

INTRODUCTION

(Daniel Pauly and Villy Christensen)

Rationale For Mass-Balance (Trophic) Models

Over the last decades, there have been massive changes of the oceanic regime in the North Pacific. These changes have resulted in increase of some major resource species, notably several species of salmon off British Columbia (B.C.) and Alaska (Beamish and Bouillon 1993), and hake off B.C. (Pitcher, this vol.). Decreases in other species, e.g., lobsters in Hawai'i have been attributed to the same climatic changes (Polovina et al. 1994).

Oceanographers, fisheries scientists and marine biologists have been tracking these changes, sometimes together, more often separately. Their common goal has been to predict future oceanographic regimes and, based thereon, the likely futures of major resources species. This research has yielded excellent results.

However, the "trophic context" of key species in north Pacific ecosystems has been largely neglected, at least since T. Laevastu and colleagues' heroic attempt at a spatially-structured simulation model of the entire Bering Sea (see Laevastu and Larkins 1981). Trophic context, as defined here encompasses food consumption and requirements of key species, and their contribution to the diet of predators. Dealing with the trophic context of resource species provides powerful insights for estimation of biomasses and of the fluxes that occur

between them. It thus provides an independent way to validate published estimates of biomasses and/or fluxes.

However, most marine and fisheries scientists have to date preferred to work on single species, or on interactions among few species, rather than to model entire ecosystems. There are many reasons for this, but the most prevalent is that "ecosystems modeling" is perceived as a specialized and long-term activity, leading to large, unwieldy products, perhaps best illustrated by the Bering Sea model alluded to above.

Practical demonstrations of the power and versatility of the Ecopath approach may help to shift emphasis to whole-system attributes, increasingly required in an age of global change.

The Ecopath approach and software

The Ecopath approach is based on the work of J.J. Polovina (1984), of the US National Marine Fisheries Service (Honolulu Laboratory). The present authors, both then at the International Center for Living Aquatic Resources Management (ICLARM) in Manila, Philippines, developed and adapted Polovina's work to a user-friendly and versatile software package for personal computers. This software allows for rapid construction and verification of mass-balance models of ecosystems (Christensen and Pauly 1992a, 1992b).

The key steps to construct a model are to:

- i) Identify the area and period for which a model is to be constructed;
- ii) Define the functional groups (i.e., "boxes") to be included;

- iii) Enter a diet matrix defining all trophic linkages by expressing the fraction that each "box" in the model represents in the diet of its consumers;
- iv) Enter the food consumption, production/biomass ratio and/or biomass, and fisheries catches, if any, for each box;
- v) Balance the model, i.e., modify entries (iii & iv) until input = output for each box;
- vi) Compare model outputs (network characteristics, estimated trophic levels and other features of each box) with estimates for the same area during another period, or with outputs of the same model type from other, similar areas, etc.

These steps are simple provided that basic parameters are available. Numerous well-documented Ecopath applications to aquatic ecosystems already exist, ranging from aquaculture ponds and flooded rice paddies to shelf systems (see Pauly and Christensen 1993, and contributions in Christensen and Pauly 1993). Other models exist which represent the North Sea (Christensen 1995), and George's Bank. Indeed, the latter model was constructed by a group of Canadian scientists (from DFO and other institutions) during a workshop run by V. Christensen, similar to the one reported upon here, and held in St. John's in late 1993.

The workshop and its outputs

The workshop was held November 6-10, 1995, at the Fisheries Centre, UBC. There were some twenty-four participants: mainly members of the scientific community in

British Columbia, and the states of Alaska and Washington, US, Fisheries Centre faculty and graduate students. Dr. Polovina was invited for the workshop to benefit from his pioneering work on Ecopath, and more recently, on regime shifts in the North Pacific gyre (Polovina et al. 1994, 1995).

Identification of key scientists was helped by discussions of the mass-balance approach at the March 1995 UBC Fisheries Centre workshop on "Impact of Changes in North Pacific Oceanographic Regimes on Coastal Fisheries." Aside from the travel arrangements, preparatory work included the briefing prospective participants on the data to be assembled, the compilation of a preliminary database and assembling relevant publications. Also, the Ecopath "module" taught (by D.P.) in September-October 1995 at the Fisheries Centre as part of "Fish 504" used the Strait of Georgia as an example, thus preparing the students to participate in the workshop, which became an element of their course.

