Traditional population models

$$\frac{dN_i}{dt} = f_i(N_1, ...N_q)\, N_i \qquad\qquad i = 1, \ldots, q$$

- All individuals are functionally identical, meaning that they have identical birth and death rates, or
- The individuals can be represented by an average type and this average does not change over time.

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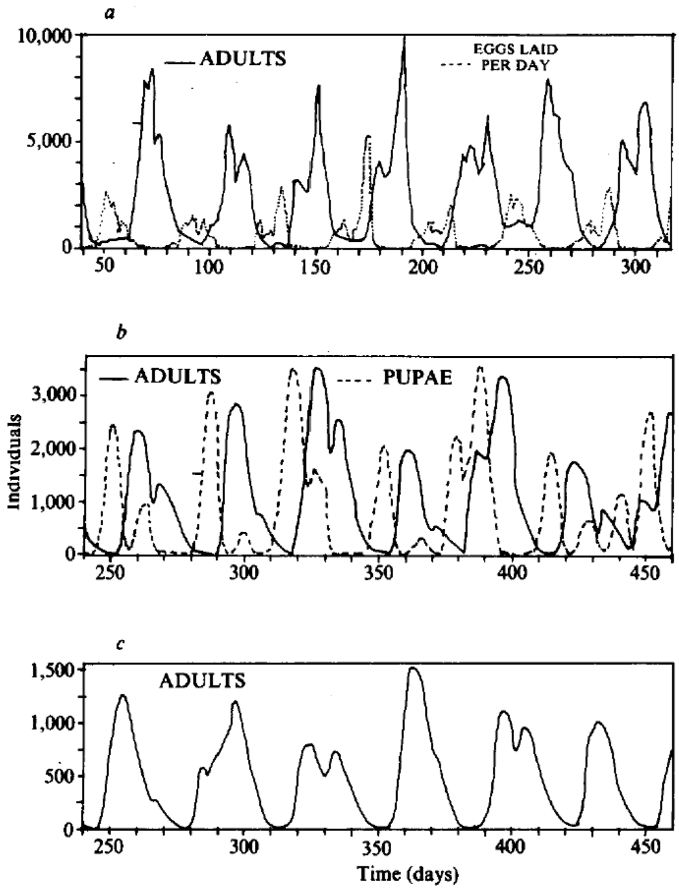

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Physiologically Structured Population Models

- explicitly model individuals and their life history, and
- derive population-level model descriptions by keeping book of the individual-level life history events (*e.g.*, reproduction, mortality) without making any further assumptions at the population-level itself.

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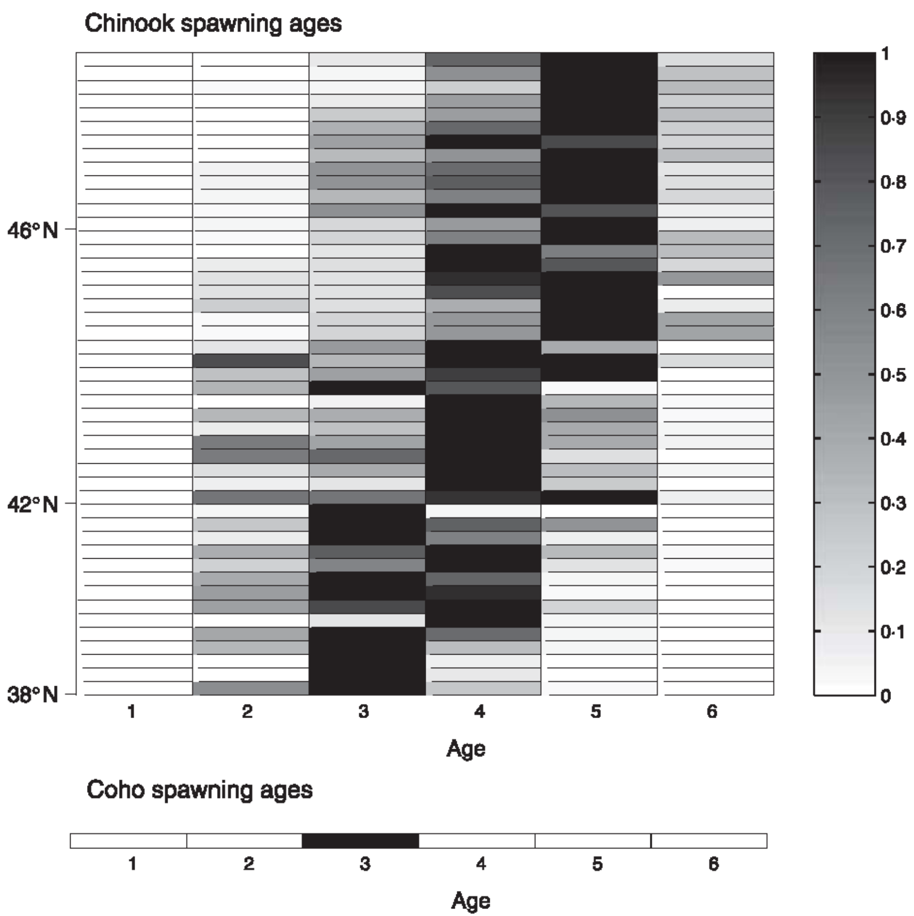
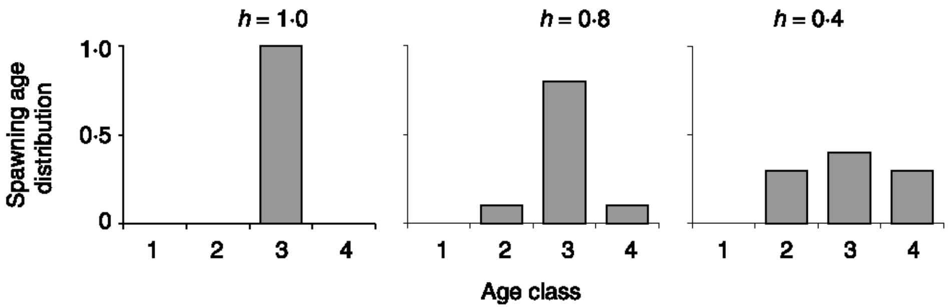
Individual, environmental and population state

