3.10 Predator satiation and handling time effects

Ecosim and Ecospace allow you to represent two factors that may limit prey consumption rates per predator (*Q/B*): i) foraging time adjustments related to predation risk and/or satiation; and ii) handling time effects. Parameters for both are specified via the Ecosim Group info form.

Satiation and/or choices to forage for short times in order to avoid higher predation risk are represented by setting non-zero values for the 'Feeding time adjustment rate' of a group: larger values of this rate represent more rapid adjustment of foraging time. Non-zero foraging time adjustment rates cause Ecosim / Ecospace to update relative foraging time during each simulation so as to represent predators as trying to maintain *Q/B* near the Ecopath input base rate. For some organisms (particularly marine mammals) this foraging time adjustment may represent animals always trying to feed to satiation (*Q/B* from Ecopath the satiation feeding rate) and taking more or less time to reach satiation depending on prey densities (and possibly also facing higher predation risk when foraging times are longer). For other organisms, the Ecopath base *Q/B* may represent a much lower feeding rate than the animal could achieve under 'safe' laboratory conditions, and in this case we view the base *Q/B* as an evolutionary 'target' rate representing results of natural selection for balancing benefits from feeding with predation risk costs of spending more time feeding.

Handling time effects represent the notion that predators have limited time available for foraging and this time can be used up by 'handling time' (pursuit/manipulation/ingestion time per prey captured) rather than searching for prey, when prey densities are high. The Ecosim Group info form allows you to set ratios of maximum to Ecopath base food consumption rates per individual (or per biomass). These ratios are set to large values (1000) by default, which allows predators to increase their feeding rates without limit as prey densities increase (i.e., not limited by time required to handle each prey). In most scenarios, limitation of prey vulnerability prevents this unreasonable assumption from having noticeable effect. But in scenarios where vulnerable prey densities of at least one type do increase greatly, setting a low value (e.g., 2 or 3) for the predator's maximum/base feeding rate ratio allows you to represent limits on feeding rate associated with time needed to handle each prey. Without such limits, your predictions of increase in predator *Q/B*, and hence productivity, at low predator density (or high prey density) might be too optimistic and lead you to errors like overestimating sustainable harvest rate for the predator. Also, ignoring handling time effects when one prey type increases greatly can cause an underestimate of the 'buffering' effect that such increases can have on predation rates felt by other prey: if the predator consumes more of the abundant prey, and spends more time handling/resting because of this, predation rates on other prey species should decrease.

Ecosim / Ecospace calculates feeding rates of predators using the 'multispecies disc equation', a generalization of Holling's type II functional response model for multiple prey types. Using the maximum/base ratio from the Group info form along with the Ecopath base food consumption rate per predator, the program calculates a maximum ration and effective handling time per prey biomass eaten (handling time = 1 / (maximum prey biomass eaten per time)). This handling time (Holling's *h* parameter) is used to calculate the denominator in the disc equation formulation Q/B_{ij} = biomass of prey type *i* consumed per time per predator *j*, $Qb_{ij} = a_{ij} V_{ij} / (1 + hj Si a_{ij} V_{ij})$ where a_{ij} is the rate of effective search by predator j for type i prey, hj is the predator handling time parameter, and V_{ij} is the instantaneous density of prey type i vulnerable to predator j.

V_{ij} is calculated by solving the 'fast dynamics' equation

$dV_{ij}/dt = v(Bi-V_{ij}) - v'V_{ij} ? a_{ij}PjV_{ij} / (1 + hj Sia_{ij} V_{ij})$for V_{ij},

while assuming the vulnerability-exploitation dynamics are fast enough to keep *dV/dt* near zero (vulnerability exchange rates *v, v'* large). The solution for V_{ij} over time involves a numerical procedure that can sometimes cause annoying 'chatter' in the Ecosim results when handling times are large (ratio of maximum/base consumption rate small). At each simulation time step the program updates an estimate of the ratio of predator search time to total time (this ratio is given by $P_{sj} = 1 / (1 + h_j S_i a_{ij} V_{ij})$ in the Holling formulation), using this update to provide an improved estimate of the V_{ij}. We do this because providing an exact value for the V_{ij} (exact solution for the nonlinear equation solutions for all the V_{ij} at the condition dV_{ij} / dt=0) at each simulation time step would require excessive computer time.

An interesting and useful feature of the algebra of multispecies disc equations is that the initial (starting simulation time) value for the Psj ratio (of search time to handling time, i.e. the denominator of the disc equation) for each predator type is given just by $P_{sj} = R_j / (R_j - 1)$, where R_j is the Group info form ratio of maximum to Ecopath base consumption rate per predator. P_{sj} is updated at each Ecosim / Ecospace time step by first calculating starting estimates of the V_{ij} using the P_{sj} from the previous (or initial) time step, then using these estimates in the sums $S_i a_{ij} V_{ij}$ that define P_{sj}.

Bioenergetics models for fish most often indicate that feeding rates are low compared to maximum ration; typical ratios of estimated to maximum ration (Hewett-Johnson 'P' parameter) are around 0.3-0.4. These estimates imply R_j (maximum/Ecopath base ration) values of at least 2-4. If you choose to use such realistic values instead of the default 1000, and if this causes Ecosim / Ecospace to Figure oscillatory behaviour, you need to consider two possibilities:

i. The oscillatory behaviour may be a numerical artifact of the procedure used to update P_{sj}; or
i. The model's 'correct' behaviour for the parameter combinations you have provided is indeed a predator-prey cycle.

If the oscillation has a period of several time steps (months), it is very likely a predator-prey cycle. Persistent predator-prey cycles are commonly predicted by models that include handling time, along with strong top-down control (high vulnerabilities v_{ij} of prey to predators). If you think the cycle is unrealistic, you should adjust the prey vulnerabilities (Ecosim Vulnerabilities form) to lower values (toward 'bottom up', prey vulnerability control) rather than just setting high R_j values. If you see very short cycles indicating numerical instability in the P_{sj} adjustment procedure (usually happens for fast turnover groups like microzooplankton), you should set higher R_j values for the offending groups. This amounts to admitting that Ecosim is limited in its ability to represent very fast dynamic changes in groups that turn over very rapidly.