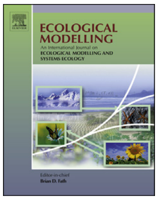
Ecological Modelling 308 (2015) 14–17

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Letter to the Editor

Ten common mistakes made in Ecopath with Ecosim modelling

Keywords:
Ecopath
Ecosim
Best practices
Ecosystem
Modelling
Fisheries

With more than 6000 registered users in 164 countries and almost 500 peer-reviewed publications (120 in Ecological Modelling), Ecopath with Ecosim (EwE) and Ecospace is by far the most commonly used ecosystem modelling platform in the world. In this software suite, Ecopath describes instantaneous biomass flows through a web of functional groups (groups of species aggregated by niche similarity) (Polovina, 1984; Christensen and Pauly, 1992), Ecosim integrates those flows over time (Walters et al., 1997) and Ecospace sets those dynamic simulations in a 2D grid (a raster) of connected cells and integrates habitat and habitat affinities (Walters et al., 1998).

This free software package has revolutionized our ability to consider fisheries and marine populations in a whole-ecosystem context. With its intuitive principles of mass-balance and conservation of energy, and its innovative application of foraging arena theory (Walters and Juanes, 1993; Walters and Martell, 2004), EwE has made complex food webs more tractable to marine science. It is an important addition to the fishery manager's toolbox (Aydin et al., 2007) and one that can help fulfill the often-stated objective of incorporating ecosystem considerations into management (e.g., MSRA, 2006; DOJ, 1996; European Community, 2002).

The most productive years lie ahead. The establishment of the Ecopath with Ecosim Consortium in November 2011 communalizes software development boosting earlier efforts to encourage subroutine development through modularization of the software. This was an effort supported by the Lenfest Ocean Program and the Pew Charitable Trusts; it allows users to develop optional plug-ins that increase functionality or substitute customized algorithms. The Consortium also provides infrastructure for additional user support. This is supplemented by innovations like the Wiki-style forum (http://www.ecopath.org/forum), automated model development routines in FishBase (Froese and Pauly, 2012; Christensen et al., 2009) and training programs offered in a variety of short and full-semester formats in Canada, the US and the UK. The range and depth of EwE applications are likely to increase in the future so there is a need to establish best practice guidelines.

In this letter to the editor, we discuss practical issues that arise in modelling and some common mistakes made in EwE literature with the hope that some pitfalls may be avoided or given due consideration by modellers. We assume some familiarity with EwE; the model system has been described in detail elsewhere (ecopath.org; Christensen and Pauly, 1992; Walters et al., 1997; Christensen and Walters, 2004). We begin with number 10 and countdown in order of increasing importance.

- *No. 10. Temporal forcing functions lower or higher than the baseline rate.* Forcing functions are functions that affect tracked variables with respect to time. The typical way to enter them in Ecosim (under the forcing functions tab) applies forcing values as multipliers of production rate or vulnerability. Vulnerability is a foraging arena parameter that defines the maximum allowable increase in predation mortality. When entering a forcing function in Ecosim, data in the first time step needs to agree logically with the initialization state of the Ecopath model. If the value of the forcing data in the first time step is greater or less than one (in the case of a relative trend), this modifies the initialization state defined in Ecopath. For example, if there is a need to enter a forcing pattern on functional group productivity less than 1 in the first year, then Ecopath must have been parameterized with too high of productivity. There may be times when this is appropriate; for example, if the Ecopath base state represents an annual average, while the forcing function adjusts for seasonality. The above logic also applies when entering absolute biomass or catch observations for the purpose of model fitting (the process in which dynamics are fine-tuned to replicate observations through parameter adjustment).
- *No. 9. Ecotrophic efficiency as a tuning parameter.* Ecotrophic efficiency (EE) is sometimes viewed as a 'catch-all' tuning parameter for Ecopath; however, it serves an important function. It describes mortality that is not captured by the model. As a general rule of thumb, species whose mortality is completely explained by dynamics that occur within the model domain and are not subject to undefined sources of mortality should be assigned a high EE, approaching 1. Low EEs imply either that there is unmodelled predation or that natural mortality (M) is dominated by unmodelled disease, physiological malfunction or aging. While these situations are probably common in reality (the M/K Beverton–Holt invariant described by Charnov, 1993 suggests that death rates increase with metabolic rates (K) whether or not there is predation mortality), there may be a tendency to leave EEs low for inappropriate functional groups. First, low EEs make Ecopath easier to balance since small adjustments to the diet matrix will less often result in EEs > 1 (a situation that denotes thermodynamic inconsistency). Second, there is never a requirement by the software to increase EEs as mass-balance is not threatened by low values. Though it is tempting to assign EE and calculate biomass or one of the other basic Ecopath parameters through the mass-balance criterion, this should be avoided wherever possible since there is no way to validate EE by empirical means.
- *No. 8. Using global EwE vulnerabilities.* Ecosim's vulnerability parameters heavily influence behaviour of the model. They are the main parameters of the foraging arena equations (Walters