- Individual or i-state: a set of (physiological) variables that characterizes an individual and is used to distinguish individuals from each other.
- Environmental or E-state: a set of variables, *e.g.*, food density, density of predators, that characterizes the environment in which the focal individual lives.
- Population or p-state: the mathematical construct to represent all individuals making up the biological population. The choice of this mathematical construct depends on the details of the modeled individual life history. It may be a vector of age- or size-class densities or a continuous distribution over an age- or size-interval.


Chinook spawning ages
46°N
42°N
38°N
1
2
3
4
5
6
Age
1
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
Coho spawning ages
1
2
3
4
5
6
Age



h = 1·0
h = 0·8
h = 0·4
Spawning age distribution
1·0
0·5
0
1
2
3
4
Age class

Mortality

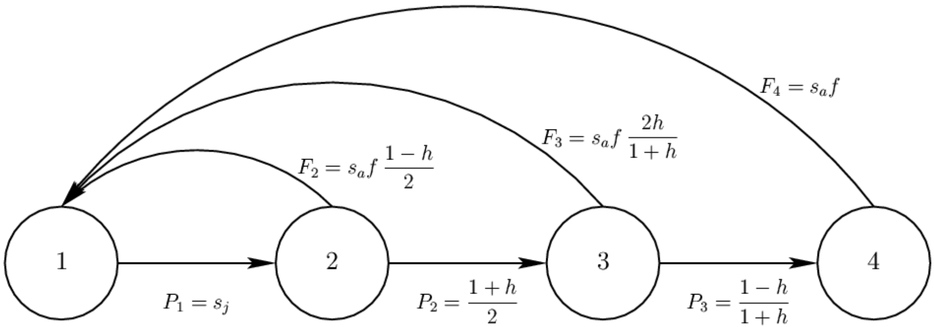
- Individuals experience mortality primarily during migration, both when migrating as smolt (1-2 years old) from their natal stream to the ocean, as well as when they migrate as adult back to their natal stream to spawn. Mortality of individuals in the ocean is negligible. The mortality that migrating juvenile individuals experience results in individuals having a probability s_j to survive their migration to the ocean (*e.g.* the survival probability from parr to smolt equals s_j). The mortality of returning adults results in these individuals having a probability s_a to survive their migration back to their natal stream.

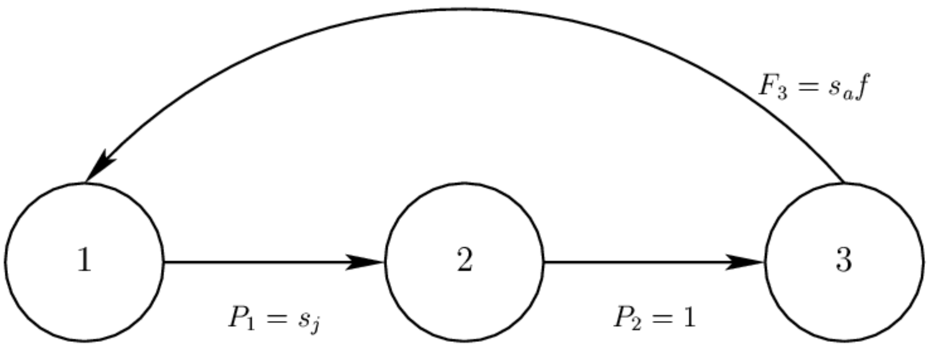
Reproduction

- Individuals return to their natal stream to spawn at an age of 2, 3 or 4 years old. With probability h they return to spawn at an age of 3 years, with probability $(1 - h)/2$ they return to spawn at either age 2 or 4 years old. On successful return to their natal stream, having survived the migration, they spawn a number of eggs that eventually yield f 1-year old individuals. Fecundity is assumed to be independent of the age at which adults spawn.

