

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

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

for time $t \in \mathbb{R}$, and weight $w \in \left[w_e(w_*), \frac{w_*}{\eta} \right]$. In general, the growth rate g and mortality rate $\bar{\mu}$ at time t depend integrals over abundances, and these abundances may change with time. However, for notational simplicity we often neglect to notate the time dependence, and write these terms as $g(w, w_*)$ and $\bar{\mu}(w, w_*)$ respectively, as the only time dependence in these terms come from their dependence upon abundances. We insist that 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, $\bar{\mu}(w, w_*)$ 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. Coexis-

tence 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 and mortality. In the classical theory, the total mortality rate of individuals with mass w and maturity weight w_* is $\mu(w, w_*)N(w, w_*, t)$, where $\mu(w, w_*)$ is the per capita mortality rate. In our model, the total mortality rate is instead

$$N(w, w_*, t)\bar{\mu}(w, w_*) := N(w, w_*, t)\mu(w, w_*)\hat{N}(w, w_*, t)^\chi \quad (4)$$

where $\mu(w, w_*)$ is the unadjusted mortality rate (before we include prey switching), and the prey switching constant $\chi \geq 0$ is some (typically small) number which abstractly represents the amount of prey switching. Also

$$\hat{N}(w, w_*, t) = N(w, w_*, t)w^\Omega w_*^\Gamma \Delta \quad (5)$$

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 mortality rate into a super linear function of the individuals 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. This assumption that predation occurs at a rate superlinear to the preys density will be adjusted for when we consider the energy input to predators. Also, the unadjusted mortality rate

$$\mu(w, w_*) = \mu_p(w) + \mu_s(w) + \mu_b(w_*) \quad (6)$$

can be written as the sum of the predation mortality rate $\mu_p(w)$, the starvation mortality rate $\mu_s(w)$ and the background mortality rate $\mu_b(w_*)$, and so we are assuming that there is also density dependence upon the death of individuals due to starvation and background effects. 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

$$\hat{N}(w, w_*, t) \approx \int_w^{(\delta+1)w} \int_{w_*}^{(\delta_*+1)w_*} N(w', w'_*, t).dw'.dw'_* \quad (7)$$

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

$$\hat{N}(w, w_*, t) \approx \int_w^{(\delta+1)w} \int_{w_*}^{(\delta_*+1)w_*} w' N(w', w'_*, t) dw' dw'_* \quad (8)$$

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

$$\int_0^\infty \int_0^\infty w' N(w', w'_*, t) s(w', w) dw' dw'_* \quad (9)$$

where

$$s(w', w) = \exp \left[- \left(\ln \left(\frac{\beta w'}{w} \right) \right)^2 / (2\sigma^2) \right] \quad (10)$$

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

$$\phi(w) = \int_0^\infty \int_0^\infty w' N(w', w'_*, t) \hat{N}(w', w'_*, t)^\chi s(w', w) dw' dw'_* \quad (11)$$

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 (11). 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

$$E_e(w) = \phi(w) \gamma w^q. \quad (12)$$

The feeding level of an individual is

$$f(w) = \frac{E_e(w)}{E_e(w) + hw^n} \quad (13)$$

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

$$E_g(w) = \alpha f(w)hw^n - kw^p. \quad (14)$$

The growth rate is now defined as

$$g(w, w_*) = \begin{cases} (1 - \psi(w, w_*)) E_g(w) & \text{if } E_g(w) > 0 \\ 0 & \text{otherwise.} \end{cases} \quad (15)$$

1.5 Mortality Rate

When we have taken account of prey switching the (per capita) mortality rate of individuals is $\bar{\mu}(w, w_*) = \mu(w, w_*) \hat{N}(w, w_*, t)^\chi$, where the unadjusted (per capita) mortality rate is

$$\mu(w, w_*) = \mu_b(w_*) + \mu_s(w) + \mu_p(w) \quad (16)$$

is the sum of the background mortality rate

$$\mu_b(w_*) = \mu_0 w_*^Q \quad (17)$$

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

and the starvation mortality rate

$$\mu_s(w) = \begin{cases} \frac{-E_g(w)}{\xi} & \text{if } E_g(w) < 0 \\ 0 & \text{otherwise.} \end{cases} \quad (18)$$

and the predation mortality rate

$$\mu_p(w) = \int_0^\infty \int_0^\infty \left(\frac{f(w') h w'^n}{E_e(w')} \right) N(w', w'_*, t) s(w, w') \gamma w'^q dw' dw'_* \quad (19)$$

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. Rearranging (13) into an equation for $E_e(w)$ and substituting it into (19) yields

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

which is the same as the expression appearing in [Hartvig].

2 Using Scale Invariance

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

$$\frac{\partial N(w, w_*, t)}{\partial t} = - \frac{\partial [N(w, w_*, t) g(w, w_*)]}{\partial w} - (\mu_b(w_*) + \mu_s(w) + \mu_p(w)) (w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1} \quad (21)$$

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 (21)). 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 (21).