http://dx.doi.org/10.1016/j.ecolmodel.2015.03.019

and Juanes, 1993; Walters and Martell, 2004) and are responsible for density-dependent modulation of feeding rates. Ideally, vulnerabilities should be adjusted to improve model fit to observational data. However, of the hundreds of EwE models that have been published, relatively few are fitted to data (Christensen and Walters, 2005; Heymans et al., 2012). In cases where historical data are lacking (or for models of the present day which have no future observations), modellers parameterize the vulnerability matrix by simpler means: for example, by assuming vulnerabilities are proportional to prey or predator trophic level (Ainsworth, 2004), or by using the default global parameter setting of 2. The interpretation of the latter case is that predation mortality, for each diet interaction, has the potential of doubling under periods of high predator abundance. Since the vulnerability index ranges from 1 to infinity, a value of 2 indicates relatively resource-dependent trophic control over the system. While there is a heuristic advantage in using a low global vulnerability setting (since it constrains the responsiveness of the model) this assumption may overestimate the resiliency of the ecosystem and underestimate extinction risk (Martell et al., 2002)—particularly in stochastic simulations. Unless the vulnerability matrix can be fitted, it is important to consider a range of global vulnerability settings to bracket predictions within an uncertainty range. Although this cannot provide a probabilistic error assessment, it is a useful technique for constraining outcomes in complex ecosystem models (Fulton et al., 2003). Moreover, accepting the default global setting should never be viewed as a means of reducing the number of assumptions introduced into the model since a global parameter set represents a powerful assumption on trophic control.