Development

- Since both mortality and reproduction are determined by the age of an individual, development from the neonate to the juvenile and eventually the adult stage is age-dependent, as well.


$F_4 = s_a f$
$F_3 = s_a f \, \frac{2h}{1+h}$
$F_2 = s_a f \, \frac{1-h}{2}$
1
2
3
4
$P_1 = s_j$
$P_2 = \frac{1+h}{2}$
$P_3 = \frac{1-h}{1+h}$


$F_3 = s_a f$
1
2
3
$P_1 = s_j$
$P_2 = 1$

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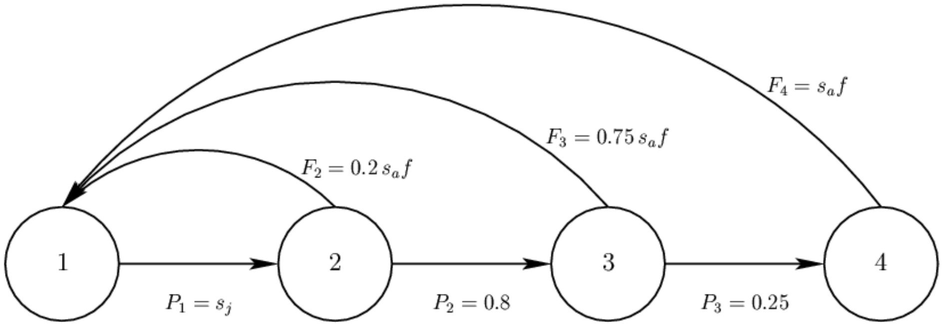


EBT-model of coho salmon

A. Definitions

a	individual age
$N_i(t)$	number of individuals in cohort i at time t
$A_i(t)$	age of individuals in cohort i at time t
$d(a)$	instantaneous mortality rate for individuals with age a
E	number of eggs spawned by an adult individual at age 3

EBT-model of coho salmon

B. Model equations

Continuous-time dynamics for all cohorts, in between two reproduction events

$$\begin{cases} \dfrac{dN_i}{dt} = -d(A_i)\,N_i \\ \dfrac{dA_i}{dt} = 1 \end{cases} \qquad i = 0, 1, 2$$

Creation of new cohort during reproduction event at $t = T, T+1, T+2, \ldots$

$$\begin{cases} N_0(t) = E\,N_2(t^-) \\ A_0(t) = 0 \end{cases}$$

Renumbering equations for all non-newborn cohorts at $t = T, T+1, T+2, \ldots$

$$\begin{cases} N_i(t) = N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \end{cases} \qquad i = 1, 2$$

EBT-model of chinook salmon

A. Definitions

a	individual age
$N_i(t)$	number of individuals in cohort i at time t
$A_i(t)$	age of individuals in cohort i at time t
$d(a)$	instantaneous mortality rate for individuals with age a
E	number of eggs spawned by an adult individual at age 3
$p(a)$	spawning probability of an individual with age $a = 1, 2, 3$ or 4

EBT-model of chinook salmon

B. Model equations

Continuous-time dynamics for all cohorts, in between two reproduction events

$$\begin{cases} \dfrac{dN_i}{dt} = -d(A_i)\,N_i \\ \dfrac{dA_i}{dt} = 1 \qquad\qquad i = 0,\dots,3 \end{cases}$$

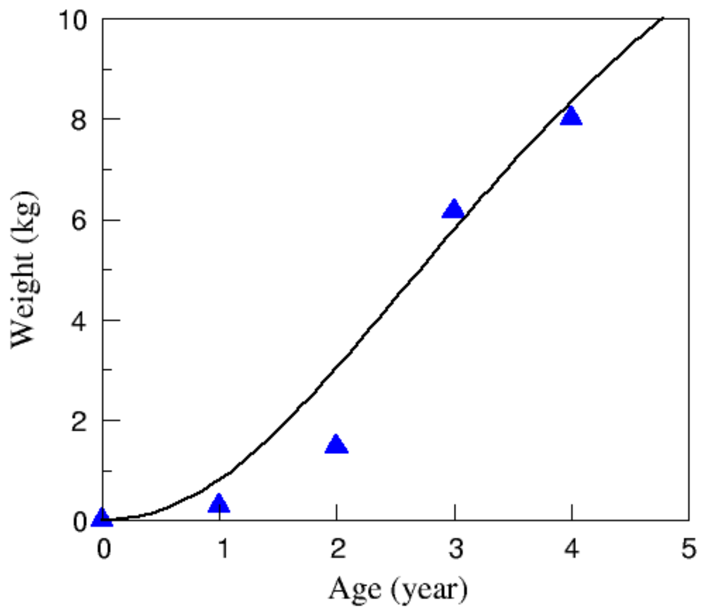
Creation of new cohort during reproduction event at $t = T, T+1, T+2, \dots$

$$\begin{cases} N_0(t) = E \displaystyle\sum_{i=1}^{3} p\left(A_i(t^-)\right)\, N_i(t^-) \\ A_0(t) = 0 \end{cases}$$