2.1 Time

To demonstrate the scale free assumption, we shall first consider how our symmetry transform alters the different terms of Equation (21), starting with the left hand side:

$$\frac{\partial N(w, w_*, t)}{\partial t} \mapsto \frac{\partial [c^\Lambda N(cw, c^A w_*, c^B t)]}{\partial t} = c^\Lambda \frac{\partial N(\tilde{w}, \tilde{w}_*, \tilde{t})}{\partial \tilde{t}} \frac{\partial \tilde{t}}{\partial t} = c^{\Lambda+B} \frac{\partial N(\tilde{w}, \tilde{w}_*, \tilde{t})}{\partial \tilde{t}} \quad (22)$$

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

2.2 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 each additive term of (21). So for example, we hope that when we apply the F_c transformation upon the term $\mu_b(w_*) (w^\Omega w_*^\Gamma \Delta)^X N(w, w_*, t)^{X+1}$ within Equation (21), we get $c^Y \mu_b(\tilde{w}_*) N(\tilde{w}, \tilde{w}_*, \tilde{t})$, where (we hope) $Y = \Lambda + B$, so that the new factors $c^{\Lambda+B}$ we introduce into Equation (21) will cancel. Our strategy will be to show that this type of effect occurs for all terms of Equation (21), and so after we have performed our F_c transformation we are left with a new expression that satisfies an equation of the same form as Equation (21), except in terms of the new, rescaled variables $\tilde{w} = cw$, $\tilde{w}_* = c^A w_*$ and $\tilde{t} = c^B t$. In order to 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 shall 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’

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

gets transformed under the F_c symmetry transform, this gives

$$(24)$$

$$\begin{aligned}
\hat{N}(w, w'_*, t)^\chi &\mapsto (c^\Lambda N(cw, c^A w_*, c^B t) w^\Omega w_*^\Gamma \Delta)^\chi \\
c^\Lambda N(cw, c^A w_*, c^B t) (w^\Omega w_*^\Gamma \Delta)^\chi &= \left(c^\Lambda N(\tilde{w}, \tilde{w}_*, \tilde{t}) \left(\frac{\tilde{w}}{c} \right)^\Omega \left(\frac{\tilde{w}_*}{c^A} \right)^\Gamma \Delta \right)^\chi \\
&= c^{\chi\Lambda - \chi\Omega - \chi\Gamma} \hat{N}(\tilde{w}, \tilde{w}_*, \tilde{t})^\chi \\
&= c^r \hat{N}(\tilde{w}, \tilde{w}_*, \tilde{t})^\chi,
\end{aligned}$$

where we define

$$r = \chi\Lambda - \chi\Omega - \chi\Gamma \quad (25)$$

We shall use expression (24) for the transformation of the prey switching modification factor a few times. For example, we can use it to determine how the factor

$$(w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1} = N(w, w_*, t) \hat{N}(w, w'_*, t)^\chi \quad (26)$$

(which multiplies the specific mortality rates in Equation (21)) is transformed under the F_c operation. In this case we see

$$(w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1} = N(w, w_*, t) \hat{N}(w, w'_*, t)^\chi \mapsto c^{\Lambda+r} N(\tilde{w}, \tilde{w}_*, \tilde{t}) \hat{N}(\tilde{w}, \tilde{w}_*, \tilde{t})^\chi \quad (27)$$

where

$$c^{\Lambda+r} N(\tilde{w}, \tilde{w}_*, \tilde{t}) \hat{N}(\tilde{w}, \tilde{w}_*, \tilde{t})^\chi = c^{\Lambda+r} (\tilde{w}^\Omega \tilde{w}_*^\Gamma \Delta)^\chi N(\tilde{w}, \tilde{w}_*, \tilde{t})^{\chi+1}. \quad (28)$$

2.3 Background Mortality

Applying the symmetry transform to the background mortality rate gives

$$\mu_b(w_*) \mapsto \mu_0 w_*^Q = \mu_0 \frac{\tilde{w}_*^Q}{c^{AQ}} = c^{-AQ} \mu_b(\tilde{w}_*). \quad (29)$$

We can use hence use expressions (27) and (29) together to get the following expression for how the total background mortality is transformed under F_c :

$$\mu_b(w_*) (w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1} \mapsto c^{\Lambda+r-AQ} \mu_b(\tilde{w}_*) (\tilde{w}^\Omega \tilde{w}_*^\Gamma \Delta)^\chi N(\tilde{w}, \tilde{w}_*, \tilde{t})^{\chi+1} \quad (30)$$

Hence the effect of the F_c transformation is to convert the additive terms $\frac{\partial N(w, w_*, t)}{\partial t}$ and $\mu_b(w_*) (w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1}$ of Equation 21 into the additive terms $c^{\Lambda+B} \frac{\partial N(\tilde{w}, \tilde{w}_*, \tilde{t})}{\partial \tilde{t}}$ and $c^{\Lambda+r-AQ} \mu_b(\tilde{w}_*) (\tilde{w}^\Omega \tilde{w}_*^\Gamma \Delta)^\chi N(\tilde{w}, \tilde{w}_*, \tilde{t})^{\chi+1}$ respectively. In order for the transformed function to satisfy 21, 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 $c^{\Lambda+B} = c^{\Lambda+r-AQ}$, for each $c > 0$, so we must have

$$\Lambda + B = \Lambda + r - AQ \quad (31)$$

We refer to refer to equations like (31) as ‘exponent balancing equations’. This one implies

$$Q = \frac{r - B}{A}. \quad (32)$$

2.4 Available Energy

Before we consider how the rest of the mortality terms transform, we shall consider how the available energy transforms under F_c as follows

