Weight, length, or age models

 sketch

The Von Foerster-McKendrik form describes the population by a number density $n(w, \mathbf{x}, t)$ giving the number (or probable number) of organisms per unit weight class and per unit volume of water. It satisfies an advection-like equation

$$\frac{\partial}{\partial t}n(w,t) + \frac{\partial}{\partial w} \Big[g(w)n(w,t)\Big] = -d_z(w)n(w,t) + \int dw' E(w|w')n(w',t) \tag{1}$$

where g represents the rate of weight gain (dw/dt), d_z the mortality, and E the rate at which new organisms at size w are created by adults at size w' reproducing.

We can simplify E by assuming:

• the newborn size does not depend on the adult size or conditions

$$E(w|w') = e_0(w)e_1(w',t)$$

• the birth rate is a function of the number of adults

$$N_A \equiv \int dw \alpha(w) n(w) \quad , \quad e_1(w) = R(N_A, t) \alpha(w) \quad \Rightarrow \quad \int dw' En = e_0(w) N_A R(N_A, t)$$

and we can normalize e_0 by

$$\int dw \ e_0(w) = 1 \quad , \quad \int dw \ w e_0(w) = w_0$$

• the weight range for newborn organisms is small – effectively a delta function

$$e_0(w) = \delta(w - w_0)$$

The last of these allows us to replace the source term in xx with a boundary condition, giving

$$\frac{\partial}{\partial t}n + \frac{\partial}{\partial w}gn = -d_z n \quad , \quad g(w_0)n(w_0, t) = N_A R(N_A) \tag{2}$$

Maps

The simplest form which makes the possibility of oscillatory/ chaotic behavior clear assumes that all reproduction occurs at a specific adult size: $\alpha(w) = \frac{g}{d_z}\delta(w-w_A)$, with the factor making α dimensionless and ensuring that $\int dw \, \alpha n$ results in a number of individuals. The reproducing population is $N_A = \frac{g}{d_z}n(w_A, t)$; all adults reproduce at a single weight. With this form, the flux of newborn animals is given by

$$gn(w_0, t) = N_A(t)R(N_A(t))$$

Finally, we can solve the equation between w_0 and w_A easily if g and d_z are constant

$$n(w_A, t) = n\left(w_0, t - \frac{w_A - w_0}{g}\right) \exp\left(-d_z \frac{w_A - w_0}{g}\right) = n(w_0, t - T) \exp(-d_z T)$$

with $T = (w_A - w_0)/g$ being the generation time. Therefore

$$N_{A}(t) = \frac{1}{d_{z}} \exp(-d_{z}T) N_{A}(t-T) R(N_{A}(t-T))$$

Thus we can algebraically map the number of adults at one generation into the number at the next. If the growth rate and death rates are not constant, the coefficient of $N_A R(N_A)$ changes, but the form remains the same.

As an example, let us assume the rate of producing offspring per adult depends on the food per adult $f = P/N_A$ in the form of a sigmoid curve

$$R = \frac{r}{T} \frac{(f/f_0)^{\beta}}{1 + (f/f_0)^{\beta}} = \frac{r}{T} \frac{1}{1 + (N/N_0)^{\beta}}$$

with $N_0 = P/f_0$ being the half-saturation value(figure .xx). Then $X_n = N(nT)/N_0$ satisfies

$$X_{n+1} = \gamma \frac{X_n}{1 + X_n^\beta} \quad , \qquad \gamma = \frac{r}{d_z T} \exp(-d_z T) \tag{3}$$

For this iterated map, we can show easily that

- The X = 0 steady state is unstable for $\gamma > 1$.
- The state $X = (\gamma 1)^{1/\beta}$ to which the system bifurcates becomes unstable for $\gamma > \beta/(\beta 2)$ to a period 2T oscillation.
- Further bifurcations to period 4T, 8T, 16T, etc. occur at shorter and shorter increments in γ , leading to a non-repeating sequence for a finite value of γ . This is the "period-doubling" route to chaos.