Renumbering equations for all non-newborn cohorts at $t = T, T+1, T+2, \dots$

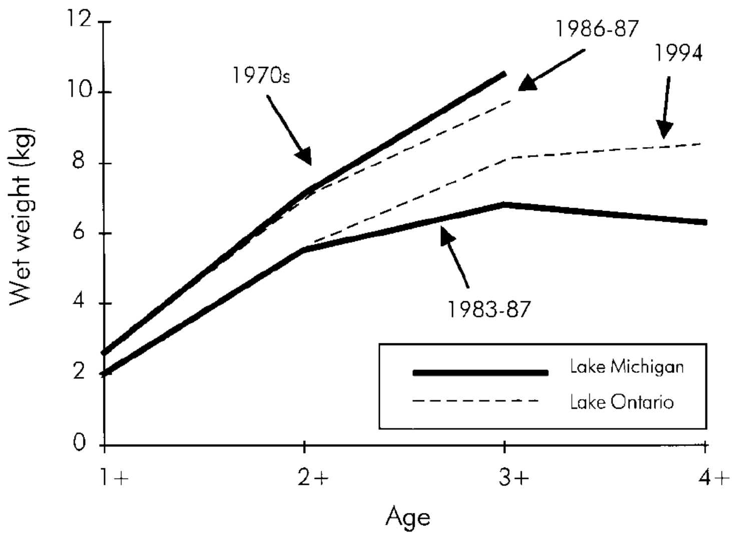
$$\begin{cases} N_i(t) = \left(1 - p\left(A_{i-1}(t^-)\right)\right)\, N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \qquad\qquad i = 1,\dots,3 \end{cases}$$

Weight-age relationship for chinook salmon



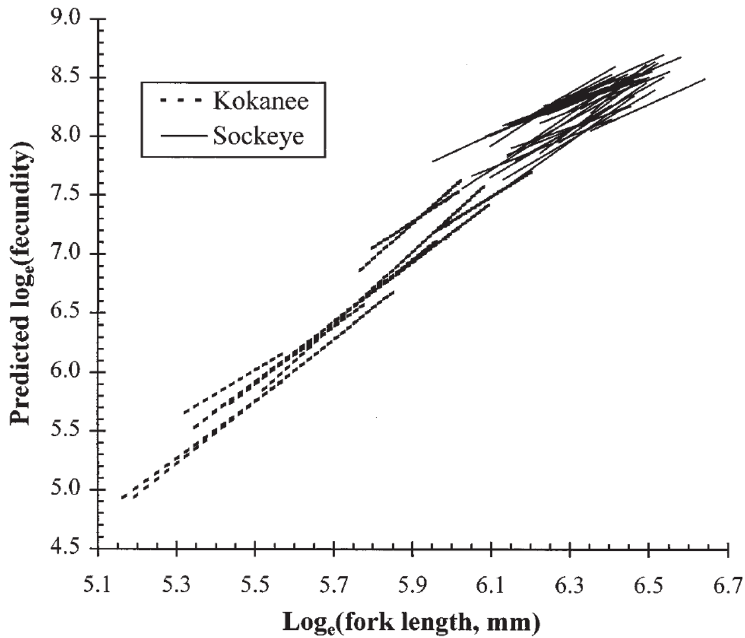
Weight-age relationship for chinook salmon in Lake Ontario. Average weight-at-age data reported by Rand & Stewart (1998) for the period 1990-1991 are shown together with a vonBertalanffy growth curve fitted by eye.

Weight-age relationship for chinook salmon



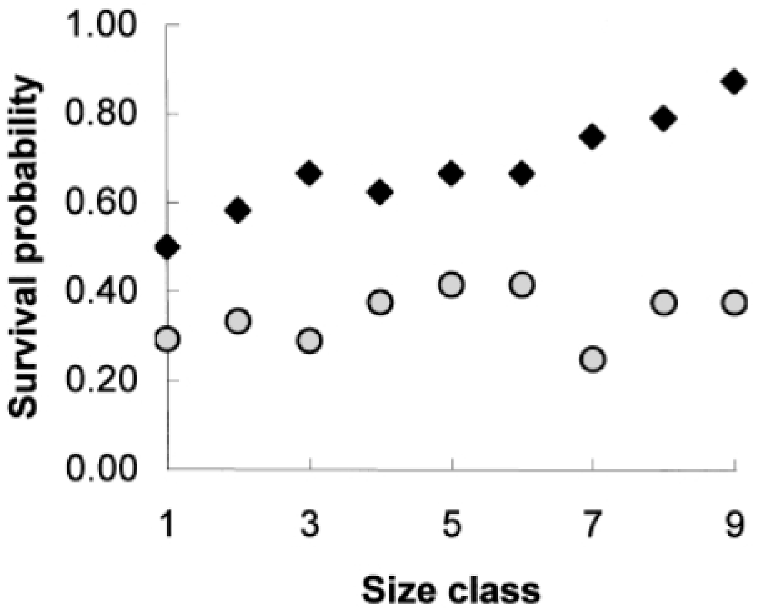
Weight-at-age for sexually mature hatchery chinook salmon from Lake Michigan and Lake Ontario. Figure redrawn from Rand & Stewart (1998), showing sampling data from Strawberry Creek, Wisconsin (Lake Michigan) and Salmon River, New York (Lake Ontario). Both reductions in size-at-age and delays in age-at-maturity have occurred in these populations over time.

