The integrated assessment of critical ecosystem dynamics in a marine fishery

Jared Woollacott*

RTI International

July 1, 2015

This work couples a Biological General Equilibrium (BGE) model with a regional economic computable general equilibrium (CGE) model to analyze the economic consequences of thresholds, tipping points, and random events in a marine ecosystem. By varying the scale and persistence of harvesting and climate forcings along with exogenous shocks to primary resources (e.g. detritus stocks, primary productivity), I identify thresholds for stable population behavior within the ecosystem and how the approach and breach of these thresholds interact with the dependent economy.

The BGE model represents multiple adaptive species in an ecosystem by positing micro-behavioral bioenergetic optimization on the part of representative species members to drive ecosystem dynamics. Earlier work by Tschirhart and Finnoff [2, 6, 7] pioneered the concept of a general equilibrium approach to ecosystem modeling. The BGE approach expands on this work by providing a novel synthesis of three veins of theoretical biology literature, optimal foraging, bioenergetic optimization, and food web dynamics, in a setup that fully exploits the rich micro-behavioral features of a CGE models. The coherence of this synthesis within a single model is therefore supported by the theory of economic general equilibrium, which provides a method and framework for identifying feasible equilibria in conservative systems (i.e. systems that conserve a quantity such as energy or economic value). The BGE model makes a hard link between the micro bioenergetics and macro population-dynamics of ecosystems that remains underdeveloped in the literature.

The underlying bioenergetic optimization takes a measure of energetic surplus as the object of maximization, as is common in the theoretical biology literature. There is clear intuitive support for this measure in as much as it proxies for robustness against evolutionary selection pressures. That is, the less energetic surplus embodied within the species, the more threaten is its survival. Conversely, the better species are able to adaptively respond to their environment to generate surpluses, the better they will be able to propagate their ge-

^{*}Contact: jwoollacott@rti.org

netic material. While a number of ecosystem models have incorporated species adaptive responses, the responses to prey-densities tend to be uniform across prey (if multiple prey are modeled) and are not typically tied to the underlying bioenergetic trade-offs. Yet, critically, bioenergetically-optimal functional responses are a prominent feature of the broader theoretical biology literature and can be generalized for sensitivity to other environmental conditions not related to prey densities (e.g. temperature, ambient toxicity).

Species optimize by producing available energy (exergy) from consumption of prey and allocating it to support their activities and propagate their genes. After sacrifices to predators and metabolic "debts" from rest processes and activity are accounted, any remaining energy surplus is allocated to ending biomass, which is carried forward to the next period. Ending biomass might take the form of structural biomass, storage biomass [3], or offspring, with selection pressure forcing species toward an optimal allocation among these to maximize genetic propagation. Optimization is thought to occur at the genetic level, not the individual [1], so that phenotypic and behavioral adaptations are made to maximize the energetic surplus of the genetic kin as a whole or from the perspective of a representative species member.

The strength and novelty of the BGE model then lies in its capacity for endogenously modeling species adaptation to changing ecosystem dynamics and external forcings. Bioenergetic functions can be tuned to generate, as an outcome of the optimization, Holling behavioral responses [5] common to the biology literature. These responses drive the trophic links in the model. Feasible ecosystem equilibria are those population (scarcity) vectors that can simultaneously satisfy bioenergetic input (consumption) and output (production) as an optimum while also conserving system aggregates.

Given a well-grounded theoretical structure for the Biological General Equilibrium (BGE) model, I program and calibrate the model to an empirical data set of the marine ecosystem surrounding the Aleutian Islands. I use an Ecosim dataset with relatively high species resolution (approximately 30 species, [4]). The data must be pre-processed to satisfy the Biological Accounting Matrix (BAM) input-output balance requirements. Once calibrated, the BGE model can be used to examine a wide cast of shocks to the ecosystem. For example, Figure 1 shows the Aleutian marine ecosystem's population responses to stochastic perturbations of primary resources and harvesting rates.¹

With balanced BAMs, I calibrate the BGE model for the Aleutian ecosystem and a state-level economic CGE model using IMPLAN data to be run in tandem in a recursive-dynamic simulation of the interacting ecosystem and economy.² Fish population levels generated by the BGE model feed resource stocks for the CGE model on an annual basis. A baseline scenario is first run to establish a "business as usual" reference point for the interacting systems.

Given a set of exogenous shocks to the ecosystem, either from the surround-

¹The Aleutian species presented in Figure 1 include, for example: flatfish (FFS), zooplankton (ZPK), pelagics (PEL), halibut (HLB), orca whales (ORC), salmon (SAL).

 $^{^{2}\}rm IMPLAN$ Group, LLC provides state-level input-output data for economic modeling, see http://implan.com/.



Figure 1: Aleutian species population responses to stochastic perturbations

ing physical environment or harvesting demands from the economy, population dynamics and their impacts on economic activity and overall welfare will be reported. Ecosystem shocks to primary resources and harvesting rates will be varied to identify thresholds for critical population dynamics such as depensation and local extinction. The variation will be both monotonic and stochastic to assess how the level and variance of ecosystem shocks influence population and economic outcomes. Last, I show how economic and ecosystem outcomes differ when reduced form representations of the coupled system are used in lieu of the fully integrated BGE-CGE model.

In sum, the BGE model adapts extant optimization-based, input-output modeling techniques common to economics to a biophysical setting where bioenergetic optimization drives species' behavior from whose interactions emerge macroscopic equilibrium outcomes for the ecosystem. This modeling approach offers a valuable tool for the analysis of ecosystems, ecosystem services, and a variety of human-environment interactions. In particular, by coupling the BGE model with an economic CGE model I show how economic activity can both generate and respond to critical dynamics in the supporting marine ecosystem. The paper will demonstrate how the integrated assessment of coupled natural and economic systems can generate substantively distinct results from the independent assessment of either system by itself.

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