## 24. Model Protocols

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In this section we describe the software selection process, balancing exercises, diagnostics protocols and scenarios applied in the Energy Modeling and Analysis eXercise (EMAX).

### A Primer on Energy Budgets and Network Models

Network models are based on the concept of a steady state ecosystem in which the energy inputs to a node are balanced by the outputs. Ecosystem network models trace the flows of energy or materials among compartments of the system. At steady state, the flows into a compartment exactly equal flows out of the compartment:

(EQ. 24.1)
$$\sum_{j=1}^{n} F_{ij} + I_i - \left( \sum_{j=1}^{n} F_{ji} + E_i \right) = 0$$

where $F_{ij}$ is the flux from compartment j to compartment I; $I_i$ is import to compartment i from outside the system; and $E_i$ is export from compartment i to outside the system. The estimates of production, consumption, and respiration described in earlier sections for each compartment are used in determining the flows among compartments. Under the assumption of steady-state conditions, these initial estimates of the flows are checked to see if the mass-balance criteria are met. If the system is not in steady-state, iterative adjustments are made to the flows in an attempt to achieve mass-balance.

Typically, all parameters necessary to determine the flows are not known and must be estimated. In general, there is not a unique solution to the system of linear equations (the problem is under-determined) and several alternative approaches were used to obtain solutions. We explored two alternative modeling approaches to examine solutions to this problem, the details of which are below.

### Caveats and Assumptions

For the purposes of this exercise, we assumed steady state equilibrium. We acknowledge that there are dynamic elements of what we modeled, but averaging estimates over a five-year period mitigates some of the inter-annual dynamics.

For EMAX we assumed no movement of animals across regions (captured by proportionality of distributions spatially and seasonally). Thus, $I_i$ was set to 0 and $E_i$ was treated as fishery removals, bycatch, and ship-strikes for each appropriate node. That is, the network models didn't consider any potential transfer of matter or energy between the different subregions (Gulf of Maine; Georges Bank; Southern New England and Mid-Atlantic Bight) on the Northeast Continental Shelf, so that each system was treated in isolation.

We recognize the potential for a wide range of results depending upon which units are used. Although network models have been constructed using energy, biomass, or elemental units, we chose to execute our model in units of biomass (wet weight) per unit area.

Given that the carbon turnover of phytoplankton and bacteria is roughly 3 days, and that of fish varies over a range of 300 - 450 days (Hakanson and Gyllenhammar, 2005), it appears that the carbon formed in photosynthesis is recycled many times before reaching fish and marine mammals. This brings into question the assumption that this recycled carbon has the same qualitative value or embodied chemical energy at different trophic levels. Schneider and Sagan (2005) discuss the importance of distinguishing between carbon which cycles and energy which flows from sources to sinks. Direct carbon flow follows the pathways of energy, while the recycled carbon flow goes along the indirect pathways. It is important to distinguish between "cycles" (indirect flows) and "network connections" (direct flows) in carbon-based networks.

In classical energy flow models where joules or kilocalories are the measure of exchange between compartments, energy flows from sources (sunlight and resultant primary production) to sinks (higher trophic levels) with a large respiratory dissipation of energy at each trophic level. This highlights the need to resolve the apparent paradox between nutrients which cycle throughout the nodes within a network and energy which flows from sources to sinks with a large respiratory tax at each trophic level. In most network models, recycled energy is implicitly modeled as flows through indirect pathways.

The EMAX network budget was based on wet weight which lies at an intermediate point on the gradient between budgets based on carbon (which explicitly consider turnover time differences between compartments) and the classical energy flow budgets (j or kcal transported from sources to sinks).

## Software and Modeling Approaches

We explored a broad selection of energy budget models, network models, and associated software packages for use in EMAX.