Fecundity-size relationship for sockeye salmon



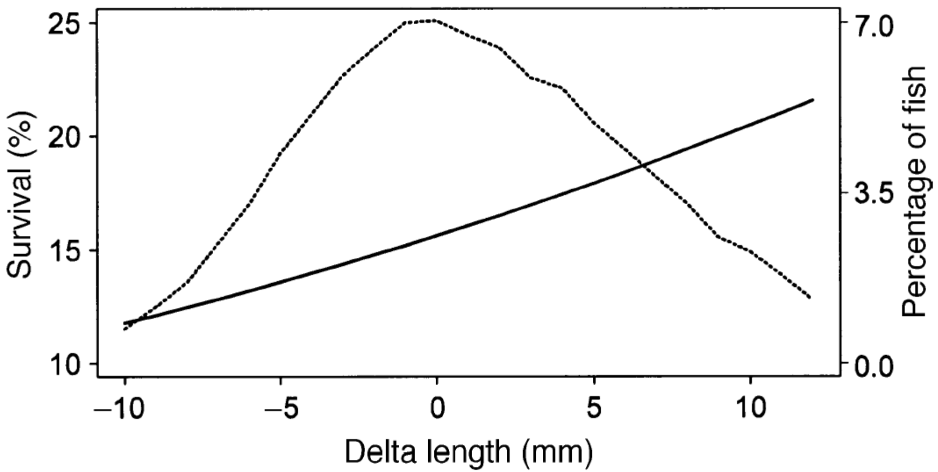
Relationship between fecundity and fork length for 11 populations of kokanee and 46 populations of sockeye salmon. Only the regression lines to the actual data on $\log_e$(fecundity) versus $\log_e$(fork length) are shown for different populations from Japan, Canada and the US. Figure redrawn from McGruk (2000).

Survial-size relationship for nasu salmon



Survival probability for different size classes of 0^+ fry of nasu salmon *Oncorhynchus nasou*. Survival was measured over a 3-week experimental period in the absence (*diamonds*) or the presence (*circles*) of a fish predator. Figure redrawn from Reinhardt *et al.* (2001).

Survial-size relationship for chinook salmon



Survival as a function of body length in chinook salmon. The solid, increasing line depicts percent survival as a function of the deviation of individual body length from the population average length. The dotted line indicates the fraction of fish in the salmon cohort with that particular body length. Figure redrawn from Zabel & Achord (2004).

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Mortality: the instantaneous mortality rate $d(s)$

- Given the variability in size-dependent survival patterns observed in natural systems, due to, for example, the type and density of predators present, we will consider only a very simple form of size-dependence in mortality rate, following the relationship

$$d(s) \;=\; \mu_\infty \;-\; (\mu_\infty \;-\; \mu_0)\; e^{-s/s_\mu}$$

  The function $d(s)$ hence is a decreasing function of our body size measure s, takes on the values μ_0 and μ_∞ for very small and very large individual, respectively, while it falls off with s at a rate determined by the parameter s_μ.

Reproduction: The number of eggs produced $E(s)$

- Data presented by Healey (2001) and Heath *et al.* (1999) indicate that per kilogram body weight chinook salmon produce somewhere between 500 and 1200 eggs. For the function $E(s)$ we wil hence assume the simple relationship

$$E(s) \;=\; \beta\, s^3$$

with scaling constant $\beta = 700$. This function implies that the number of eggs produced at spawning scales linearly with individual body weight $(= s^3)$ and that per kilogram weight 700 eggs are produced.

Development: The individual growth rate $g(s)$

- This function represents the right-hand side of the ODE that describes the growth of the individual in body size:

$$\frac{ds}{dt} = g(s) \qquad s(0) = s_0$$

in which the parameter $s_0 = 0.16$ equals the cubic root of the weight of a newborn individual at birth ($W_0 = 0.004$) and the growth function $g(s)$ is defined as

$$g(s) = \gamma\,(s_\infty - s)$$

with parameters $\gamma = 0.4$ and $s_\infty = 2.5$.

