

A Trait Based Model From Scale Free Assumptions

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1 Model Definition

1.1 The Basics

We model our ecosystem by keeping track of the abundance $N(w, w_*, t)$ of fish of weight w at time t . Here w_* denotes the weight of the fish at maturity. We suppose the maturity weight w_* represents the species of the fish, in the sense that fish of the same weight can act differently in our model, only if they have different maturity weights. We allow w and w_* to vary continuously, and to take any positive values, and hence we are assuming a continuum of species, characterized by different size traits w_* . The abundance $N(w, w_*, t)$ is defined such that

$$\int_{w_1}^{w_2} \int_{w_{*1}}^{w_{*2}} N(w, w_*, t) . dw . dw_* \quad (1)$$

is the number of fish per unit volume which have a weight $w \in [w_1, w_2]$ and a maturity weight $w_* \in [w_{*1}, w_{*2}]$.

The abundance $N(w, w_*, t)$ of fish with a particular maturity weight w_* vary according to the McKendrick–von Foerster equation

$$\frac{\partial N(w, w_*, t)}{\partial t} = - \frac{\partial [N(w, w_*, t) g(w, w_*)]}{\partial w} - \mu(w, w_*) N(w, w_*, t) \quad (2)$$

for time $t \in \mathbb{R}$, and weight $w \in \left[w_e(w_*), \frac{w_*}{\eta} \right]$. The abundance $N(w, w_*, t)$ of fish with weight $w \notin \left[w_e(w_*), \frac{w_*}{\eta} \right]$ must be zero.

We further insist that our abundances $N(w, w_*, t)$ must satisfy the boundary condition:

$$g(w_e(w_*), w_*) N(w_e(w_*), w_*, t) = \frac{\epsilon}{2w_e(w_*)} \int_0^\infty N(w, w_*, t) E_g(w) \psi(w, w_*) . dw, \quad (3)$$

the left hand side of which represents the flux of new offspring into the system, and the right hand side of which represents how the amount of such new offspring is obtained by integrating over the reproducing fish of different weights. An abundance function $N(w, w_*, t)$ is a solution to our system if and only if it satisfies (2) and (3) for each $w_* > 0$, $t \in \mathbb{R}$, and $w \in \left[w_e(w_*), \frac{w_*}{\eta} \right]$, while $w \notin \left[w_e(w_*), \frac{w_*}{\eta} \right] \Rightarrow N(w, w_*, t) = 0$.

Here $g(w, w_*)$ is the growth rate, $\mu(w, w_*)$ is the mortality rate, $w_e(w_*)$ is the egg size of species with w_* as their maturity weight, $\frac{w_*}{\eta}$ is the asymptotic weight of such a species, ϵ is the reproductive efficiency, $E_g(w)$ is the energy available for reproduction and growth, and $\psi(w, w_*)$ is the fraction of such energy which a fish uses for reproduction. We shall describe these quantities in more detail later.

1.2 Scale Free Assumption

Setting up a size spectrum model required the definition of many functions representing features of the feeding, growth, death and reproduction of fish. Often the real world nature of these functions is poorly understood, or the model becomes analytically intractable once there are modeled in sufficient detail. Therefore various assumptions are often introduced, such as the assumption of constant feeding level in Hartvig. Instead of this, our main simplifying assumption is that our model should be scale invariant, in the sense that if we apply particular kinds of rescaling upon the units of weight, maturity weight, time, and abundance, we get another solution to our system. Using this assumption gives us natural constraints on the forms of functions we should use which are often in remarkable agreement to function forms justified by other researchers for other reasons. Applying our particular type of rescaling to an abundance function $N : \mathbb{R}_+ \times \mathbb{R}_+ \times \mathbb{R} \rightarrow \mathbb{R}$ using a scaling constant $c > 0$ yields a new abundance function $F_c[N] = \tilde{N}$ where $\tilde{N} : \mathbb{R}_+ \times \mathbb{R}_+ \times \mathbb{R} \rightarrow \mathbb{R}$ is defined such that $\tilde{N}(w, w_*, t) = c^\Lambda N(cw, c^A w_*, c^B t)$ for each $w, w_* > 0$ and each $t \in \mathbb{R}$. Here \mathbb{R}_+ denotes the set of positive reals. Sometimes we call F_C a symmetry transform because it represents a type of rescaling that we require the key features of our model to be invariant under. Formally, our scale free assumption is that: if the abundance function N satisfies our system, then we require the rescaled abundance function $F_c[N]$ to also be a solution to the system, for each $c > 0$.