(33)

$$\begin{aligned} \phi(w) &\mapsto \int_0^\infty \int_0^\infty w' c^{\Lambda+r} N(\tilde{w}', \tilde{w}'_*, \tilde{t}) \hat{N}(\tilde{w}', \tilde{w}'_*, \tilde{t})^\chi s(w', w) dw' dw'_* \\ &= \int_0^\infty \int_0^\infty \frac{\tilde{w}'}{c} c^{\Lambda+r} N(\tilde{w}', \tilde{w}'_*, \tilde{t}) \hat{N}(\tilde{w}', \tilde{w}'_*, \tilde{t})^\chi s(\tilde{w}', \tilde{w}) \frac{d\tilde{w}'}{c} \frac{d\tilde{w}'_*}{c^A} \\ &= c^{\Lambda+r-2-A} \phi(\tilde{w}) \end{aligned}$$

where we changed our integration variables to $\tilde{w}' = cw'$ and $\tilde{w}'_* = c^A w'_*$ and used the fact $s(w', w) = s(cw', cw) = s(\tilde{w}', \tilde{w})$.

2.5 Encountered Energy

The encountered energy $E_e(w)$ transforms under F_c as

$$E_e(w) \mapsto c^{\Lambda+r-2-A} \phi(\tilde{w}) \gamma w^q = c^{\Lambda+r-2-A-q} E_e(\tilde{w}) = c^{\hat{e}} E_e(\tilde{w}), \quad (34)$$

where we define $\hat{e} = \Lambda + r - 2 - A - q$.

2.6 Feeding level

The feeding level $f(w)$ transforms under F_c as

$$f(w) \mapsto \frac{c^{\hat{e}} E_e(\tilde{w})}{c^{\hat{e}} E_e(\tilde{w}) + c^{-n} h \tilde{w}^n}, \quad (35)$$

and by looking at where $f(w)$ appears in our different terms, we come to the conclusion that our scale free assumption implies that we must have $f(w) \mapsto c^Z f(\tilde{w})$ for some Z . However, by looking at the transformed expression (35), we see that this can only be so if all our multipliers cancel out. In other words, we must have $\hat{e} = -n$, and this implies that we simply have that $f(w) \mapsto f(\tilde{w})$.

2.7 Energy For Growth And Reproduction

The energy for growth and reproduction $E_g(w)$ transforms under F_c as

$$E_g(w) \mapsto \alpha f(\tilde{w}) h \frac{\tilde{w}^n}{c^n} - k \frac{\tilde{w}^p}{c^p} \quad (36)$$

and so our scale invariance assumption implies that we must have $n = p$ and

$$E_g(w) \mapsto c^{-n} E_g(\tilde{w}) \quad (37)$$

2.8 Growth Rate

The growth rate $g(w, w_*)$ is zero when $E_g(w) \leq 0$ and otherwise, the growth rate has the form $g(w, w_*) = (1 - \psi(w, w_*)) E_g(w)$. In order for this to satisfy our scale invariance assumption, the reproduction function $\psi(w, w_*)$ must transform under F_c so that

$$\psi(w, w_*) \mapsto \psi(\tilde{w}, \tilde{w}_*) \quad (38)$$

and it follows that our growth rate transforms so (in general, irrespective of the sign of $E_g(w)$), we have that the growth rate transforms under F_c so that

$$g(w, w_*) \mapsto c^{-n} g(\tilde{w}, \tilde{w}_*). \quad (39)$$

We can now see that the term of our central equation (21) involving a weight derivative transforms under F_c as

$$\frac{\partial[g(w, w_*)N(w, w_*, t)]}{\partial w} \mapsto c^{\Lambda-n} \frac{\partial[g(\tilde{w}, \tilde{w}_*)N(\tilde{w}, \tilde{w}_*, t)]}{\partial w} = c^{\Lambda-n+1} \frac{\partial[g(\tilde{w}, \tilde{w}_*)N(\tilde{w}, \tilde{w}_*, t)]}{\partial \tilde{w}} \quad (40)$$

We want the new factor $c^{\Lambda-n+1}$ that is introduced here to cancel with the factor $c^{\Lambda+B}$ that was introduced when we transformed the time derivative (22). This leads to our next exponent balancing equation

$$\Lambda + B = \Lambda - n + 1 \quad (41)$$

hence we require $n = 1 - B$.

2.9 Starvation Mortality Rate

The per capita starvation mortality rate

$$\mu_s(w) = \begin{cases} 0 & \text{if } E_g(w) > 0 \\ -\frac{E_g(w)}{\xi w^d} & \text{otherwise} \end{cases} \quad (42)$$

this transforms under F_c as

$$\mu_s(w) \mapsto \begin{cases} 0 & \text{if } E_g(\tilde{w}) > 0 \\ -\frac{c^{-n} E_g(\tilde{w})}{\xi} \frac{c^d}{w^d} & \text{otherwise} \end{cases} \quad (43)$$

and so we have

$$\mu_s(w) \mapsto c^{d-n} \mu_s(\tilde{w}) \quad (44)$$

So the total starvation rate appearing as a term in (21)

$$\mu_s(w) (w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1} = \mu_s(w) N(w, w_*, t) \hat{N}(w, w'_*, t)^\chi$$