Age/size structured life history model of chinook salmon

A. i-state variables and life history parameters

Symbol	*Unit*	*Value*	*Interpretation*
a	y		individual age
s	$\text{kg}^{1/3}$		individual body size
s_0	$\text{kg}^{1/3}$	0.16	body size of newborn individual
s_∞	$\text{kg}^{1/3}$	2.5	maximimum body size
γ	y^{-1}	0.4	growth rate constant
β	kg^{-1}	700	weight-specific fecundity
μ_0	y^{-1}	2	mortality rate of very small individual
μ_∞	y^{-1}	1	mortality rate of very large individual
s_μ	$\text{kg}^{1/3}$	0.5	body size scaling constant of mortality

B. Life history model equations

Function	*Interpretation*
$g(s) = \gamma\,(s_\infty - s)$	growht rate in body size
$E(s) = \beta\, s^3$	number of eggs spawned by an adult individual
$d(s) = \mu_\infty - (\mu_\infty - \mu_0)\, e^{-s/s_\mu}$	instantaneous mortality rate
$p(a) = \begin{cases} 0 & \text{for } a = 1 \\ 0.2 & \text{for } a = 2 \\ 0.75 & \text{for } a = 3 \\ 1.0 & \text{for } a = 4 \end{cases}$	age-specific spawning probability

Age/size-structured EBT-model of a chinook salmon

Continuous-time dynamics for all cohorts, in between two reproduction events

$$\begin{cases} \dfrac{dN_i}{dt} = -d(S_i)\,N_i \\ \dfrac{dA_i}{dt} = 1 \\ \dfrac{dS_i}{dt} = g(S_i) & i = 0, \dots, 3 \end{cases}$$

Creation of new cohort during reproduction event at $t = T, T+1, T+2, \dots$

$$\begin{cases} N_0(t) = \displaystyle\sum_{i=1}^{3} E\left(S_i(t^-)\right)\, p\left(A_i(t^-)\right)\, N_i(t^-) \\ A_0(t) = 0 \\ S_0(t) = s_0 \end{cases}$$

Renumbering equations for all non-newborn cohorts at $t = T, T+1, T+2, \dots$

$$\begin{cases} N_i(t) = \left(1 - p\left(A_{i-1}(t^-)\right)\right)\, N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \\ S_i(t) = S_{i-1}(t^-) & i = 1, \dots, 3 \end{cases}$$

Food dependent life history model of chinook salmon

A. i-state variables and life history parameters

Symbol	*Unit*	*Value*	*Interpretation*
a	y		individual age
s	$kg^{1/3}$		individual body size
s_0	$kg^{1/3}$	0.16	body size of newborn individual
s_m	$kg^{1/3}$	2.5	maximimum body size at very high food levels
γ	y^{-1}	0.4	growth rate constant
β	kg^{-1}	700	weight-specific fecundity
μ_0	y^{-1}	2	mortality rate of very small individual
μ_∞	y^{-1}	1	mortality rate of very large individual
s_μ	$kg^{1/3}$	0.5	body size scaling constant of mortality
α	$g/kg^{2/3}$	1	maximum ingestion rate scaling constant
F_h	g/L	0.5	body size scaling constant of mortality

Food dependent life history model of chinook salmon

B. Life history model equations

Function	*Interpretation*
$g(s,F) = \gamma\left(s_m \dfrac{F}{F_h+F} - s\right)$	growht rate in body size
$E(s) = \beta\, s^3$	number of eggs spawned by an adult individual
$d(s) = \mu_\infty - (\mu_\infty - \mu_0)\, e^{-s/s_\mu}$	instantaneous mortality rate
$p(a) = \begin{cases} 0 & \text{for } a=1 \\ 0.2 & \text{for } a=2 \\ 0.75 & \text{for } a=3 \\ 1.0 & \text{for } a=4 \end{cases}$	age-specific spawning probability
$I(s,F) = \alpha\, s^2 \dfrac{F}{F_h+F}$	resource ingestion rate

Food dependent EBT-model of chinook salmon

Continuous-time dynamics for all cohorts, in between two reproduction events

$$\begin{cases} \dfrac{dN_i}{dt} = -d(S_i)\,N_i \\ \dfrac{dA_i}{dt} = 1 \\ \dfrac{dS_i}{dt} = g(S_i, F) \end{cases} \qquad i = 0, \ldots, 3$$

Creation of new cohort during reproduction event at $t = T, T+1, T+2, \ldots$

$$\begin{cases} N_0(t) = \displaystyle\sum_{i=1}^{3} E\left(S_i(t^-)\right)\, p\left(A_i(t^-)\right)\, N_i(t^-) \\ A_0(t) = 0 \\ S_0(t) = s_0 \end{cases}$$

Renumbering equations for all non-newborn cohorts at $t = T, T+1, T+2, \ldots$

$$\begin{cases} N_i(t) = \left(1 - p\left(A_{i-1}(t^-)\right)\right)\, N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \\ S_i(t) = S_{i-1}(t^-) \end{cases} \qquad i = 1, \ldots, 3$$

Dynamics of resource density

$$\frac{dF}{dt} = \rho\,(K - F) - \sum_{i=0}^{3} I\,(S_i, F)\; N_i(t)$$

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Comupational stages in EBT-model

1. The numerical integration of all sets of ODEs that determine the life history of the individuals in a cohort, more specifically their development, aging and mortality.