First we examined EcoNetwrk and constructed a preliminary model for the Gulf of Maine region. This approach uses reconstructed flows as the state variables (see Ulanowicz 2004 for an overview). Balancing the network proved to be challenging, as this model balances mainly by constraining respiration and consumption, and is a statistical minimization rather than a true optimization solution. Assumptions about primary production and detrital processing were key. We also explored Netwrk, the precursor to EcoNetwrk, which we decided was not likely to be an improvement over EcoNetwrk, particularly because it did not reside in a graphical user interface (GUI) environment.

We also constructed a preliminary model for Ecopath. This approach uses estimates of standing stocks as the state variables (see Christensen and Pauly 1992, Walters *et al.* 1997). Although initial balance was achieved, we were uncertain how much was due to detritus. This model balances primarily off ecotrophic efficiencies and uses a true optimization protocol.

Other software packages we investigated were WAND, WAND Balance, DR. LOOP, and SIMULOOP. They may be useful for additional analyses once balanced budgets are formed using the two primary software packages, because they feature some useful cybernetic metrics. However, they are not likely to provide a balancing package of any improvement over the first two programs. Many packages provide useful information and analytical capabilities, but are not readily amenable for balancing a budget or easily translatable into the fisheries management context. Other models we evaluated as potentially very useful but rejected were redundant; focused on more qualitative network properties; were less user-friendly; or obfuscated their underlying model structure.

We also noted the potential for using some of the outputs from a concurrent GLOBEC Phase IV project, which could provide some MATLAB software to conduct energy budget balancing. Additionally, we made explorations into AD Model Builder and At-Risk/Excel, tools used to build models from scratch. Neither option, however, could be implemented in a timely manner.

After several iterations, we settled on using EcoPath (Christensen and Pauly 1992; Walters *et al.* 1997) and EcoNetwrk (Ulanowicz and Kay 1991; Ulanowicz 2004) as our primary tools. The pros and cons of each have been noted elsewhere (e.g., Walters *et al.* 1997; Heymans and Baird 2000; Hollowed *et al.* 2000; Whipple *et al.* 2000; Allesina and Bondavalli 2003; Kavanagh *et al.* 2004; Ulanowicz 2004). There is a subtle difference in the underlying philosophy and numerical solutions between the two programs (Heymans and Baird 2000).

The production (flows) for the heterotrophic compartments in EcoNetwrk can be expressed as:

(EQ. 24.2)
$$P = C - R - E$$

where P is production; *C* is consumption; R is respiration; and E is egestion (unassimilated food). The autotrophic compartment(s) considers respiration losses to gross primary production (GPP) to yield net primary production. Fishery yields are treated as exports from the system.

The mass balance EcoPath model can be expressed as:

(EQ. 24.3)
$$B_i(P/B)_i EE_i = C_i + \sum_j B_j (Q/B)_j DC_{ij}$$

where $B_i$ is the biomass in the compartment; $(P/B)_i$ is the production to biomass ratio; $EE_i$ is the ecotrophic efficiency (fraction of total production consumed by predators or exported from the system); $C_i$ is the catch for compartment i; $B_j$ is the biomass for predator j; $(Q/B)_j$ is the consumption to biomass ratio for predator j; and $DC_{ij}$ is the diet composition of predator j (fraction of biomass comprising prey i in the diet of predator j).

The benefit of using the two packages instead of choosing one is that their strengths and weaknesses can be played off against one another. The detritus box is the main weakness of Ecopath, while in EcoNetwrk it is egestion. Ecopath is an optimization program, whereas EcoNetwrk is a minimization procedure. These programs use two different methods to arrive at working, balanced solutions: Ecopath emphasizes P, while EcoNetwrk emphasizes R. Both use convergence of values with repeated (auto) balancing as the main way to verify model finalization. Even though the two models have a conceptually different approach (Ecopath is more top-down while EcoNetwrk is more bottom-up), both have highlighted the same deficiencies in our data matrix. A positive outcome of using both software packages is that we improve our input data and systemic understanding more than we would have by changing the model parameters using only one package. This also suggests that our results are robust to model choice.