transforms under F_c as

$$(45)$$

$$\begin{aligned} \mu_s(w) N(w, w_*, t) \hat{N}(w, w'_*, t)^\chi &\mapsto c^{d-n} \mu_s(\tilde{w}) c^{\Lambda+r} N(\tilde{w}, \tilde{w}_*, \tilde{t}) \hat{N}(\tilde{w}, \tilde{w}_*, \tilde{t})^\chi \\ &= c^{\Lambda+r+d-n} \mu_s(\tilde{w}) (\tilde{w}^\Omega \tilde{w}_*^\Gamma \Delta)^\chi N(\tilde{w}, \tilde{w}_*, \tilde{t})^{\chi+1} \end{aligned}$$

and so, since the same factor must be introduced here as in our considerations of the time derivative (Equation (22)), so we get our next exponent balancing equation:

$$\Lambda + B = \Lambda + r + d - n \quad (46)$$

It is interesting to compare this to our previous observation that $c^{\Lambda+B} = c^{\Lambda+r-AQ}$, since this means

$$\Lambda + r + d - n = \Lambda + r - AQ \quad (47)$$

and hence $n - d = AQ$.

If one chooses exponents $d = A = 1$, as they do in [Harvig], you get $Q = n - 1$, which is the value they use in [Harvig].

2.10 Predation Mortality

The per capita predation mortality rate

$$\mu_p(w) = \int_0^\infty \int_0^\infty (1 - f(w')) N(w', w'_*, t) s(w, w') \gamma w'^q dw' dw'_* \quad (48)$$

transforms under F_c as

$$\begin{aligned} \mu_p(w) &\mapsto \int_0^\infty \int_0^\infty (1 - f(\tilde{w}')) c^\Lambda N(\tilde{w}', \tilde{w}'_*, t) s(\tilde{w}, \tilde{w}') \gamma \frac{\tilde{w}'^q}{c^q} \frac{d\tilde{w}'}{c} \frac{d\tilde{w}'_*}{c^A} \\ &= c^{\Lambda-q-1-A} \mu_p(\tilde{w}) \end{aligned}$$

So the total predation rate appearing as a term in (21) transforms under F_c as

$$\begin{aligned} \mu_p(w) (w^\Omega w_*^\Gamma \Delta)^\chi N(w, w_*, t)^{\chi+1} &\mapsto c^{\Lambda+r} N(\tilde{w}, \tilde{w}_*, \tilde{t}) \hat{N}(\tilde{w}, \tilde{w}_*, \tilde{t})^\chi = c^{\Lambda-q-1-A} \mu_p(\tilde{w}) c^{\Lambda+r} (\tilde{w}^\Omega \tilde{w}_*^\Gamma \Delta)^\chi N(\tilde{w}, \tilde{w}_*, \tilde{t})^{\chi+1} \\ &= c^{2\Lambda+r-q-1-A} \mu_p(\tilde{w}) (\tilde{w}^\Omega \tilde{w}_*^\Gamma \Delta)^\chi N(\tilde{w}, \tilde{w}_*, \tilde{t})^{\chi+1} \end{aligned}$$

and the factor balancing we require in order for the scale invariance assumption to hold we need the following exponent balancing Equation to hold

$$\Lambda + B = 2\Lambda + r - q - 1 - A \quad (49)$$

and hence if we choose

$$q = \Lambda + r - 1 - A - B \quad (50)$$

Rearranging Equation (32) into terms of B gives

$$B = r - AQ \quad (51)$$

2.11 Exponent Balancing

Gathering together the different exponent balancing equations which have to hold to get our scale invariance assumption gives us

$$\Lambda + B = \Lambda - n + 1 = \Lambda + r - AQ = \Lambda + r + d - n = 2\Lambda + r - q - 1 - A \quad (52)$$

where the equated quantities correspond to the exponents of c which the respective terms of (21) get multiplied by when we apply the F_c transform. These equations hold if and only if

$$(53)$$

$$\begin{aligned} n &= 1 - B \\ d &= 1 - r \\ Q &= \frac{n - d}{A} = \frac{r - B}{A} \\ q &= \Lambda + r - 1 - A - B \end{aligned}$$

Clearly then for any choice of A, B, Λ , and whatever value r takes (according to its definition $r = \chi\Lambda - \chi\Omega - \chi\Gamma$), we can select exponents n, d, Q, q that lead to a satisfaction of the scale free assumption (at least, with respect to Equation (21), and we will show the boundary condition is also satisfied).

Since $B = 1 - n$, if we introduce a new constant defined as $\Lambda - 1 = \mathring{\lambda}$ then the final Equation of (53) can be rewritten as

$$q = \mathring{\lambda} + r - A - (1 - n) \Leftrightarrow \mathring{\lambda} = 1 + A + q - n - r \quad (54)$$

and when $A = 1$ and $r = 0$, as is done in [Hartvig], this gives us the familiar expression $\mathring{\lambda} = 2 + q - n$.

2.12 PDE obeys symmetry

So we have applied our F_c transformation to each term of (21), and shown that for appropriately chosen exponents, the result of performing the F_c transform is that the newly introduced $c^?$ factors cancel, and this results in a new partial differential equation, in terms of \tilde{w} , \tilde{w}_* and \tilde{t} , which has precisely the same form as (21), except with new variable names. It follows that the transformed solution also satisfies equation (21), and hence we only have to show that the boundary condition is still satisfied after the symmetry transform, and we will have finished demonstrating that the scale invariance assumption holds.

