundance’ with  $\kappa^{(1)} = \dots = \kappa^{(s)} = \kappa$ , and it no longer has single shaped solutions, but by tuning the species specific background mortality, we can set things up.

\* For a feeding kernel homogeneous, unlimited intake, size spectrum model, we know how to construct a power law aggregate abundance steady state that is single shaped (stable\_community.R does this type of thing). Using the linearity of the growth and death rates in this case

\* An unlimited intake size spectrum model in state  $N$  has ‘power law aggregate abundance’ when it has power law sum aggregate abundance and when  $k = 1, B_1 = \dots = B_s = 1, \theta_{ij} = 1, D_1 = \dots = D_s = 1$ . This is the standard power law case for which we can obtain a complete analytic solution. In other words, an unlimited intake size spectrum model in state  $N$  has ‘power law aggregate abundance’ if  $\theta_{ij} = 1$ , and

\* A generalization of the above case is to allow  $B_1, \dots, B_s, D_1, \dots, D_s$  to take general values.

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We shall consider heterogeneous multispecies size spectrum models as described in the mizer vignette, except with  $\theta_{ij} = 1$  the resource dynamics turned off. For simplicity suppose we have an unlimited feeding level (so  $h_i \rightarrow \infty, \forall i$ ).

Suppose we have such a system, and we have free choice over all the usual system parameters we want to use, except for the background resource level  $N_R(w)$  and the background death rate  $\mu_{b.i}(w)$  and the reproductive efficiency  $\epsilon_i$  which we shall pick to take specific values later in order to construct a steady state.

The steady state  $N$  we shall construct has the following properties:

$$\sum_i N_i(w) + N_R(w) = \kappa w^{-\lambda} \quad (13)$$

$$\mu_i[N](w) = \mu_{0.i} w^{n-1} = \mu_{b.i}[N](w) + \mu_{p.i}[N](w) = \mu_{b.i}[N](w) + \int_0^\infty \phi_i\left(\frac{w}{w'}\right) w'^q \left( \sum_j \gamma_j \theta_{ji} N_j(w', t) \right) dw', \forall \quad (14)$$

where  $\kappa$  and  $\mu_{0.1}, \dots, \mu_{0.s}$  are chosen by us initially. The construction is as follows:

1. Let be the unscaled steady state solution of the Mvf, for each species  $i$ .

Here  $g_i^*(w)$

$$g_i^*(w) = \hbar_i w^n (1 - \psi_i(w)) \quad (15)$$

$$\mu_i^*(w) = \hbar w^n (1 - \psi_i(w)) \quad (16)$$

$$f_i(w) = \frac{1}{g_i^*(w)} \exp \left( - \int_{w_{e.i}}^w \frac{\mu_i^*(w')}{g_i^*(w')} dw' \right) \quad (17)$$

2. Choose any abundance multipliers  $A_1, \dots, A_s \geq 0$  such that  $\sum_i A_i f_i(w) \leq \kappa w^{-\lambda}, \forall w > 0$ .

Suppose we have a size spectrum model with  $s$  heterogeneous species.

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## Affine Structure Result

If  $N^1, \dots, N^k$  are steady states of an unlimited intake ( $\hbar_i \rightarrow \infty, \forall i$ ) size spectrum model that all induce the same death and growth rates (in the sense that  $\mu_i[N^1](w) = \dots = \mu_i[N^k](w) =: M_i(w)$  and  $g_i[N^1](w) = \dots = g_i[N^k](w) =: G_i(w)$ ) and  $N^* = \lambda_1 N^1 + \dots + \lambda_k N^k : \lambda_1 + \dots + \lambda_k = 1$  is an affine combination of the steady states then  $N^*$  is a steady state.

Proof

In this type of system, for any state  $N$ , the death and growth rates are

$$\mu_{p.i}[N](w) = \int_0^\infty w'^q \left( \sum_j \phi_j\left(\frac{w}{w'}\right) \gamma_j \theta_{ji} N_j(w', t) \right) dw' \quad (18)$$

$$g_i[N](w) = (1 - \psi_i(w)) \alpha_i w^q \int_0^\infty \phi_i\left(\frac{w'}{w}\right) w' \left( \gamma_i \left( N_R(w') + \sum_j \theta_{ij} N_j(w') \right) \right) dw'. \quad (19)$$

are linear in  $N$ , so that for any pair of states  $N$  and  $N'$  we have  $g_i[N + N'](w) = g_i[N'](w) + g_i[N](w)$ .

Since the growth rates  $G$  and death rates  $M$  are the same for all steady states,  $N^1, \dots, N^k$  they must satisfy the MvF steady state condition for such growth and death rates and so  $\forall e \in \{1, \dots, k\} \forall i \in \{1, \dots, s\}$  there exists  $A_i^e$  such that  $N_i^e(w) = A_i^e \frac{1}{G_i(w)} \exp\left(-\int_{w_{e,i}}^w \frac{M_i(w')}{G_i(w')} dw'\right)$ . Now note that since  $N^*$  is written as an affine combination of such states, it must also have a similar form, in the sense that  $\forall e \in \{1, \dots, k\} \forall i \in \{1, \dots, s\}$  there exists  $B_i^e$  such that

$$N_i^{*e}(w) = B_i^e \frac{1}{G_i(w)} \exp\left(-\int_{w_{e,i}}^w \frac{M_i(w')}{G_i(w')} dw'\right) \quad (20)$$

And so all we have to do is to show that the death and growth rates  $\mu_i[N^*](w)$  and  $g_i[N^*](w)$  induced by state  $N^*$  are the same as those death and growth rates  $M_i(w) = \mu_i[N^1] = \dots = \mu_i[N^k]$  and  $G(w) = g_i[N^1] = \dots = g_i[N^k]$  which are experienced in each of our steady states  $N^1, \dots, N^k$ .

To see that  $g[N^*] = G$  note that since  $g[N^1] = \dots = g[N^k] =: G$  we have

$$g[N^*] = g[\lambda_1 N^1 + \dots + \lambda_k N^k] = \lambda_1 g[N^1] + \dots + \lambda_k g[N^k] = (\lambda_1 + \dots + \lambda_k) G = G \quad (21)$$

a similar argument shows that the death rates in  $N^*$  are the same as those that were in the steady states  $N^1, \dots, N^k$ .

It follows that  $N^*$  can be written in the form

$$N_i^{*e}(w) = B_i^e \frac{1}{g_i[N^*](w)} \exp\left(-\int_{w_{e,i}}^w \frac{\mu_i[N^*](w')}{g_i[N^*](w')} dw'\right) \quad (22)$$

and so it is also a steady state.  $\square$

Loose ends

need to demonstrate (and similarly for mortality rates) that

$$g_i[N^1 + N^2](w) = g_i[N^1] + g_i[N^2](w)$$

$$\text{and } \lambda g_i[N](w) = g_i[\lambda N](w)$$