## Balancing Protocols

We made an initial calculation of the difference between the inflows and outflows from each compartment according to the specification of the input variables. For compartments exhibiting large discrepancies, we reexamined the input information for consistency, made comparisons with similar inputs from other systems, and made adjustments as necessary. We then employed balancing options in both software packages to provide estimates of the steady-state flows. EcoNetwrk employs a manual balancing procedure in which an extended matrix comprising elements for the exchanges among compartments, respiration, imports, and exports is adjusted using successive transformations of this structural matrix (see Allesina and Bondavalli 2003). EcoNetwrk allows for "locking" estimates thought to be well determined and therefore provides an implicit weighting procedure. EcoPath employs a statistical balancing procedure using Singular Value Decomposition to constrain the estimates for the underdetermined system of equations. EcoPath allows the specification of an index of reliability (or "pedigree") for each element to provide weighting options for estimation. Following each balancing procedure, we reevaluated inputs showing large deviations from mass balance or unrealistic estimates for certain diagnostic measures such as the ratio of production to consumption and respiration to consumption in EcoNetwrk, and the ecotrophic efficiency in EcoPath. Adjustments were made to the inputs to obtain more realistic estimates and the balancing protocols were repeated until stable estimates were obtained.

One of the benefits of this exercise and approach is that we identified major information/ data gaps for the GOM (and generally NEUS) ecosystem (Table 24.1).

## Ecopath Considerations

For the EcoPath model we initially investigated entering uncertainties globally rather than using the pedigree of data option on individual nodes. We used a 50% coefficient of variation (CV) on diet and Q:B values, and a 10% CV on biomass and P:B values.

The EcoPath model provided a range of options for autobalancing based either on minimizing maximum ecotrophic efficiencies, minimizing the sum of excess EEs, or minimizing the current EE. We chose the first two options simultaneously. Additionally, we used the Ecopath pedigree table to set confidence values for biomass, P:B, Q:B, diet and catch for autobalancing (Table 24.1). After examining several runs, the group decided that the pedigree approach was more desirable since it provided a way to weight the data sources with their relative degree of confidence.

Next, we began an iterative process whereby we modified the input/initial matrix and attempted to rebalance the network, primarily keying off EE < 1. For the initial Ecopath runs, P:C anomalies (P:C >0.5) appeared to be the result of low consumption values rather than high production values. Using autobalancing based on ecotrophic efficiencies (EEs) worked well without causing major changes to network structure.

Large-scale changes were necessary to for gelatinous zooplankton, squid, demersal omnivores, macrobenthos - other, and shrimp. We reduced the C:B ratio, diet composition, and B for gelantinous zooplankton; C:B and P:B of demersal ominivores; C:B of macrobenthos mollusks; B and C:B of macrobenthos – other; diet composition of predators of small pelagics; and P:B and B of shrimp.

Since the balancing approach was iterative, we had to ask: When do we have a balanced model? The model was considered sufficiently balanced when we reran it starting at the solution and verified that it provided the same solution, conditioned upon minimizing EE via several numerical solution methodologies.

### EcoNetwrk Considerations

For the EcoNetwrk model, we used an iterative approach similar to the one used for Ecopath. Repeated use of the balancing protocol (DATBAL, similar to AUTOBAL in Ecopath) was required to find a more global solution that would be responsive to input parameter changes.

The major consideration was to “close the loop” in EcoNetwrk by ensuring that the detrital node received unassimilated consumption from the other nodes in the network. We took the unassimilated fractions of all the consumptive flows (portions relegated to detritus), summed them and made microbial respiration equal to that sum. We also added 15% of primary production (phytoplankton direct contribution to detritus) to that sum to account for that flow, and the model then seemed to be more solvable.

Once these solutions were implemented, we carried out an iterative balancing process. For this we modified the input data matrix and attempted to rebalance the network primarily by keying off the R:C ratio. As a caveat, biomasses and C:B ratios seemed reasonable, but assimilation efficiencies (AE) were all >0.9. Again, the R:C ratio was a useful constraint in solving these multiple concerns.