2.13 Boundary Condition

We shall suppose that individuals of weight w_* lay eggs of weight

$$w_e(w_*) = Gw_*^{\frac{1}{A}}. \quad (55)$$

Note that this function has the property that

$$cw_e(w_*) = w_e(\tilde{w}_*) \quad (56)$$

Under The left hand side of the boundary condition (3) transforms under F_c so that

$$\begin{aligned} g(w_e(w_*), w_*)N(w_e(w_*), w_*, t) &\mapsto c^{\Lambda-n}g(cw_e(w_*), \tilde{w}_*)N(w_e(\tilde{w}_*), \tilde{w}_*, \tilde{t}) \\ &= c^{\Lambda-n}g(w_e(\tilde{w}_*), \tilde{w}_*)N(w_e(\tilde{w}_*), \tilde{w}_*, \tilde{t}) \end{aligned}$$

and the right hand side transforms so that

$$\begin{aligned} \frac{\epsilon}{2w_e(w_*)} \int_0^\infty N(w, w_*, t) E_g(w) \psi(w, w_*) . dw &\mapsto \frac{\epsilon c}{2w_e(\tilde{w}_*)} \int_0^\infty c^\Lambda N(\tilde{w}, \tilde{w}_*, \tilde{t}) c^{-n} E_g(\tilde{w}) \psi(\tilde{w}, \tilde{w}_*) . \frac{d\tilde{w}}{c} \\ &= c^{\Lambda-n} \frac{\epsilon}{2w_e(\tilde{w}_*)} \int_0^\infty N(\tilde{w}, \tilde{w}_*, \tilde{t}) E_g(\tilde{w}) \psi(\tilde{w}, \tilde{w}_*) . d\tilde{w} \end{aligned}$$

and hence our factors balance, and the boundary condition is satisfied, so we have shown that our system satisfies the scale invariance assumption.

3 A Steady State Solution

Let $\hat{\mu}(w, w_*) = (\mu_b(w_*) + \mu_s(w) + \mu_p(w)) (w^\Omega w_*^\Gamma \Delta)^\chi$. We shall rewrite Equation (21) as

$$\frac{\partial N(w, w_*, t)}{\partial t} = -\frac{\partial [N(w, w_*, t)g(w, w_*)]}{\partial w} - \hat{\mu}(w, w_*)N(w, w_*, t)^{\chi+1} \quad (57)$$

We shall assume that the system is at steady state, so that

$$\frac{\partial [N(w, w_*)g(w, w_*)]}{\partial w} = -\hat{\mu}(w, w_*)N(w, w_*)^{\chi+1}. \quad (58)$$

where we neglect to write the t 's because N is time invariant in this case. To solve ODE (58), we rewrite it in terms of

$$X(w, w_*) = N(w, w_*)g(w, w_*) \quad (59)$$

to get

$$-\frac{1}{\chi} \frac{\partial [X(w, w_*)^{-\chi}]}{\partial w} = \frac{\partial X(w, w_*)}{\partial w} X(w, w_*)^{-\chi-1} = -\frac{\hat{\mu}(w, w_*)}{g(w, w_*)^{\chi+1}}. \quad (60)$$

Hence

$$\frac{\partial [X(w, w_*)^{-\chi}]}{\partial w} = \frac{\chi \hat{\mu}(w, w_*)}{g(w, w_*)^{\chi+1}}, \quad (61)$$

and so there exists $w_0 \in \mathbb{R}$ such that

$$\frac{X(w, w_*)}{g(w, w_*)} = N(w, w_*) = \frac{1}{g(w, w_*)} \left(\chi \int_{w_0}^w \frac{\hat{\mu}(w', w_*)}{g(w', w_*)^{\chi+1}} dw' \right)^{-1/\chi} \quad (62)$$

Another way to express this solution is to say that there exists a constant $D(w_*)$ such that

$$N(w, w_*) = \frac{1}{g(w, w_*)} \left(\chi \left(D(w_*) + \int_{w_e(w_*)}^w \frac{\hat{\mu}(w', w_*)}{g(w', w_*)^{\chi+1}} dw' \right) \right)^{-1/\chi} \quad (63)$$

3.1 A Scale Free Steady State

In order to be able to evaluate the terms within the steady state solution (62), we shall assume that our abundance function N is unaltered by the symmetry transform F_c for any $c > 0$. It follows that

$$N(w, w_*, t) = c^\Lambda N(cw, c^A w_*, c^B t), \quad (64)$$

since we are at steady state, there is no time dependence, so we can write

$$N(cw, c^A w_*) = c^{-\Lambda} N(w, w_*), \quad (65)$$

and choosing $w_* = 1, c^A = v_*$ we get

$$N(wv_*^{\frac{1}{A}}, v_*) = c^{-\Lambda} N(w, 1), \quad (66)$$

and so if we can solve (58) for $N(w, w_*, t)$ for a particular maturity weight w_* we can use (66) to give us the form of the abundance function on different maturity weights.

The assumption that our solution is unaltered by any symmetry transform F_c constraints the forms of $g(w, w_*)$ and $\hat{\mu}(w, w_*)$ so that we can write down an expression for the solution to (58).