This map demonstrates the potential for chaotic, unpredictable population fluctuations. N0=1.5 N0=2.0 N0=2.5 bifurcations

Finite Range of Reproducing Adults

The iterated map version has a number of oddities: the cycles from each starting time in the range [0, T) are independent of each other. Allowing reproduction over a range of sizes will couple neighboring times together, leading to smooth behavior; therefore, we might worry that the chaotic behavior disappears. To examine this issue, consider another case where all animals with weights greater than or equal to w_A are reproducing. Then $\alpha(w) = \mathcal{H}(w - w_A)$. We can find an equation for the number of adults

$$N_A = \int_{w_A}^{\infty} dw n(w)$$

by integrating over the same limits

$$\frac{\partial}{\partial t}N_A = -d_z N_A + g(w_A)n(w_A)$$

Using the solution for n gives a delay-differential equation

$$\frac{\partial}{\partial t}N_A(t) = -d_z N_A(t) + e^{-d_z T} N_A(t-T) R(N_A(t-T))$$

with $T = (w_A - w_0)/g$ again being the generation time. Because of the delay term, this equation is not just a first order equation, and it can exhibit complex behavior.

We use the same form for R, define $X = N_A/N_0$, and nondimensionalize time by T to find

$$\frac{\partial}{\partial t}X(t) = -dX(t) + d\gamma \frac{X(t-1)}{1 + X(t-1)^{\beta}} \quad , \quad d = d_z T \tag{4}$$

2.5-2.9 4-5 7-8

Coupling to food source

To link this kind of model to lower trophic levels, we need to consider the implied biomass changes. Although the numbers in any weight class other than w_0 can only decrease, the movement of numbers from one class to a larger class imply an increase in biomass which must have derived from the animals' food source. For a single organism, the rate of change of biomass is just

$$\frac{d}{dt}w = g$$

(in the Lagrangian sense), and the net biomass changes by

$$\frac{d}{dt}b = n\frac{d}{dt}g = ns = \frac{g}{w}b$$

(not counting biomass loss by death, which do not affect the food source). This, then, represents the rate of biomass assimilation by ZP at size w. To derive this from the number equation, we examine changes in the the net biomass

$$\frac{\partial}{\partial t} \int wn = w_0 N_A R - \int w \frac{\partial}{\partial w} gn - \int d_z wn$$
$$= w_0 N_A R + \int gn - \int d_z wn$$

The first two terms represent biomass increases; we must relate these to depletion of the resources. Of course, ZP of different weights may draw from different PP groups, in which case the terms can be suitably partitioned.

As written, the reproduction draws directly on the prey for its biomass. We would then think of both R and g as being functions of P, functions which vanish as $P \to 0$. Therefore, we have a PP equation of the form

$$\frac{\partial}{\partial t}P = uptake - \frac{1}{a}\int g(P, w)n - \frac{1}{a}w_0R(P, N_A)N_A - death$$

As an alternative, suppose that the biomass of offspring is drawn from the adult biomass directly at a rate which could be independent of the food supply. Then the $w_0 N_A R$ term must be offset by one of the other two integrals – either the death rate must increase or the growth rate decrease to compensate. We can represent these possibilities as

$$d_z \to d_z + \frac{w_0}{w} R \alpha$$

(so that the integral of the last term times wn cancels $w_0 N_A R$) or

$$g \to g(P, w) - w_0 R \alpha$$

(with the integral times n providing the reproductive biomass). In those cases, the PP equation will be

$$\frac{\partial}{\partial t}P = uptake - \frac{1}{a}\int g(P, w)n - death$$

EXAMPLE:

Let us consider the equivalent of the NPZ model using a structured zooplankton population. We assume that the growth rate is $g = G(P)g_w(w)$, the assimilation efficiency is constant, and the birth rate is $R = R_e(P)$ ($R_i = 0$), so that reproduction biomass derives from food intake. The equations become

$$\frac{\partial}{\partial t}P = \mu P \left(N_T - P - \int dw \, wn\right)$$
$$-\frac{1}{a}G(P) \int dw \, g_w n - \frac{1}{a}w_0 R(P) \int \alpha n - d_p P$$
$$\frac{\partial}{\partial t}n = -G(P) \frac{\partial}{\partial w}g_w n - d_z n$$
$$G(P)g_w(w_0)n(w_0) = R(P) \int \alpha n$$
(5b)

For future use, we note that the ZP biomass $Z = \int wn$ satisfies

$$\frac{\partial}{\partial t}Z = G(P)\int g_w n + w_0 R(P)\int \alpha n - \int d_z w n$$

SIMPLIFICATION:

Numerical solutions show that the shape of n remains constant even when the amplitude is fluctuating. This result suggests the continuous model can have a solution

$$n(w,t) = Z(t)\frac{\overline{n}(w)}{\int w\overline{n}}$$

where the normalization ensures that Z is the biomass. If we substitute this into the equation 12b, we find

$$\overline{n}\frac{\partial}{\partial t}Z = Z\left[-G(P)\frac{\partial}{\partial w}g_w\overline{n} - d_z\overline{n}\right]$$
$$= Z\left[\frac{G(P)}{G(\overline{P})}d_z\overline{n} - d_z\overline{n}\right]$$

and

$$ZG(P)g_w(w_0)\overline{n}(w_0) = ZR(P)\int \alpha \overline{n} = Z\frac{R(P)G(\overline{P})}{R(\overline{P})}g_w(w_0)\overline{n}(w_0)$$

which holds since $R(P)/R(\overline{P}) = G(P)/G(\overline{P})$. Therefore, the ZP dynamics becomes

$$\frac{\partial}{\partial t}Z = Z\left[\gamma G(P) - d_z\right]$$

The PP equation

$$\frac{\partial}{\partial t}P = P(N_T - P - Z) - \frac{1}{a}G(P)Z\frac{\int g_w\overline{n}}{\int w\overline{n}} - \frac{w_0}{a}R(P)Z\frac{\int \alpha\overline{n}}{\int w\overline{n}} - d_pP$$

can be transformed using the integral of w times the equation for \overline{n} to

$$\frac{\partial}{\partial t}P = P(N_T - P - Z) - \frac{1}{a}d_z \frac{G(P)}{G(\overline{P})}Z - d_pP$$
$$= P(N_T - P - Z) - \frac{1}{a}\gamma G(P)Z - d_pP$$

so that the two equations for Z and P are precisely the ODE forms with $\gamma = d_z/G(\overline{P})$.

SECOND EXAMPLE:

Most problems cannot be simplified in the manner above, and the dynamics including a structured ZP population will generally be richer than the standard ODE models. To illustrate this, we consider the case where the reproduction biomass is drawn from the adult population. We assume that $R_i = R$ is simply a constant, that G(P) = P to match the QNPZ model, and that the biomass of the offspring can be neglected $(w_0\alpha/w \to 0)$. The last assumption is not necessary but simplifies the problem significantly; numerically, we can show that the finite w_0 case is quite similar to the results from the approximated set:

$$\frac{\partial}{\partial t}P = \mu P\left(N_T - P - \int dw \, wn\right) - \frac{1}{a}P \int dw \, g_w n - d_p P \tag{6a}$$

$$\frac{\partial}{\partial t}n = -P\frac{\partial}{\partial w}g_wn - d_zn\tag{6b}$$

$$Pg_w(0)n(0) = R \int dw \,\alpha n \tag{6c}$$

instability P, NA, n(w,t) comparison

SIMPLIFICATION

The previous discussion concentrated on cases where the structured model differs from the stable, steady QNPZ model. However, for some parameter values (or $g_w(w)$, $\alpha(w)$ functional forms), the structured model still has steady solutions, and we might wish to explore simplifying the model to obtain a much lower dimension system which can be used in simulations with space or time-dependent variability. If we write n(w,t) as a product of the biomass, Z, and the weight structure $\hat{n}(w,t)$

$$n(w,t) = Z(t)\hat{n}(w,t) \quad , \quad \int dw \, w \hat{n}(w,t) = 1$$

and sustitute into the dynamics, we find

$$\hat{n}\frac{\partial}{\partial t}Z + Z\frac{\partial}{\partial t}\hat{n} = -ZP\frac{\partial}{\partial w}g_w\hat{n} - d_z Z\hat{n}$$

Multiplying by w and integrating gives

$$\frac{\partial}{\partial t}Z = PZ\gamma(t) - d_z Z$$

with $\gamma = \int g_w \hat{n}$ and a structure equation

$$\frac{\partial}{\partial t}\hat{n} = -P\frac{\partial}{\partial w}g_w\hat{n} - P\gamma\hat{n} \quad , \qquad Pg_w(0)\hat{n}(0,t) = R\int dw\,\alpha\hat{n}$$

The PP equation

$$\frac{\partial}{\partial t}P = \mu(N_T - P - Z) - \gamma P Z - d_p P$$

likewise has the appropriate form. As a comparison, consider the case when the light level varies seasonally, so that the PP uptake rate varies. We presume a sinusoidal dependence with μ changing from 0.6 to 1.4 times the mean value. The simplification works quite well in the stable case; when limit cycles occur, the approximation represents the average trajectory reasonably well, but does not produce the large cyclic variations. However, the detailed cycling depends on initial conditions and thus is not likely to be realistic. The simplified model compares reasonably well to the average of runs of the full model with different starting phases; although there is a noticeable offset in the ZP field.