Significant changes to gelatinous zooplankton (B, C:B); macrobenthos - other (B, R:B, C:B); larval fish (B); and shrimp (B, C:B, R:B) were initially required before we even came close to achieving network balance. These are similar to network nodes requiring similar changes in the EcoPath model version, our prebalance, and are noted as groups with lower data certainty (Table 24.1). We then modified megabenthos filterers, macrobenthos mollusks, medium pelagics, demersal omnivores, small pelagics anadromous, and small copepods.

## Diagnostics

The input matrices and some diagnostic measures we used are provided in Appendix 1. Foremost is that once we identified a major constraining factor based upon the underlying assumption of the model software (i.e., EE or R:C), other key ratios were then examined. These model outputs must make sense relative to expert knowledge among EMAX personnel, and be consistent with literature values. In this way our exercise was unique; the large amount of extant, reasonable quality data allowed for a model reality check.

Many of these diagnostics (e.g., mean trophic level, ascendancy, input-output analysis, size spectra metrics, imbalance sum, pyramidal structure, connectance, etc.) might form the basis for indicators to be translated and incorporated into ecosystem approaches to fisheries management.

## Scenarios

Once a balanced, baseline model was obtained for both software packages, various changes were made to the network (e.g., multiplying key nodes by various scalars such as 1/100th, ½, 10, 100, singularly and in various combinations), which was then rebalanced. Although we have preliminary balanced networks for all four subregions, we chose to initially evaluate the various scenarios for only one of them, the Gulf of Maine. We executed the scenario rebalancing as a psuedo-dynamic modeling process to see where the perturbed system would redistribute biomass and production after the changes were imposed. We executed all scenarios in both model packages.

For comparisons across regions and across scenarios, we examined a set of network, cybernetic, and ecological statistics common to both software packages. However, to highlight the role of small pelagics in particular, we primarily evaluated a set of biomass ratios and similar indicators (Link 2005).

The bulk of the results and interpretation of these (and other) scenarios and the model balancing exercise are intended for presentation in other venues, but the main highlights are:

- Overall changes to major fish groups resulted in compensating changes to other fishes.
- The upper trophic levels (TLs) had minimal impact on the rest of the network.
- Changes to marine mammals sometimes had a counterintuitive effect on fish.
- Categorically across all scenarios, gelatinous zooplankton and macrobenthos decreased whereas most other zooplankton increased. Could that be a possible hardwiring artifact of the network structure?
- In terms of biomass, production, energy flows, and importance for upper trophic levels, small pelagics are a keystone group in this ecosystem.

## References and Bibliography

Allesina, S; Bondavalli, C. 2003. Steady state of ecosystem flow networks: a comparison between balancing procedures. *Ecol. Model*. 165:221-229.

Allesina, S; Bondavalli, C. 2004. WAND: an Ecological Network Analysis user-friendly tool. *Env. Model. Software* 19:337-340.

Allesina, S; Bodini, A. 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading exctinctions. *J. Theor. Biol*. 230(3);351-358.

Allesina, S; Ulanowicz, RE. 2004. Cycling in ecological networks: Finn's index revisited. *Comput. Biol. Chem*. 28(3):227-233.

Baird, D; Glade, JM: Ulanowicz, RE. 1991. The comparative ecology of six marine ecosystems. *Philos. Trans. R. Soc. Lond*. 333:15-29.

Baird, D; Ulanowicz, RE. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr*. 59:329-364.

Baird, D; Ulanowicz, RE. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Mar. Ecol. Prog. Ser*. 99:221-237.

Bax, NJ. 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals on six marine ecosystems. *ICES* (Int. Counc. Explor. Sea) *Mar. Sci. Symp.* 193:217-224.