1.3 Prey Switching

The problem of coexistence, is the problem of making an ecological model where multiple different species competing for common resources can coexist. Coexistence is not generally possible in the classical size spectrum models of [Hartvig] for example, and this can be seen by noting that there are no steady state of the McKendrick–von Foerster equation they use, where all species coexist, that satisfies the boundary conditions for each maturity weight w_* . We resolve this

problem by adding a small amount of extra density dependence into the dynamics of predation. In the classical theory, the total predation mortality rate of individuals with mass w and maturity weight w_* is $\check{\mu}_p(w)N(w, w_*, t)$, where $\check{\mu}_p(w)$ is the per capita predation mortality rate. In our model, the total predation mortality rate is instead $\check{\mu}_p(w)N(w, w_*, t)\hat{N}(w, w_*, t)^\chi$ where the prey switching constant $\chi \geq 0$ is some (typically small) number which abstractly represents the amount of prey switching, and

$$\hat{N}(w, w_*, t) = N(w, w_*, t)w^\Omega w_*^\Gamma \Delta \quad (4)$$

where Δ, Ω and Γ are constants. We do not give a direct ecological interpretation to this new prey switching factor, but the result of adding the factor is that it makes the total predation mortality rate into a super linear function of the prey's density in a way which works well with our scale free assumption. Adding such density dependence seems justified ecologically since large groups of prey are more likely to be targeted by predators. Also, only a small amount of prey switching (e.g., $\chi = 0.05$) is often required to make it possible for a solution of (2) to satisfy the boundary conditions (3). Perhaps the simplest form of prey switching would be to pick $\Omega = \Gamma = 0$, in which case the prey switching corresponds to a simple additional dependence upon the abundance. Similar biomass based prey switching can be encoded by setting $\Omega = 1, \Gamma = 0$. If one lets $\Omega = 1, \Gamma = 1$ and $\Delta = \delta\delta_*$ then the prey switching term approximates the number of individuals (per unit volume) with nearby weights and maturity weights, in the sense that

$$\hat{N}(w, w_*, t) \approx \int_w^{(\delta+1)w} \int_{w_*}^{(\delta_*+1)w_*} N(w', w'_*, t).dw'.dw'_* \quad (5)$$

in this case. If one lets $\Omega = 2, \Gamma = 1$ and $\Delta = \delta\delta_*$ then the prey switching term approximates the total biomass (per unit volume) of individuals with nearby weights and maturity weights, in the sense that

$$\hat{N}(w, w_*, t) \approx \int_w^{(\delta+1)w} \int_{w_*}^{(\delta_*+1)w_*} w' N(w', w'_*, t).dw'.dw'_* \quad (6)$$

in this case.

