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Supplement A: Assumptions and Equations in Ecopath with Ecosim

Governing Equations

The Ecopath module of EwE is a static, mass-balance ecosystem model that uses two governing equations for each species and age group (Christensen and Walters 2004). The first governing equation describes each species group's production for a time period, i.e., production (*P*) is the sum of fishery catch (*F*), predation (*M2*), net migration (immigration, *I*, and emigration, *E*), biomass accumulation (*BA*), and mortality from other sources ('other mortality', *M0*):

$$P = F + M2 + (I - E) + BA - M0$$

The second governing equation is based on the principle of conservation of matter within a group, and is designed to balance the energy flows of a biomass pool, i.e., consumption (*C*) equals the sum of production (*P*), respiration (*R*), and unassimilated food (*U*):

$$C = P + R + U$$

At a minimum, Ecopath requires inputs of diet composition ($DC_{i,j,}$ where *i* is predator and *j* is prey), fishery catch (Y_i), and three of the following four parameters for each model group (*i*): biomass (B_i), production-to-biomass ratio (P_i/B_i), consumption-to-biomass ratio (Q_i/B_i), and the ecotrophic efficiency (EE_i, the fraction of the production that is used in the system and does not move directly to the detritus pool). Mass-balance principles are then used to estimate the fourth parameter. P/B is the annual production rate of the population in Ecopath. Under equilibrium conditions, the P/B ratio of fish is equivalent to its total annual instantaneous mortality (*Z*) (Allen 1971). The total instantaneous mortality rate is the sum of fishing mortality, predation mortality, and ‘other mortality’ sources (disease, senescence, etc.). Balance of the energy equation is achieved by ensuring that respiration, the difference between the consumption, production, and unassimilated food, is positive and that ecotrophic efficiency is less than 1.

The Ecosim module provides a dynamic simulation of trophic interactions and biomass accumulation over time. The Ecosim basic equations are a set of coupled differential equations that re-express the first governing equation of the Ecopath model:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{j,i} - \sum_k Q_{i,k} - (M_i + F_i + E_i - I_i)\, B_i$$

where dB_i/dt represents the biomass accumulation rate during the time interval dt of group (*i*), g_i is the growth efficiency (production-to-consumption ratio), M_i is the natural mortality rate from sources other than predation (i.e. disease), F_i is fishing mortality rate, E_i is emigration rate, and I_i is immigration rate. The two summations are estimates of consumption rate Q, with the first expressing the total consumption by group *i* on prey *j*, and the second expressing the total predation by all predators on the same group *i*. In Ecosim, the consumption ($C_{i,j}$) of predator *i* on prey *j* was calculated as follows:

$$C_{i,j} = \frac{a_{i,j} \cdot v_{i,j} \cdot T_j \cdot T_i \cdot B_i \cdot B_j}{v_{i,j} + v_{i,j} \cdot T_j + a_{i,j} \cdot T_i \cdot B_j}$$

where search rate ($a_{i,j}$) is defined in Ecopath as the following:

$$a_{i,j} = \frac{\left(\frac{Q}{B}\right)_i \cdot B_i \cdot DC_{i,j}}{B_i . B_j}$$

Feeding time of group *i* (T_i) was calculated based on the ratio of consumption at the last time step ($C_{i,t-1}$) and the optimal consumption ($C_{i,opt}$) and feeding time at a previous time step ($T_{i,t-1}$):

$$T_{i,t} = T_{i,t-1}(1 - a + \frac{a \cdot C_{i,opt}}{C_{i,t-1}})$$

where a is a pre-defined constant for feeding time adjustment rate (=0.5 by default). The consumption is based on the 'forage arena' concept, where prey are divided into vulnerable and invulnerable components (Ahrens et al. 2012), and the transfer rate (vulnerability coefficient, $v_{i,j}$) between these two components. High vulnerability coefficients indicate high prey availabilities to predators. When consumption decreases, feeding time will increase in the next time step, in order to increase consumption. However, the feeding time is constrained by a user-defined value, the maximum relative feeding time, with default of two times the feeding time in the Ecopath model. In addition, longer feeding time will result in higher other mortality.