Brown, MT. 2004. A picture is worth a thousand words: energy systems language and simulation. *Ecol. Model*. 178: 83-100.

Brown, MT; Buranakarn, V. 2003. Energy indices and ratios for sustainable material cycles and recycle options. *Resources Conserv. Recycl*. 38:1-22.

Brown, MT; Herendeen, RA. 1996. Embodied energy analysis and energy analysis: a comparative view. *Ecol. Econ*. 19:219-235.

Brown, MT; McClanahan, TR. 1996. Energy analysis perspectives of Thailand and Mekong River dam proposals. *Ecol. Model*. 91(1-3):105-130.

Brown, MT; Ulgiati, S. 1999. Energy evaluation of the biosphere and natural capital. *Ambio* 28(6):486-493.

Brown, MT; Ulgiati, S. 2004a. Energy quality, energy, and transformity: H.T. Odum's contributions to quantifying and understanding systems. *Ecol. Model*. 178:201-213.

Brown, MT; Ulgiati, S. 2004b. *Energy analysis and environmental accounting. Encyclopedia of Energy, Volume 2*. New York, NY: Elsevier.

Bodini, A. 1991. What is the role of predation on stability of natural communities? A theoretical investigation. *BioSys*. 26:21-30.

Bodini, A. 1996. Uncertainty and resource exploitation: exploration based on qualitative modeling. *Statist. Appl*. 8 (1):185-199.

Bodini, A. 1998. Representing ecosystem structure through signed digraphs. Model reconstruction, qualitative predictions and management: the case of a freshwater ecosystem. *Oikos* 83:93-106.

Bodini, A. 2000. Reconstructing trophic interactions as a tool for understanding and managing ecosystems: application to a shallow eutrophic lake. *Can. J. Fish. Aq. Sci*. 57:1999-2009.

Bodini, A; Bondavalli, C. 2002. Toward a sustainable use of water resources. A whole-ecosystem approach using network analysis. *Int. J. Env. Pollut*. 15:463-485.

Bodini, A; Giavelli, G. 1989. The qualitative approach in investigating the role of species interactions on stability of natural communities. *Biosys*. 22:289-299.

Bodini, A; Giavelli, G. 1992. Multicriteria analysis as a tool to investigate the compatibility between conservation and development on Salina Island, Aeolian Archipelago, Italy. *Env. Manag*. 16:633-652.

Bodini, A; Giavelli, G; Rossi, O. 1994. The qualitative analysis of community food webs: implications for wildlife management and conservation. *J. Env. Manag*. 41:49-65.

Bodini, A; Puccia, CJ; Giavelli, G. 1990. Understanding resource management strategies under different ecological constraints: the case of oligotrophic and eutrophic lakes. *In*: Ravera, O. ed. *Terrestrial and Aquatic Ecosystems: Perturbation and Recovery*. London, UK: Ellis Horwood; p. 583-592.

Bodini, A; Ricci, A; Viaroli, P. 2000. A multi-methodological approach for the sustainable management of perifluvial wetlands of the Po river (Italy). *Env. Manag.* 26:59-72.

Bondavalli, C; Naldi, M; Christian, RR. 1998. Cs-137 circulation in an eutrophic lagoon: a modeling approach. *Ver. Internat. Verein. Limnol*. 26:1422-1425.

Bondavalli, C; Ulanowicz, RE. 1999. Unexpected effects of predators upon their prey: the case of the American alligator. *Ecosys*. 2: 49-63.

Bondavalli, C; Ulanowicz, RE; Bodini, A. 2000. Insights into the processing of carbon in the South Florida Cypress Wetlands: a whole-ecosystem approach using network analysis. *J. Biogeog*. 27:697-710.

Bundy, A. 2005. Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s. *Can. J. Fish. Aquat. Sci*. 62:1453-1473.

Christensen, V; Pauly, D. 1992. On steady-state modeling of ecosystems. *In*: Christensen, V; Pauly, D eds. *Trophic models of aquatic ecosystems*. ICLARM (Int. Center Liv. Aq. Resour. Manag.) *Conf. Proc.* 26*:*14-19.