2. The simultaneous integration of the ODEs that determine the dynamics of all environmental factors, such as food density. These ODEs are coupled with the cohort ODEs through the influence these factors (*e.g.* food density) have on individual life history and, in turn, the population-level feedback of the cohorts on them, for example through feeding.

3. The creation of a new cohort of individuals at the moment that a reproduction event occurs, and

4. The renumbering of all existing cohorts in the population at the moment of a reproduction event to conserve an appropriate order in the indexes of the cohorts.

The population state or p-state

The mathematical object or construct that represents a biological population in a dynamic model. The type of the mathematical object depends on the life history model:

- In the chinook salmon model:

$$\begin{pmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{pmatrix}, \quad \begin{pmatrix} A_0(t) \\ A_1(t) \\ A_2(t) \\ A_3(t) \end{pmatrix} \quad \text{or} \quad \begin{pmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{pmatrix}, \quad \begin{pmatrix} S_0(t) \\ S_1(t) \\ S_2(t) \\ S_3(t) \end{pmatrix}$$

- In the *Daphnia* model with continuous reproduction:

$$n(t, \ell)$$

The individual state or i-state

A collection of, usually physiological, statistics that characterizes the individual organism and that is used to distinguish individuals from each other. Formally, the individual state should be a collection of individual properties

1. that at any one time completely determines, possibly together with the present state of its environment, the individual's probability to die or give birth and its influence on the environment (its contribution to the overall population dynamics), and

2. whose future values are completely determined by its present values plus the time course of the intervening environmental history, as encountered by the individual.

The environmental state or E-state

Every factor that can modify the life history of an individual organisms and that is not one of its own physiological traits, is considered part of its environment. Three distinct classes can be recognized:

- *Abiotic modulation*: completely external factors that neither the individual itself, nor the population it belongs to, nor any other population in the community that the population is part of can influence. This type of environmental influence therefore does not lead to density dependence!

The environmental state or E-state

- *Direct density dependence*: Influences of the population itself on the life history of its individuals (nursery competition, interference, cannibalism). This density dependence operates in a very direct way, because it is the population abundance that directly modifies the vital rates.

- *Environmental feedback*: Environmental feedback represents a form of density dependence that operates indirectly: for example, high population densities will lead to lower resource levels, which in turn will slow down individual growth and development, as well as negatively affect individual reproduction and survival.

Basic features of Daphnia life history models

1. the feeding rate of individual *Daphnia* strongly increases with individual size and is an increasing but decelerating function of food density,
2. individual *Daphnia* mature on reaching a fixed size, and
3. ultimate size and growth rate increase with food availability.

Model variables and life history parameters of Daphnia

Symbol	*Unit*	*Value*	*Interpretation*
ℓ	mm		individual length
ν	mgC/mm^2	0.007	maximum ingestion rate scaling constant
F_h	mgC/L	0.164	half-saturation food density in functional response
ℓ_b	mm	0.6	length at birth
ℓ_j	mm	1.4	length at maturation
ℓ_m	mm	3.5	maximimum length at very high food levels
γ	d^{-1}	0.11	growth rate constant
r_m	mm^{-2}	1.0	maximum reproduction rate scaling constant
μ	d^{-1}	0.05	size-independent, background mortality rate

B. Life history model equations

Function	*Interpretation*
$g(\ell, F) = \gamma \left(\ell_m \dfrac{F}{F_h + F} - \ell \right)$	growht rate in length
$b(\ell, F) = \begin{cases} r_m \, \ell^2 \dfrac{F}{F_h + F} & \text{if } \ell_j < \ell \\ 0 & \text{if } \ell \leq \ell_j \end{cases}$	reproduction rate
$d(\ell, F) = \mu$	instantaneous mortality rate
$I(\ell, F) = \nu \, \ell^2 \dfrac{F}{F_h + F}$	Feeding rate

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EBT-model of Daphnia with continuous reproduction

A. Population variables and parameters

Symbol	*Unit*	*Value*	*Interpretation*
$N_i(t)$	#/L		number of individuals in cohort i at time t
$L_i(t)$	mm		average length of individuals in cohort i at time t
$B_0(t)$	mm/L		Length-based measure of individuals in cohort 0 at time t
$F(t)$	mgC/L		resource density in the environment
ρ	d^{-1}	0.5	semi-chemostat resource regrowth rate
K	mgC/L	0.25	maximum resource density in absence of consumers