Ecosim is driven by external forcing, such as fishery catches and nutrient loads. Time series of fishery catches are converted into a loss term (F_i). The time series of nutrient loads (phosphorus in this study) are ratios of nutrient loads (L_t) of simulation year t to the nutrient load of the beginning (L_0) of the simulation (Ecopath year). For an ecosystem in equilibrium, the total nutrient at time t ($N_{T,t}$) is assumed to be proportional to the nutrient loads: $N_{T,t} = \beta L_t$. Thus, $N_{T,t}$ can be calculated as:

$$N_{T,t} = f_t \cdot N_{T,0},$$

where the f_t is the time series of nutrient load ratios, and $N_{T,0}$ is the Ecopath base estimate of total nutrient. The free nutrient that is available to primary producers (N_f) is the difference between total nutrient and the nutrient in biomass pools (N_B), which is calculated in Ecosim assuming a fixed nutrient content per unit of biomass. The primary production of group i (P_i) is calculated using Michaelis-Menten relationship.

$$P_i = B_i \left(\frac{P}{B}\right)_{max,i} \left(\frac{N_f}{N_f + K_i}\right)$$

where $(P/B)_{max,i}$ is the maximum production to biomass ratio for group i, and K_i is a half-saturation constant estimated by Ecosim.

The estimation of biomass and consumption to biomass ratio for non-leading stanza fish groups in the Ecopath model (Dr. Yu-Chun Kao, University of Michigan, personal communication, also see Kao (2015) Appendix F)

Most fishes undergo ontogenetic changes in diet from early stages to adults. EwE models fish groups by separating them into several life-history stages in which one stage recruits to the next one after a time lag and each stage has different input parameters. The biomass of fish group *i* in stage *s* (*s = larva, juvenile, adult…etc*.) can be expressed as:

$$B_i(s) = \sum_{a=a_{\min,i}(s)}^{a_{\max,i}(s)} N_i(a) \times W_i(a) \qquad \text{(S.A.1)}$$

where $B_i(s)$ is the biomass in stage *s*, $N_i(a)$ and $W_i(a)$ are the number of individuals and the mean weight of an individual at age *a*, and $a_{max,i}(s)$ and $a_{min,i}(s)$ are the maximum and the minimum ages of stage *s*, respectively. $N_i(a)$ is derived based on the assumption of constant total mortality and recruitment rates over each life-history stage by solving the following equation:

$$dN_i(t)/dt = -Z_i(t) \times N_i(t) + (BA/B)_i \times N_i(t)$$

$$\Rightarrow N_i(a) \propto \exp\left[-\sum_a Z_i(a) + a \times (BA/B)_i\right] \qquad \text{(S.A.2)}$$

where $Z_i(a)$ is the total mortality rate at age *a*, and $(BA/B)_i$ is the population growth rate. The weight of an individual at age *a* is modeled by the von Bertalanffy growth model (von Bertalanffy 1938) with an assumption that weight is proportional to the length-cubed:

$$W_i(a) \propto \left[L_{\infty,i}\left(1-e^{-K_i a}\right)\right]^3 \propto \left(1-e^{-K_i a}\right)^3 \qquad \text{(S.A.3)}$$

where $L_{\infty,i}$ is the maximum length, and K_i is the von Bertalanffy growth parameter. Combining Eqs. S.A.1–S.A.3, the biomass at life stage (*s*) can be expressed as:

$$B_i(s) \propto \sum_{a=a_{\min,i}(s)}^{a_{\max,i}(s)} \exp\left[-\sum_a Z_i(a) + a \times (BA/B)_i\right] \times \left(1 - e^{-K_i a}\right)^3 \qquad \text{(S.A.4)}$$

Again, based on the von Bertalanffy growth model (Essington et al. 2001), an individual's consumption rate is assumed to be proportional to the 2/3 power of its body weight:

$$Q_i(s) \propto \sum_{a=a_{\min,i}(s)}^{a_{\max,i}(s)} N_i(a) \times \left[W_i(a)\right]^{2/3} \qquad \text{(S.A.5)}$$

Combining Eqs. S.A.4 and S.A.5, the consumption/biomass ratio at stage *s*, $(Q/B)_i(s)$, can be expressed as:

$$(Q/B)_i(s) = \frac{Q_i(s)}{B_i(s)} \propto \frac{\sum_{a=a_{\min,i}(s)}^{a_{\max,i}(s)} \exp\left[-\sum_a Z_i(a) + a \times (BA/B)_i\right] \times \left(1 - e^{-K_i a}\right)^2}{\sum_{a=a_{\min,i}(s)}^{a_{\max,i}(s)} \exp\left[-\sum_a Z_i(a) + a \times (BA/B)_i\right] \times \left(1 - e^{-K_i a}\right)^3} \qquad \text{(S.A.6)}$$

In the EwE modeling approach, biomass and consumption/biomass ratio of one life-stage are required inputs for a fish group. Biomass and consumption/biomass ratio for other stages are modeled using Eqs. S.A.4 and S.A.6. More details about modeling multi-stanza fish groups in the EwE modeling approach can be obtained in Christensen et al. (2005).

Supplemental References

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