Christensen, V; Pauly, D. 2004. Placing fisheries in their ecosystem context, an introduction. *Ecol. Model*. 172:103-107.

Cohen, EB; Grosslein, MD; Sissenwine, MP. 1982. Energy budget of Georges Bank. *Can. Spec. Publ. Fish. Aquat. Sci*. 59:95-107.

Fogarty, MJ; Murawski, SA. 1998. Large-scale disturbance and the structure of marine systems: Fishery impacts on Georges Bank. *Ecol. Appl*. 8(S1):S6-S22.

Giavelli, G; Bodini, A. 1990 Plant-ant-fungus communities investigated through qualitative modeling. *Oikos* 57: 357-365.

Giavelli, G; Bodini, A; Rossi, O. 1990. An extension of the complexity concept derived from the analysis of colonisation processes in small island environments. *Coenoses* 5: 1-5.

Grosslein, M; Langton, R; Sissenwine, MP. 1980. Recent fluctuations in pelagic fish stocks of the northwest Atlantic, Georges Bank region, in relation to species interactions. *Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer.* 177:374-404.

Heymans, JJ; Baird, D. 2000. Network analysis of the northern Benguela ecosystem by means of NETWRK and ECOPATH. *Ecol. Model*. 131:97-119.

Heymans, JJ; Ulanowicz, RE; Bondavalli, C. 2002. Network analysis of the South Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems. *Ecol. Model*. 149:5-23.

Hollowed, AB; Bax, N; Beamish, R; Collie, J; Fogarty, M; Livingston, P; Pope, J; Rice, JC. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES* (Int. Counc. Explor. Sea) *J. Mar. Sci.* 57:707-719.

Jollands, N; Lermit, J; Patterson, M. 2004. Aggregate eco-efficiency indices for New Zealand--a principal components analysis. *J. Env. Manag*. 73:293-305.

Jorgensen, SE. 1992. Exergy and ecology. *Ecol. Model*. 63:185-214.

Kang, D; Park, SS. 2002. Energy evaluation perspectives of a multipurpose dam proposal in Korea. *J. Env. Manag*. 66:293-306.

Kavanagh, P; Newlands, N; Christensen, V; Pauly, D. 2004. Automated parameter optimization for Ecopath ecosystem models. *Ecol. Model*. 172:141-149.

Larkin, PA. 1996. Concepts and issues in marine ecosystem management. *Rev. Fish Biol. Fish.* 6:139-164.

Lindeman, RL. 1942. The trophic-dynamic aspect of ecology. *Ecol*. 23:399-418.

Link, JS. 2005. Translation of ecosystem indicators into decision criteria. *ICES ICES* (Int. Counc. Explor. Sea) *J. Mar. Sci.* 62:569-576.

Mageau, MT ; Constanza, R; Ulanowicz, RE. 1998. Quantifying the trends expected in developing ecosystems. *Ecol. Model*. 112:1-22.

Monaco, M; Ulanowicz, RE. 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. *Mar. Ecol. Prog. Ser*. 161:239-254.

Morisette, L; Despatie, S-P; Savenkoff, C; Hammill, MO; Bourdages, H; Chabot, D. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). *Can. Tech. Rep. Fish. Aquat. Sci.* no. 2497; 100 p.

Odum, E. 2004. Energy analysis of shrimp mariculture in Ecuador: a review. *Ecol. Model.* 178:239-240.

Odum, HT. 1988a. Energy, environment and public policy: a guide to the analysis of systems. *UNEP* (United Nations Environment Program) *Regional Seas Report;* Study #95.

Odum, HT. 1988b. Self organization, transformity, and information. *Science* 242:1132-1139.

Odum, HT. 1996. *Environmental Accounting: Energy and Environmental Decision Making*. New York, NY: John Wiley & Sons.