The first day of the workshop proper was devoted to a formal review of the concepts behind the Ecopath approach (Box 1) and informal presentations and discussions on its various features, both positive and negative. The following multi-authored text presents the following:

- Estimated "summer" biomasses of the major components in three marine ecosystems: the Alaska Gyre, on the shelf of Southern B.C., and in the Strait Georgia;
- Mass-balance models describing the trophic flows in these three ecosystems, and largely pertaining to the late 1980s;

- Parameter estimates for the construction of “winter” models for these same areas, and hence for studying seasonal cycles;
- A basis for comparisons with similar ecosystems in other parts of the world; and, most importantly:
- A basis for formulating hypotheses about the likely effect of future changes of oceanographic and/or fisheries regimes on food webs and

biomasses of key species in the three model areas .

We hope these results will be seen as useful by the scientific community in the Pacific Northwest, and contribute to a renaissance of studies linking ecological models and applied fisheries work. We also hope that the overview of ecosystems we present here will also lead to more consideration of local knowledge on their interrelationships of their component species (see Haggan, this vol.).

Box 1 Basic equations, assumptions and parameters of the Ecopath approach.

The mass-balance modelling approach used in this workshop combines an approach by Polovina and Ow (1983) and Polovina (1984, 1985) for estimation of biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem (the original "ECOPATH") with an approach proposed by Ulanowicz (1986) for analysis of flows between the elements of ecosystems. The result of this synthesis was initially implemented as a DOS software called "ECOPATH II", documented in Christensen and Pauly (1992a, 1992b), and more recently in form of a Windows software, Ecopath 3.0 (Christensen and Pauly 1995, 1996). Unless noted otherwise the word "Ecopath" refers to the latter, Windows version.

The ecosystem is modeled using a set of simultaneous linear equations (one for each group i in the system), i.e.

Production by (i) - all predation on (i) - nonpredation losses of (i) - export of (i) = 0, for all (i) .

This can also be put as

$$P_i - M2_i - P_i(1 - EE_i) - EX_i = 0 \quad 1)$$

where P_i is the production of (i) , $M2_i$ is the total predation mortality of (i) , EE_i is the ecotrophic efficiency of (i) or the proportion of the production that is either exported or predated upon, $(1 - EE_i)$ is the "other mortality", and EX_i is the export of (i) .

Equation (1) can be re-expressed as

$$B_i * P/B_i - \sum_j B_j * Q/B_j * DC_{ij} - P/B_i * B_i(1 - EE_i) - EX_i = 0$$

or

$$B_i * P/B_i * EE_i - \sum_j B_j * Q/B_j * DC_{ij} - EX_i = 0 \quad ..2)$$

where B_i is the biomass of (i) , P/B_i is the production/biomass ratio, Q/B_j is the consumption/biomass ratio and DC_{ij} is the fraction of prey (i) in the average diet of predator (j) .

Based on (2), for a system with n groups, n linear equations can be given in explicit terms:

$$B_1 P/B_1 EE_1 - B_1 Q/B_1 DC_{11} - B_2 Q/B_2 DC_{21} - \dots - B_n Q/B_n DC_{n1} - EX_1 = 0$$

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$$B_2 P/B_2 EE_2 - B_1 Q/B_1 DC_{12} - B_2 Q/B_2 DC_{22} - \dots - B_n Q/B_n DC_{n2} - EX_2 = 0$$

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$$B_n P/B_n EE_n - B_1 Q/B_1 DC_{1n} - B_2 Q/B_2 DC_{2n} - \dots - B_n Q/B_n DC_{nn} - EX_n = 0$$

This system of simultaneous linear equations can be solved through matrix inversion. In Ecopath, this is done using the generalized inverse method described by MacKay (1981), which has features making it generally more versatile than standard inverse methods.

Thus, if the set of equations is overdetermined (more equations than unknowns) and the equations are not consistent with each other, the generalized inverse method provides least squares estimates which minimize the discrepancies. If, on the other hand, the system is undetermined (more unknowns than equations), an answer that is consistent with the data (although not unique) will still be output.

Generally only one of the parameters B_i , P/B_i , Q/B_j , or EE_i may be unknown for any group i . In special cases, however, Q/B_j may be unknown in addition to one of the other parameters (Christensen and Pauly 1992b). Exports (e.g., fisheries catches) and diet compositions are always required for all groups.

A box (or "state variable") in an Ecopath model may be a group of (ecologically) related species, i.e., a functional group, a single species, or a single size/age group of a given species.