two year cycle R=0.4 R=1 R=1 phase av 20 classes 4 modes

Size-spectrum models

sketch

Model formulation

Logarithmic size classes are commonly used to allow spanning a wide range of lengths or weights. If we take the weight W (in nitrogen units) as our underlying variable, then $\omega = \ln(W/W_0)$ will be our coordinate, with W_0 the size of the smallest autotroph. At times, we shall discuss the "length" L taken to be the equivalent spherical radius $\rho_0 \frac{4\pi}{3}L^3 = W$. The variable P_j measures the biomass in the log-size class centered at $(j + \frac{1}{2})\Delta$: $j\Delta < \omega < (j + 1)\Delta$ where Δ is the logarithmic width of each class. For the heterotrophs, the smallest class will be ω_Z , and Z_j represents the biomass with log-size centered at $\omega_Z + (j + \frac{1}{2})\Delta$. The smallest classes of P and Z may be photosynthesizing bacteria (e.g., prochlorococcus) and protozoans, respectively; however, we shall use "phytoplankton" ("PP") and "zooplankton" ("ZP") as shorthand names for the two groups.

Food for ZP in size class i:

$$F_i = p_{ij} P_j \tag{7}$$

where p_{ij} expresses the range of PP which will be grazed (non-zero values) and the preference or ability to forage for different-sized prey. (1) the entries represent relative preferences so that $\sum_j p_{ij} = 1$, (2) the ZP of size $\ell_Z + j\Delta$ can only ingest prey of size $j\Delta$ and smaller $(p_{ij} = 0 \text{ for } j > i)$, and (3) the preferences or foraging abilities are fixed, independent of whether there is prey in a particular size class or not. For example, if the food available for Z_2 is $(P_0 + P_1 + P_2)/3$, it will remain so even if $P_1 = 0$, not switch to $(P_0 + P_2)/2$. These assumptions interact with the presumption that there is a minimum weight W_0 in subtle ways; alterations in them may have unexpected effects on the system.

Grazing rate:

$$g_i \frac{F_i}{F_{1/2,i} + F_i}$$

so that the rate of removal of PP in class j by ZP in size i is

$$g_i \frac{F_i}{F_{1/2,i} + F_i} \frac{P_j}{F_i} = g_i \frac{P_j}{F_{1/2,i} + F_i}$$

Of the grazed food, a fraction a_i is assimilated (although we could use a_{ij} if the ZP assimilate different prey differently). Our equation for Z_i becomes

$$\frac{\partial}{\partial t}Z_i = Z_i \left[a_i g_i \frac{F_i}{F_{1/2,i} + F_i} - d_{zi} \right]$$
(8)

and the PP equation is

$$\frac{\partial}{\partial t}P_i = P_i \left[\mu_i \frac{N}{N_{1/2,i} + N} - \frac{g_j p_{ji} Z_j}{F_{1/2,j} + F_j} - d_{pi} \right]$$
(9)

The continuum equations follow by replacing sums with integrals

$$F(\omega) = \int d\omega' p(\omega, \omega') P(\omega')$$
(10)

$$\frac{\partial}{\partial t}P(\omega) = P(\omega) \left[\frac{\mu(\omega)N}{N_{1/2}(\omega) + N} - \int d\omega' \, \frac{g(\omega')p(\omega',\omega)Z(\omega')}{F_{1/2}(\omega') + F(\omega')} - d_p(\omega)\right] \tag{11}$$

$$\frac{\partial}{\partial t}Z(\omega) = Z(\omega) \left[\frac{a(\omega)g(\omega)F(\omega)}{F_{1/2}(\omega) + F(\omega)} - d_z(\omega)\right]$$
(12)

The number of parameters seems now to be unmanageably large: for each PP class, we must specify μ_i , $N_{1/2,i}$, d_{pi} , and for each ZP class g_i , a_i , d_{zi} , $F_{1/2,i}$, and a preference matrix p_{ij} .

For functions such as $\mu_i = \mu(\omega_i)$ or $g(\omega_i)$, we invoke allometric relations

$$\mu(\omega_i) = \mu_0 \left(\frac{W}{W_0}\right)^{\beta_{\mu}} = \mu_0 \exp(\beta_{\mu}\omega)$$

where μ_0 and β_{μ} are the constants which define the shape of the curve. Allometric relationships make a lot of sense: many biological characteristics scale with the length, surface area, or weight.