EBT-model of Daphnia with continuous reproduction

Continuous time dynamics during cohort cycle

Continuous-time dynamics for boundary cohort

$$\begin{cases} \dfrac{dN_0}{dt} = -d(\ell_b, F)N_0 - \dfrac{\partial}{\partial \ell} d(\ell_b, F)B_0 \\ \qquad + \displaystyle\sum_{i>0} b\left(L_i, F\right) N_i\ ^{\ddagger} \\ \dfrac{dB_0}{dt} = g(\ell_b, F)N_0 + \dfrac{\partial}{\partial \ell} g(\ell_b, F)B_0 \\ \qquad - d(\ell_b, F)B_0 \end{cases}$$

Continuous-time dynamics for other cohorts

$$\begin{cases} \dfrac{dN_i}{dt} = -d(L_i, F)N_i \\ \dfrac{dL_i}{dt} = g(L_i, F) \qquad\qquad i = 1, 2, \ldots \end{cases}$$

Dynamics of resource density in environment

$$\frac{dF}{dt} = \rho\left(K - F\right) - \sum_i I\left(L_i, F\right)\ N_i(t)\ ^{\ddagger}$$

‡ Include the boundary cohort in the sum if $N_0 \neq 0$; use $L_0 = \ell_b + B_0/N_0$.

EBT-model of Daphnia with continuous reproduction

Transformation and renumbering equations

Transformation and new initial values for boundary cohort at end of cohort cycle $(t = t^*, t^* + \Delta, \ldots)$

$$\begin{cases} N_1(t^* + \Delta) = N_0(t^* + \Delta^-) \\ L_1(t^* + \Delta) = \ell_b + \dfrac{B_0(t^* + \Delta^-)}{N_0(t^* + \Delta^-)} \\ N_0(t^* + \Delta) = 0 \\ B_0(t^* + \Delta) = 0 \end{cases}$$

Renumbering equations for other cohorts at end of cohort cycle $(t = t^*, t^* + \Delta, \ldots)$

$$\begin{cases} N_i(t^* + \Delta) = N_{i-1}(t^* + \Delta^-) \\ L_i(t^* + \Delta) = L_{i-1}(t^* + \Delta^-) \qquad i = 2, 3, \ldots \end{cases}$$

Partial differential equation formulation of the Daphnia model

Daphnia dynamics

$$\frac{\partial n(t,\ell)}{\partial t} + \frac{\partial g(\ell,F)\,n(t,\ell)}{\partial \ell} = -\,d(\ell,F)\,n(t,\ell)$$

$$g(\ell_b,F)\,n(t,\ell_b) = \int_{\ell_b}^{\ell_m} b(\ell,F)\,n(t,\ell)\;d\ell$$

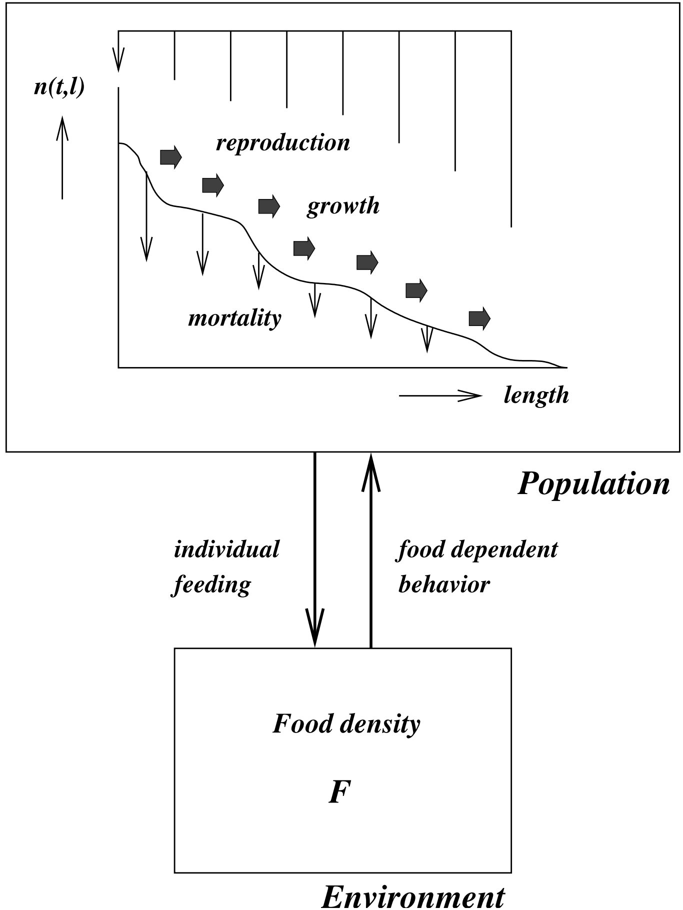
Algal dynamics

$$\frac{dF}{dt} = \rho\,(K - F) - \int_{\ell_b}^{\ell_m} I(\ell,F)\,n(t,\ell)\;d\ell$$

Initial conditions

$$n(0,\ell) = \Psi(\ell)$$

$$F(0) = F_0$$


n(t,l)
reproduction
growth
mortality
length
Population
individual
feeding
food dependent
behavior
Food density
F
Environment