Odum, HT. 2000. *Energy of Global Processes (Folio#2).* Gainesville, FL: Univ. of Florida Center Env. Pol.; 30 p.

Odum, HT; Arding, JE. 1991. *Energy Analysis of Shrimp Mariculture in Ecuador*. Narragansett, RI: University of Rhode Island Coastal Resources Center; 114 p.

Odum, HT; Brown, MT; Brandt-Williams, S. 2000. *Introduction and Global Budget (Folio#1)*. Gainesville, FL: Univ. of Florida Center Env. Pol.; 16 p.

Odum, HT; Odum, EC. 2000. *Modeling for All Scales: An Introduction of Systems Simulation*. San Diego, CA: Academic Press.

Odum, HT; Odum, EP. 2000. The energetic basis for valuation of ecosystem services. *Ecosys*. 3:21-23.

Savenkoff, C; Bourdages, H; Swain, DP; Despatie, S-P; Hanson, JM; Methot, R; Morissette, L; Hammill, MO. 2004. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). *Can. Tech. Rep. Fish. Aquat. Sci*. no. 2529; 111 p.

Savenkoff, C; Castonguay, M; Vezina, AF; Despatie, S-P; Chabot, D; Morisette, L; Hammill, MO. 2004. Inverse modelling of trophic flow through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. *Can. J. Fish. Aquat. Sci*. 61:2194-2214.

Savenkoff, C; Vezina, AF; Bundy, A. 2001. Inverse analysis of the structure and dynamics of the whole Newfoundland-Labrador Shelf ecosystem. *Can. Tech. Rep. Fish. Aquat. Sci*. no. 2354; 64 p.

Savenkoff, C; Vezina, AF; Roy, S; Klein, B; Lovejoy, C; Therriault, J-C; Legendre, L; Rivkin, R; Berube, C; Tremblay, J-E; Silverberg, N. 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 1. Seasonal variations. *Deep-Sea Res. II* 47(3-4):585-607.

Savenkoff, C; Vezina, AF; Smith, PC; Han, G. 2001. Summer transports of nutrients in the Gulf of St. Lawrence estimated by inverse modelling. *Estuar. Coast. Shelf Sci.* 52: 565-587.

Schneider, ED; Sagan, D. 2005. Into the Cool: Energy Flow, Thermodynamics and Life. University of Chicago Press; Chicago, Il.; 378 p.

Ulanowicz, RE. 1986. *Growth and development: ecosystems phenomenology.* New York, NY: Springer-Verlag.

Ulanowicz, RE. 1995. Trophic flow networks as indicators of ecosystem stress. *In*: Polis, GA; Winemiller, KO. eds. *Food webs: integration of patterns and* dynamics. New Yor, NY: Chapman and Hall; p. 358-368.

Ulanowicz, RE. 2000. Toward the measurement of ecological integrity. *In*: Pimentel, D; Westra, L; Noss, RF. eds. *Ecological Integrity: Integrating Environment, Conservation and Health*. Washington, DC: Island Press; p. 102-113.

Ulanowicz, RE. 2004. Quantitative methods for ecological network analysis. Comput. Biol. Chem. 28(5-6):321-339.

Ulanowicz, RE; Kay, JJ. 1991. A package for the analysis of ecosystem flow networks. *Environ. Software* 6:131-142.

Ulanowicz, RE; Platt, TC. 1985. Ecosystem theory for biological oceanography. *Can Bull. Fish. Aquatic Sci.* no. 213; 260 p.

Ulanowicz, RE; Wulff, F. 1991. Comparing ecosystem structures: the Chesapeake Bay and the Baltic Sea. *In*: Cole, J; Lovett, G; Findlay, S. eds. *Comparative analysis of ecosystems, pattern, mechanism, and theories*. New York, NY: Springer-Verlag.