Since adding a prey switching term $\hat{N}(w, w_*, t)$ (of whatever form) will effect the total predation mortality rate, there will be a corresponding modification to the term $\phi(w)$ which denotes the total amount of energy available to a size w predator. The classical expression for available energy in [Hartvig] was essentially

$$\int_0^\infty \int_0^\infty w' N(w', w'_*, t) s(w', w) dw' dw'_* \quad (7)$$

where

$$s(w, w') = \exp \left[- \left(\ln \left(\frac{\beta w'}{w} \right) \right)^2 / (2\sigma^2) \right] \quad (8)$$

represents the preference that a predator of weight w has for a prey of weight w' . Here β is the preferred predator-prey mass ratio, and σ represents the width of sizes of prey which the predator will tolerate. When we include our prey switching, the expression for available energy changes to

$$\phi(w) = \int_0^\infty \int_0^\infty w' N(w', w'_*, t) \hat{N}(w, w'_*, t)^\chi s(w', w) dw' dw'_* \quad (9)$$

and so when prey switching is present (i.e., when $\chi > 0$) the amount of food extracted from the prey goes up super-linearly with their abundance.

1.4 Growth Rate

The available energy (i.e., the food available) $\phi(w)$ to a weight w predator is given by Equation (9). To get the energy encountered $E_e(w)$ by such a predator $\phi(w)$ must be multiplied by the volumetric search rate γw^q so

$$E_e(w) = \phi(w) \gamma w^q. \quad (10)$$

The feeding level of an individual is

$$f(w) = \frac{E_e(w)}{E_e(w) + hw^n} \quad (11)$$

where 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 α 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. It follows that the energy available for growth and reproduction is

$$E_g(w) = \alpha f(w)hw^n - kw^p. \quad (12)$$

The growth rate is now defined as

$$g(w, w_*) = \begin{cases} (1 - \psi(w, w_*)) E_g(w) & \text{if } E_g(w) > 0 \\ 0 & \text{otherwise.} \end{cases} \quad (13)$$

1.5 Mortality Rate

The (per capita) mortality rate

$$\mu(w, w_*) = \mu_b(w_*) + \mu_s(w) + \mu_p(w) \quad (14)$$

is the sum of the background mortality rate

$$\mu_b(w_*) = \mu_0 w_*^Q \quad (15)$$

(note in [Hartvig] they chose $Q = n - 1$, constraining the rescaling exponent choices A, B, Λ)

and the starvation mortality rate

$$\mu_s(w) = \begin{cases} \frac{-E_g(w)}{\xi} & \text{if } E_g(w) < 0 \\ 0 & \text{otherwise.} \end{cases} \quad (16)$$

and the predation mortality rate

$$\mu_p(w) = \hat{N}(w, w'_*, t)^\chi \int_0^\infty \int_0^\infty \left(\frac{f(w') h w'^n}{E_e(w')} \right) N(w', w'_*, t) s(w', w) \gamma w'^q dw' dw'_* \quad (17)$$

where $\left(\frac{f(w') h w'^n}{E_e(w')} \right)$ is the energy income of the weight w' predators, divided by the total energy encountered. This equals the fraction of encountered individuals they consume. The remaining terms inside the integral represent the amount of weight w prey encountered by predators. We multiply the integral by $\hat{N}(w, w'_*, t)^\chi$ to account for prey switching. Rearranging (11) into an equation for $E_e(w)$ and substituting it into (17) yields

$$\mu_p(w) = \hat{N}(w, w'_*, t)^\chi \int_0^\infty \int_0^\infty (1 - f(w')) N(w', w'_*, t) s(w', w) \gamma w'^q dw' dw'_* \quad (18)$$

which is the same as the expression appearing in [Hartvig] except that we have an additional prey switching factor.

2 Using Scale Invariance

The McKendrick–von Foerster equation (2) can be rewritten as

$$\frac{\partial N(w, w_*, t)}{\partial t} = - \frac{\partial [N(w, w_*, t) g(w, w_*)]}{\partial w} - (\mu_b(w_*) + \mu_s(w)) N(w, w_*, t) - \mu_p^*(w) N(w, w_*, t)^{\chi+1} \quad (19)$$

where

$$\mu_p^*(w) = (w^\Omega w_*^\Gamma \Delta)^\chi \int_0^\infty \int_0^\infty (1 - f(w')) N(w', w'_*, t) s(w', w) \gamma w'^q dw' dw'_* \quad (20)$$