3.2 The prey community spectrum

The prey community spectrum, modified by prey switching, as encountered by a predator is

$$N_{prey}(w) = \int_0^\infty N(w, w'_*, t) \hat{N}(w, w'_*, t)^\chi dw'_* = \int_0^\infty \left(w^\Omega (w'_*)^\Gamma \Delta \right)^\chi N(w, w'_*, t)^{\chi+1} dw'_*, \quad (67)$$

Since we are assuming that N is invariant under F_c , we must have that $N_{prey}(w)$ is invariant under F_c and so $N_{prey} \mapsto J$ where

$$\begin{aligned} N_{prey}(w) &= J(w) = \int_0^\infty \left(w^\Omega (w'_*)^\Gamma \Delta \right)^\chi c^{\Lambda(\chi+1)} N(cw, c^A w'_*, c^B t)^{\chi+1} dw'_* \\ &= \int_0^\infty \left(\left(\frac{\tilde{w}}{c} \right)^\Omega \left(\frac{\tilde{w}'_*}{c^A} \right)^\Gamma \Delta \right)^\chi c^{\chi\Lambda+\Lambda} N(\tilde{w}, \tilde{w}'_*, \tilde{t})^{\chi+1} \frac{d\tilde{w}'_*}{c^A} \\ &= c^{r+\Lambda-A} N_{prey}(cw) \end{aligned}$$

where $r = \chi\Lambda - \chi\Omega - \chi\Gamma$, $\tilde{w} = cw, \tilde{w}'_* = c^A w'_*$ and $\tilde{t} = c^B t$.

Letting $w = 1$ and $c = v$ in the expression $N_{prey}(cw) = c^{A-r-\Lambda} N_{prey}(w)$ gives us $N_{prey}(v) = v^{A-r-\Lambda} N_{prey}(1)$ so we have

$$N_{prey}(w) = w^{A-r-\Lambda} N_{prey}(1) = \kappa_R^* w^{-\lambda_*} \quad (68)$$

where we define $\lambda_* = \Lambda + r - A$ to be the exponent of the χ modified community spectrum, and $\kappa_R^* = N_{prey}(1)$ is the associated prefactor.

Now note that since $q = \Lambda + r - 1 - A - B$, we have $q + 1 + A + B = \Lambda + r$ and so

$$\begin{aligned} \lambda_* &= q + 1 + B \\ &= q + 2 - n \end{aligned}$$

which is the same as the value it gets in [Hartvig].

3.3 The unaltered community spectrum

The community spectrum in the absence of prey switching, is the spectrum of the community of predators in the predation mortality equations. This is

$$N_{pred}(w) = w^{A-\Lambda} N_{pred}(1) = \kappa_R w^{-\lambda} \quad (69)$$

where we define $\lambda = \Lambda - A$ to be the exponent of the unmodified community spectrum, and $\kappa_R = N_{pred}(1)$ is the associated prefactor. Hence

$$\begin{aligned} \lambda_* &= \lambda + r \\ &= \lambda + \chi\Lambda - \chi\Omega - \chi\Gamma \\ &= \lambda + \chi(\lambda + A) - \chi\Omega - \chi\Gamma \\ &= (\chi + 1)(\lambda + A) - A - \chi\Omega - \chi\Gamma \end{aligned}$$

3.4 Growth Rate At Steady State

When we are at a F_c invariant steady state, we have

$$E_g(w) \mapsto c^{-n} E_g(cw) = E_g(w)$$

and so we get $E_g(w) = E_g(1)w^n = \alpha f(w)hw^n - kw^n = \hbar w^n$ and $g(w, w_*) = \hbar w^n(1 - \psi(w, w_*))$, where $\alpha f\hbar - k$ and \bar{f} is the feeding level (which must be constant at such an F_c invariant state).

3.5 Predation Mortality Rate

At our F_c invariant steady state the predation mortality rate is such that

$$\begin{aligned} \mu_p(w) &= \int_0^\infty \int_0^\infty (1 - f(w')) N(w', w'_*, t) s(w, w') \gamma w'^q dw' dw'_* \\ &= c^{\Lambda - q - 1 - A} \mu_p(cw) \end{aligned}$$

Letting $c = \frac{1}{w}$ gives

$$\mu_p(w) = w^{1+q+A-\Lambda} \mu_p(1)$$

The prefactor was determined Equations (A.2) and (A.3) of [Hartvig] for there case, where prey switching was absent. Also see Appendix B of [Andersen]. We can modify approach.

3.6 Case Without Starvation Or Background Mortality

We shall suppose that $\mu_0 = 0$ and that there is no starvation mortality so $\mu_s(w) = 0, \forall w$. In this case we have $\hat{\mu}(w', w_*) = \alpha_p w^{n-1}$ and $g(w, w_*) = \hbar w^n (1 - \psi(w, w_*))$, and so the expression for our solution is

$$N(w, w_*) = \frac{1}{g(w, w_*)} \left(\chi \left(D(w_*) + \int_{w_e(w_*)}^w \frac{\alpha_p w^{n-1}}{(\hbar w^n (1 - \psi(w, w_*)))^{\chi+1}} dw' \right) \right)^{-1/\chi} \quad (70)$$

where we wish to choose $D(w_*)$ so that the boundary condition

$$g(w_e(w_*), w_*) N(w_e(w_*), w_*) = \frac{\epsilon}{2w_e(w_*)} \int_0^\infty N(w, w_*) \hbar w^n \psi(w, w_*) dw, \quad (71)$$

is satisfied.