Vezina, AF; Savenkoff, C. 1999. Inverse modeling of carbon and nitrogen flows in the pelagic food web of the northeast subarctic Pacific. *Deep-Sea Res. I*I 46(11-12): 2909-2939.

Vezina, AF; Savenkoff, C; Roy, S; Klein, B; Rivkin, R; Therriault, J-C; Legendre, L. 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. *Deep-Sea Res. II* 47(3-4): 609-635.

Walters, CJ; Christensen, V; Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish*. 7:139-172.

Whipple, SJ; Link, JL; Garrison, LP; Fogarty, MJ. 2000. Models of predation and fishing mortality in aquatic ecosystems. *Fish. Fish*. 1:22-40.

Table 24.1. Data pedigree for all nodes modeled in EMAX. Lower numbers or bluer colors are less certain/resolved estimates, and higher numbers or redder colors are more confident estimates (modified from a similar Ecopath module). B = Biomass, P:B = production, Q:B = consumption, Diet = diet composition, Catch = landed removals.

| Group | B | P:B | Q:B | Diet | Catch |
|---|---|---|---|---|---|
| Phytoplankton - primary producers | 5 | 5 | --- | --- | --- |
| Bacteria | 2 | 2 | 2 | 2 | --- |
| Microzooplankton | 2 | 2 | 2 | 2 | --- |
| Small Copepods | 4 | 3 | 3 | 2 | --- |
| Large Copepods | 4 | 3 | 3 | 2 | --- |
| Gelatinous Zooplankton | 3 | 2 | 2 | 2 | 0 |
| Micronekton | 3 | 2 | 2 | 2 | --- |
| Mesopelagics | 3 | 2 | 2 | 3 | --- |
| Macrobenthos - polychaetes | 4 | 3 | 3 | 2 | 0 |
| Macrobenthos - crustaceans | 4 | 3 | 3 | 2 | 0 |
| Macrobenthos - molluscs | 4 | 3 | 3 | 2 | 0 |
| Macrobenthos - other | 4 | 3 | 3 | 2 | 0 |
| Megabenthos - filterers | 4 | 3 | 3 | 2 | 4 |
| Megabenthos - other | 3 | 3 | 3 | 2 | 4 |
| Shrimp *et al.* | 5 | 3 | 3 | 2 | 5 |
| Larval and juvenile fish | 3 | 2 | 2 | 3 | 0 |
| Small Pelagics - commercial | 5 | 7 | 7 | 5 | 5 |
| Small Pelagics - other | 4 | 5 | 5 | 4 | 3 |
| Small Pelagics - squid | 4 | 5 | 5 | 4 | 5 |
| Small Pelagics - anadromous | 4 | 5 | 5 | 4 | 4 |
| Medium Pelagics (piscivores and other) | 4 | 5 | 5 | 5 | 5 |
| Demersals - benthivores | 5 | 5 | 7 | 5 | 5 |
| Demersals - omnivores | 5 | 5 | 7 | 5 | 5 |
| Demersals - piscivores | 5 | 5 | 7 | 5 | 5 |
| Sharks - pelagics | 3 | 4 | 4 | 4 | 3 |
| Sharks - coastal | 3 | 4 | 4 | 4 | 3 |
| HMS (highly migratory species) | 3 | 6 | 4 | 4 | 3 |
| Pinnipeds | 4 | 3 | 3 | 3 | 3 |
| Baleen Whales | 4 | 3 | 3 | 3 | 3 |
| Odontocetes | 4 | 3 | 3 | 3 | --- |
| Sea Birds | 4 | 3 | 3 | 4 | --- |
| Fisheries - demersal | --- | --- | --- | --- | 3 |
| Fisheries - pelagic | --- | --- | --- | --- | 3 |
| Discards | --- | --- | --- | --- | 3 |
| Detritus - POC | 2 | 1 | 1 | 1 | 1 |
| DOC | 2 | 1 | 1 | 1 | 1 |

🟦 Worse
🟦
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🟨
🟧
🟧
🟥 Better