In this section we shall demonstrate how particular choices of parameters can lead to a model that satisfies our scale free assumption. We shall assume that $N : \mathbb{R}_+ \times \mathbb{R}_+ \times \mathbb{R}$ is a solution to our system (so it satisfies (3) and (19)). In this section, we write $\mathcal{A} \mapsto \mathcal{B}$ to denote that expression \mathcal{B} is obtained by

taking expression \mathcal{A} and replacing each $N(w, w_*, t)$ with $c^\Lambda N(cw, c^A w_*, c^B t)$. Essentially the notation $\mathcal{A} \mapsto \mathcal{B}$ denotes that expression A transforms to expression B when we apply the symmetry transform F_c for generic $c > 0$. We shall now demonstrate that (for appropriate parameter choices) our scale free assumption holds, in the sense that after we replace the N 's with $F_c[N]$'s the resulting expression still satisfies (3) and (19).

2.1 Time

To demonstrate the scale free assumption, we shall first consider how our symmetry transform alters the different terms of Equation (19), starting with the left hand side:

$$\frac{\partial N(w, w_*, t)}{\partial t} \mapsto \frac{\partial [c^\Lambda N(cw, c^A w_*, c^B t)]}{\partial t} = c^\Lambda \frac{\partial N(\tilde{w}, \tilde{w}_*, \tilde{t})}{\partial \tilde{t}} \frac{\partial \tilde{t}}{\partial t} = c^{\Lambda+B} \frac{\partial N(\tilde{w}, \tilde{w}_*, \tilde{t})}{\partial \tilde{t}} \quad (21)$$

where we use notation $\tilde{w} = cw$, $\tilde{w}_* = c^A w_*$ and $\tilde{t} = c^B t$.

2.2 Background Mortality

Applying the symmetry transform to the total background mortality rate gives

$$\mu_b(w_*)N(w, w_*, t) \mapsto \mu_0 w_*^Q c^\Lambda N(cw, c^A w_*, c^B t) = \mu_0 \frac{\tilde{w}_*^Q}{c^{AQ}} c^\Lambda N(cw, c^A w_*, c^B t) = c^{\Lambda-AQ} \mu_b(\tilde{w}_*)N(\tilde{w}, \tilde{w}_*, \tilde{t}) \quad (22)$$

Hence the effect of the F_c transformation is to convert the additive terms $\frac{\partial N(w, w_*, t)}{\partial t}$ and $\mu_b(w_*)N(w, w_*, t)$ of Equation 19 into the additive terms $c^{\Lambda+B} \frac{\partial N(\tilde{w}, \tilde{w}_*, \tilde{t})}{\partial \tilde{t}}$ and $c^{\Lambda-AQ} \mu_b(\tilde{w}_*)N(\tilde{w}, \tilde{w}_*, \tilde{t})$, respectively. In order for the transformed function to satisfy 19, with respect to the rescaled variables $\tilde{w} = cw$, $\tilde{w}_* = c^A w_*$, $\tilde{t} = c^B t$ the new factors, multiplying these terms, that our symmetry transform introduced, must cancel out. In other words, we must have $c^{\Lambda+B} = c^{\Lambda-AQ}$, for each $c > 0$, so we must have $Q = -\frac{B}{A}$.

2.3 Prey Switching Term

In order to demonstrate the scale free assumption, we wish to show that the symmetry transform has the same type of effect upon the other terms of Equation (19), as we witnessed in Subsection 2.2, and hence we must consider how the other terms change when we apply our F_c transform, and since these terms are mostly written in terms of different functions of integrals, we must consider how the more elementary functions describing energy transfer etc. change under the F_c transform. We start by how the ‘prey switching modification factor’

$$\hat{N}(w, w'_*, t)^x = N(w, w_*, t) w^\Omega w_*^\Gamma \Delta \quad (23)$$

which appears as a factor within integral (9), gets transformed under the F_c symmetry transform.