- *No. 7. Amplitude of forcing functions.* A new development with the release of EwE V6 is that one can now enter a physical forcing pattern such as sea surface temperature (SST), and apply it to one or more functional groups. This is in contrast to EwE V5 in which the functional group was linked directly to the forcing pattern using a 'pool code' in the forcing function input file. Though V6 uses a more flexible and intuitive approach, there may be a temptation to associate the forcing pattern to multiple groups without regard to the appropriate amplitude for the parameter and group being affected. For example, a 2-fold increase in fish recruitment may be a reasonable response to SST forcing, while a 2-fold increase in primary productivity will result in a much larger effect in the model and may be inappropriate. Several versions of the SST trend may need to be inputted using different scaling factors on amplitude (applied outside of EwE) to make the climate series appropriate for the parameters and groups of interest. An example of this is found in Ainsworth et al. (2011).
- *No. 6. Overreliance on automated tuning facilities.* As with any complex model, there are numerous ways to achieve an equivalent goodness of fit: a measure of how well the model reproduces observed time series such as catch, biomass or fishing mortality in a historical reconstruction simulation. The vulnerability matrix and climate anomalies are the data inputs most often used to tune dynamics to time series because Ecosim has automated parameter search facilities for these. However, adjusting the diet matrix is a powerful and underused method for improving fit. Each predator provides a 'signature' pattern of predation mortality that can be viewed on the 'Ecosim group plots' tab. Adjusting the importance of that predator through the diet matrix emphasizes or deemphasizes its contribution to the overall mortality trend. Strategic use of predation in this way provides a good deal of dexterity for modifying predicted biomass if predation mortality is a dominant driver of population dynamics. Note that adjusting the vulnerability matrix, climate anomalies or the diet matrix each affords alternative explanations for observations in terms of animal behaviour, climate, and trophic dynamics, respectively. By only using the automated parameter search functions the user may miss an opportunity to improve the diet matrix, instead relying solely on changes to vulnerabilities to adjust the predation mortality trends.
- *No. 5. Model domain as a bath tub.* Representing an open system presents challenges in any localized ecosystem model. It becomes problematic if the modelled area is small (capturing a small fraction of the stock range for a large number of groups) or if the focus of attention is on migratory species. In these cases, population changes may not be predictable from drivers and dynamics occurring within the model. In EwE, there is an implicit assumption often overlooked that any mortality rates incurred within the model domain are representative of the entire spatial range occupied by a functional group. This may not be a bad assumption in the case of predation and fishing mortality, however any incidental or localized source of mortality (e.g., through interaction with coastal pollution or other human industries) needs to be adjusted downwards in proportion to the total time spent in the model domain (e.g., Busch et al., 2013).

  The sophisticated option for representing seasonal movement in EwE is Ecospace's integrated migration routine. This 'Eulerian' approach (Walters et al., 1998; Christensen and Walters, 2004; Walters and Martell, 2004) moves the centroid of the population to predefined waypoints throughout the year, while concentration parameters define the spread of mass. However, this method only handles movement within the model domain and may not be practical to apply to wide-ranging migratory stocks. A large area is needed for this which limits the spatial resolution under the usual computational constraints. Habitat representation suffers. Intraannual dynamics in general are difficult to justify unless seasonality is fully represented (e.g., primary production).

  Alternatively, Ecosim can be used to represent biomass flux entering and leaving the model domain. The simplest approach is to include 'import' in a migrator's diet. Diet import is a limitless prey resource (taxonomically undefined) that does not dynamically interact with any groups in the model. However, since diet import is not subject to variation in availability (e.g., due to fluctuations in system productivity or trophic dynamics) this introduces a stabilizing effect on migrators that can impart unrealistic resilience to trophodynamic variability. This issue also affects diadromous fishes that feed in freshwater systems, potentially during critical life stages.

  A more involved method in Ecosim is to include 'outside' predators or prey as groups in the model, representing spatial segregation through the diet matrix. Described in Christensen et al. (2005), this method is seldom used except to represent predation from sea birds and terrestrial animals (e.g., Watkinson, 2001; Lima et al., 2014). Unfortunately it complicates the use of Ecospace as there is no practical way to spatially partition the outside groups. Using diet import terms on the outside prey and predators of the migrator may serve as a partial solution because unwanted interactions can be eliminated.

  Each method of representing migration has strengths and weaknesses. If the focus of policy exploration is on non-migrating groups it may be worthwhile to treat migrator biomass as an input (e.g., Ainsworth et al., 2008). Alternatively, the 'Lagrangian' approach (Walters et al., 1998) conceptually treats the model (Ecospace or Ecosim) as if the boundaries were constantly moving to follow the migrating population. This is practical only for simple models focused on migrators as it requires the assumption that the organismal community is subject to similar feeding opportunities and mortality risks as they move.
- *No. 4. Hard-wired system behaviour.* It is possible to parameterize a functional group so that a biomass decline is ensured only because the carrying capacity of the ecosystem lies below the initial biomass value. In this case, the decline is 'hard wired' into the