Ranges and Steady States

Phytoplankton will only be able to grow in the range $0 \le \omega \le \omega_{Pmax}$ where the maximum possible size is given by

$$\mu(\omega_{Pmax}) = d_p(\omega_{Pmax})$$

However, not all of this range may be occupied, depending on parameters such as

$$N_T = N + \int d\omega \ P(\omega) + \int d\omega \ Z(\omega)$$

Zooplankton require

$$a(\omega)g(\omega) > d_z(\omega)$$

but will generally be restricted by the amount of available food.

SOLUTION PROCEDURE: (6) implies

$$F(\omega) = \frac{ag}{ag - d_z} F_{1/2}$$

Solve integral eqn/ linear system (4) for $P(\omega)$; choose N, solve similar linear system

$$\int d\omega' p(\omega',\omega) \frac{g(\omega')Z(\omega')}{F_{1/2}(\omega') + F(\omega')} = d_p(\omega) - \frac{\mu(\omega)N}{N_{1/2}(\omega) + N}$$

for $gZ/(F_{1/2}+F)$ and hence Z. Iterate on N until $N + \int P + \int Z = N_T$.

steady states

Fhalf=100 time evolution 40 classes stability Fhalf=10 stability Carnivory

In the quadratic case, we just include terms

$$a(\omega) \int d\omega' \tilde{p}(\omega, \omega') Z(\omega') - \int d\omega' \tilde{p}(\omega', \omega) Z(\omega')$$

The changes from the herbivore case are significant; the microzooplankton's death rate increases dramatically, and eventually, we see the larger carnivores. (Note: this is a qradratic model which should stabilize it!) Grazing structure.

Putting it all together

We have the pieces required to construct a model such as the original figure: transfer of biomass between trophic levels, multiple limitations, size-dependent processes, and growth in size within a population. We can easily rephrase the size-structured model in terms of weight classes instead of length classes; the $L^{-3/4}$ allometric rules become $w^{-1/4}$. We can also reformulate the structured-population model in terms of biomass in weight classes by multiplying xx by w

$$\frac{\partial}{\partial t}b = -w\frac{\partial}{\partial w}\frac{g}{w}b - db$$

or
$$\frac{\partial}{\partial t}b = -\frac{\partial}{\partial w}gb + \frac{g}{w}b - db$$
$$g(w_0)b(w_0) = \int dw r(w,s)b(w,s)$$

In the second form, the $\frac{\partial}{\partial w}$ term moves biomass $(b \, dw)$ conservatively from weight to weight while the gb/w terms represents the biomass which must be added for the organisms to gain weight. Transfer of biomass from other parts of the size-species domain must be adequate to account for this term as well as any residual biomass gain needed for reproduction (recognizing, of course, the inefficiency of grazing).

The somewhat different form of the reproduction term just makes connecting the newborn biomass produced by adults of weight w to intake easier. Competitive nonlinearities can still be included, both here and in the growth term, by making r(w, s) and/or g(w, s)functionals of b(w, s).

To connect species s to the others on which it feeds or for which it is prey, we define the transfer function p(w, s|w', s') – the amount of food from weight class w' in species s'available to weight class w in s. From this, we have the total food available

$$F(w,s) = \int dw' ds' \, p(w,s|w',s') b(w',s')$$

(recall that we are considering "species" as a continuous variable; in any case, the integral will be replaced by sums for numerical evaluation.) If we use the Monod form for limitation in food uptake, the gain by species s organisms at weight w is

$$G(w,s) = a(w,s)g_w(w,s)\frac{F(w,s)}{1 + F(w,s)/C(w,s)}$$

and the losses by predation are

$$D(w,s) = \int dw' ds' \frac{g_w(w',s')p(w',s'|w,s)}{1 + F(w',s')/C(w's')} b(w',s');$$

Some of the input is assimilated and allocated to growth (a_g) and some to reproduction $(a - a_g)$; for illustrative purposes, we shall assume that all the newborn biomass comes from this intake so that

$$g = wa_g G$$
 , $r = (a - a_g)G$

with the $a - a_g$ factor acting like α to isolate the adult portion of the weight spectrum.