3.7 Solution in a specific case

We shall here consider a specific case, with realistic parameter settings, within which we can numerically determine $D(w_*)$ such that the expression in (70) satisfies (71). For this case we shall assume $A = 1$ and $k = 0$ (so there is no metabolic cost or starvation) and use a reproduction function of the form

$$\psi(w, w_*) = \left[1 + \left(\frac{w}{w_*} \right)^{-u} \right]^{-1} \left(\frac{w_*}{w} \right)^{n-1} \eta^{1-n}$$

as they do in [Hartvig], where u determines the width of the step function which the square bracketed factor acts like. We shall assume $u \gg 1$ so ψ raises initially like an abrupt step. We also use additional parameter values as follows:

$$\begin{aligned}
\bar{f} &= 0.4 \\
A &= 1 \\
\alpha &= 0.6 \\
h &= 30 \\
q &= 0.9 \\
k &= 0 \\
\mu_0 &= 0 \\
\chi &= 0.05 \\
\Delta &= 1 \\
\Omega = \Gamma &= 0 \\
\kappa_R &= 0.005 \\
\gamma &= 600.4424 \\
\beta &= 100 \\
\sigma &= 1.3 \\
w_* &= 149.871063 \\
w_e &= 0.001 \\
\epsilon &= 0.1
\end{aligned}$$

where we use formulas

$$\hbar = \alpha h \bar{f} - k$$

$$\lambda_* = q + 2 - n$$

$$\lambda + \chi(\lambda + A) - \chi\Omega - \chi\Gamma$$

$$\lambda + \chi(\lambda + A) - \chi\Omega - \chi\Gamma$$

$$\lambda_* = \lambda(1 + \chi) + A\chi - \chi\Omega - \chi\Gamma$$

$$\lambda = \frac{\lambda_* - A\chi + \Omega\chi + \Gamma\chi}{(1 + \chi)}$$

Also note

$$B = 1 - n$$

$$r = \chi\Lambda - \chi\Omega - \chi\Gamma$$

$$n = p$$

Q and d are irrelevant

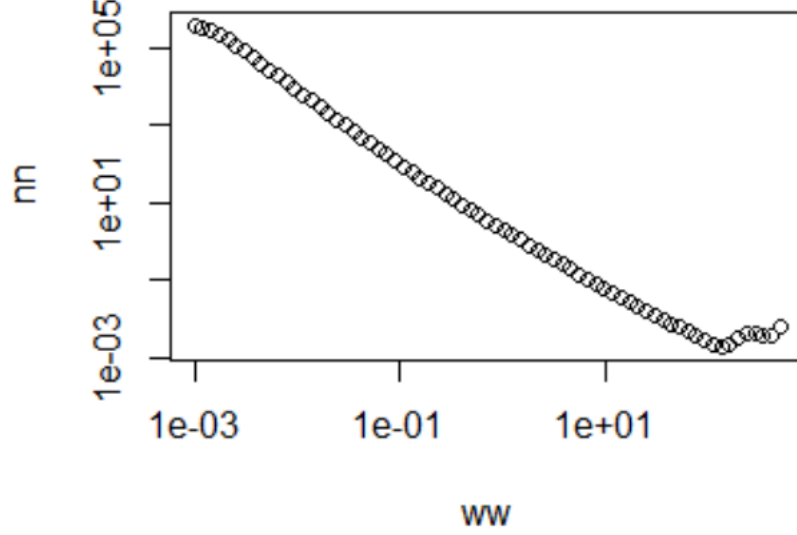
also note

$$\Lambda = \lambda_* + A - r.$$

In this case numerical simulations at

https://github.com/gustavdelius/mizer/blob/aggregate/R/Experimental%20Code/solution_testing.R

show that the boundary condition is satisfied for integration constant $D = 11.73$, and this leads to the resulting plot of w vs $N(w, w_*)$.



3.8 Evaluation strategy

In order to use the above procedure, we must select κ and κ^* , (inputs) which will lead to a particular value of f (which we should have computed, rather than assumed, via numeric evaluation of E_g using the community power law). Having done this we can determine our growth and mortality rates, and then perform the integrals, and solve for the boundary condition to get a particular value of $N(w, w_*^\#)$, for some particular maturity weight $w_*^\#$. Say we know function for $w_*^\# = 1$. In this case we use the relation

$$N(w, w_*) = (w_*)^{-\Lambda/A} N\left(\frac{w}{w_*^{1/A}}, 1\right) \quad (72)$$

to evaluate

$$N_{pred}(w) = \int_0^\infty N(w, w_*) \cdot dw_* = \kappa w^{-\lambda} \quad (73)$$

and to determine κ output. Similarly we should evaluate

$$N_{prey}(w) = \int_0^\infty N(w, w'_*) \hat{N}(w, w'_*, t)^\chi dw'_* = \kappa_* w^{-\lambda_*} \quad (74)$$

to determine κ_* output.

We wish to find a case where $\kappa_{input} = \kappa_{output}$ and $\kappa_{*input} = \kappa_{*output}$.

3.9 Practical Procedure

Choose κ_* , and κ .

(\&)

Choose n and q . Let $\lambda_* = q + 2 - n$. Choose β, σ so that $s(\cdot)$ is defined.
evaluate

$$\phi(w) = \int_0^\infty \int_0^\infty w' N(w', w'_*, t) \hat{N}(w', w'_*, t)^\chi s(w', w) dw' dw'_* = \int_0^\infty w' s(w', w) N_{prey}(w') dw' \quad (75)$$

where

$$N_{prey}(w) = \int_0^\infty N(w, w'_*, t) \hat{N}(w, w'_*, t)^\chi dw'_* = \kappa_* w^{-\lambda_*} \quad (76)$$

Choose γ, h , evaluate

$$f(w) = \frac{\gamma w^q \phi(w)}{\gamma w^q \phi(w) + h w^n} = \bar{f} \quad (77)$$

Choose α, ψ define

$$g(w, w_*) = \alpha \bar{f} h w^n (1 - \psi(w, w_*)) \quad (78)$$

Use

$$\begin{aligned} \mu_p(w) &= \mu_p(w) = w^{1+q+A-\Lambda} \mu_p(1) \\ &= \int_0^\infty (1 - f(w')) N_{pred}(w') s(w, w') \gamma w'^q dw' \end{aligned}$$

to evaluate predation mortality, and note that

In our case $\Omega = \Gamma = 0$ so

$\Lambda + r = \Lambda(1 + \chi) = \lambda_* + A$ so

$$\Lambda = \frac{\lambda_* + A}{1 + \chi}.$$

[[This agrees with simu, but we need to extend support of community spectrum]].

Pick $w_e(w_*^\#)$ to be typical egg size,

For $w_*^\#$, evaluate

$$N(w, w_*^\#) = \frac{1}{g(w, w_*^\#)} \left(\chi \left(D(w_*) + \int_{w_e(w_*^\#)}^w \frac{\hat{\mu}(w', w_*^\#)}{g(w', w_*^\#)^{\chi+1}} dw' \right) \right)^{-1/\chi} \quad (79)$$

Determine $D(w_*)$ so that boundary condition

$$g(w_e(w_*^\#), w_*^\#) N(w_e(w_*^\#), w_*, t) = \frac{\epsilon}{2w_e(w_*^\#)} \int_0^\infty N(w, w_*^\#, t) E_g(w) \psi(w, w_*^\#) dw, \quad (80)$$

Use N to evaluate

$$N_{pred}(w) = \int_0^\infty N(w, w_*) . dw_* = \kappa' w^{-\lambda} \quad (81)$$

using

$$N(w, w_*) = \left(\frac{w_*^\#}{w_*} \right)^{\frac{\Lambda}{A}} N \left(w \left(\frac{w_*^\#}{w_*} \right)^{\frac{1}{A}}, w_*^\# \right) \quad (82)$$

and determine output κ' . Similarly, evaluate

$$N_{prey}(w) = \int_0^\infty N(w, w'_*, t) \hat{N}(w, w'_*, t)^\chi dw'_* = \kappa'_* w^{-\lambda_*} \quad (83)$$

In our case with $\Omega = \Gamma = 0$ and $\Delta = A = 1$ we have

$$N_{prey}(w) = \int_0^\infty N(w, w'_*, t)^{\chi+1} dw'_* \quad (84)$$

$$\begin{aligned} N_{prey}(w) &= \int_0^\infty N(w, w'_*, t)^{\chi+1} dw'_* \\ &= \int_0^\infty \left(\frac{w_*^\#}{w_*} \right)^{\Lambda(\chi+1)} N \left(w \left(\frac{w_*^\#}{w_*} \right), w_*^\# \right)^{\chi+1} dw'_* \\ &= w w_*^\# \int_0^\infty \left(\frac{w_*^\#}{y} \right)^{\Lambda(\chi+1)} N(y, w_*^\#)^{\chi+1} y^{-2} dy \end{aligned}$$

where we use

$$y = w \left(\frac{w_*^\#}{w_*} \right)$$

$$\frac{dy}{dw_*} = -w w_*^\# w_*^{-2} = -\frac{y^2}{w w_*^\#}$$

Use these results to determine κ'_* .

Go to (&) and iterate round until the same kappa values are outputted as were inputted.

References

[Harvig]=Martin Hartvig, K. H. Andersen, and Jan E. Beyer. Food web framework for size-structured populations RID c-4303-2011. Journal of Theoretical Biology, 272(1):113{122, March 2011. ISSN 0022-5193. doi: 10.1016/j.jtbi.2010.12.006. WOS

<https://arxiv.org/pdf/1004.4138.pdf>

[Andersen]=K. H. Andersen and J. E. Beyer, “Asymptotic Size Determines Species Abundance in the Marine Size Spectrum” (Am. Nat., vol. 168, no. 1, p. 54)

3.10 To Do

Go through exponent constraints from scale invariance

Go through how F_c invariant terms are described, and what this implies for power law

Go back and argue about egg size properly

Add in different terms for reproduction term,

Evaluate ODE in most general case possible

Show Harvig +r is a special case, and go through numerical solution in this case

Use special case to get stock recruitment etc.

what about the scale free time variant solutions, do they decay to the steady state scale free solution

what about if one proposes a background traveling wave rather than a background power law

are there any non-steady states for which a non-trivial time transformation on N has the same effect as performing a symmetry transform on N ,

Lit review

Put multiple eggs in, and code in mizer.