With these definitions and choices, the equation becomes

$$\frac{\partial}{\partial t}b = -w\frac{\partial}{\partial w}a_gGb - (D+d)b$$

$$a_g(w_0)w_0G(w_0)b(w_0) = \int (a-a_g)Gb$$
(13)

with the various quantities being functions of w and s. If we integrate with respect to weight, we find the biomass equation $[Z(s) = \int dw b(w, s)]$:

$$\frac{\partial}{\partial t}Z = wa_g Gb\Big|_{w_0} + \int a_g Gb - \int (D+d)b = \int (aG - D - d)b$$

Fixed Size Structure Species

Under some rather strong restrictions, we can again find solutions with a stable population structure for species s so that $b(w, s, t) = Z(s, t)\overline{b}(w)$. In the general equation, the \overline{b} factors will cancel out if G can be factored into a part dependent on weight, but not environment (food, temperature, etc.) and a weight-independent environmental term, $G = \hat{G}g_w$. D and d must be independent of weight. The reproductive term was already assumed to be proportional to G. The resulting structure equation is

$$\hat{G}_{0}w\frac{\partial}{\partial w}a_{g}g_{w}\overline{b} = -(D_{0}+d)\overline{b}$$

$$a_{g}(w_{0})w_{0}g_{w}(w_{0})\overline{b}(w_{0}) = \int (a-a_{g})g_{w}\overline{b}$$

$$\Rightarrow$$

$$\int ag_{w}\overline{b} = \frac{D_{0}+d}{\hat{G}_{0}}$$
(14)

where \hat{G}_0 and D_0 are constants, chosen to give a value of $(D_0 + d)/\hat{G}_0$ making the solution to the structure equation consistent with the boundary condition. With this form, the temporal changes of the biomass satisfy

$$\frac{\partial}{\partial t}Z = Z\frac{\hat{G}}{\hat{G}_0}\int a\hat{G}_0g_w\overline{b} - DZ - dZ = Z\left[\frac{\hat{G}}{\hat{G}_0}(D_0 + d) - D - d\right]$$
(15)

For the conditions to apply for species s, F and D must be independent of w so that p = p(s|w', s') for all s' which are prey and p = p(s', w'|s) for all s' which are predators. As an example, consider single-celled organisms which reproduce by cell division: we can think of $\alpha_g = 1$ so that all intake of nutrient goes to growth. Reproduction takes the flux into weight $2w_0$ and redirects it to new cells at weight w_0 so that $g(w_0)b(w_0) = g(2w_0)b(2w_0)$ or $r = \delta(w - 2w_0)g(w)$. We replace the integral condition by $G(w_0)b(w_0) = G(2w_0)b(2w_0)$. The factorization of G and the idea that grazers do not distinguish between cell sizes seem quite reasonable, and the reproduction indeed scales the same way with environmental variability as growth. Of course, we do need to account for the variations in parameters with different species. Even for single-celled organisms, however, this picture may be oversimplified: Pascual and Caswell (19xx) discuss the case where only part of the cell cycle proceeds at a nutrient-dependent rate and demonstrate that cell numbers can have oscillatory or chaotic fluctuations with, respectively, steady or periodic in nutrient supply. Thus even the simplest organisms may show significant effects from varying weight distribution.

If we carry the fixed-weight distribution idea to an (unwarranted) extreme, by assuming p = p(s|s'), C = C(s), d = d(s), all species will have fixed distributions

$$b = Z(s,t)\overline{b}(w,s)$$
 , $\int dw \,\overline{b} = 1$

with the equations for the structure and the dynamics given above; the food, grazing, and predation mortality are set by

$$F(s) = \int ds' p(s|s') Z(s')$$

$$\hat{G}(s) = \frac{F(s)}{1 + F(s)/C(s)}$$

$$D(s) = \int ds' p(s'|s) \frac{Z(s')}{1 + F(s')/C(s')} \left[\int dw' g_w(w,s') \overline{b}(w,s') \right]$$
(16)

(If a is independent of weight, the last integral becomes $[D_0(s') + d(s')]/[a(s')\hat{G}_0(s')]$ but this is not a fundamental change.) In essence, the model reduces to a multispecies "compartment" model, conceivably with a much larger set of variables (limiting to the case where s is treated as continuous).

While some of the effects of weight have been removed, the previous models can still be developed within this context; indeed, the grouping chosen in that section could be just as well be phrased in terms of s rather than w. If species are sorted by their mean weight, then the allometric relationships still make sense. (However, such scaling for the grazing rates does not account for differences in preference among prey species which have similar mean weights; this kind information can be incorporated, but makes specification of p(s|s') more complex.)