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On Steady-State Modelling of Ecosystems*

V. CHRISTENSEN and D. PAULY
International Center for Living
Aquatic Resources Management
MCPO Box 2631, 0718 Makati
Metro Manila, Philippines

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Abstract

This paper provides a brief description of the rationale behind steady-state modelling, and of the implementation of the ECOPATH II software system, a system for straightforward construction, parametrization, and balancing of steady-state trophic models of (aquatic) ecosystems. ECOPATH II is written for MS DOS computers and is available as a public domain software from the ICLARM Software Project.

ECOPATH II is structured around a system of linear equations initially proposed by J.J. Polovina and coworkers. Also, it incorporates routines for computation of several maturity and network flow indices proposed by various theoretical ecologists, notably the Odum brothers and R.E. Ulanowicz.

Modelling of Ecosystems

The word "model" has several meanings; for scientists and, more specifically, for biologists working at the ecosystem level, "models" may be defined as *consistent* descriptions, emphasizing certain aspects of the system investigated, as required to *understand* their function.

Thus, models may consist of a text ("word models") or a graph showing the interrelationships of the various components of a system. Models may also consist of equations, whose parameters describe "states" (the elements included in the models) and "rates" (of growth, mortality, food consumption, etc.) of the elements of the model.

The behavior of mathematical models is difficult (often impossible) to explore without computers. This is especially the case for "simulation models", i.e., those representations of ecosystems which follow, through time, the interactive behavior of the (major) components of an ecosystem.

Simulation models are difficult to build, and even more difficult to get to simulate realistically the behavior of a system over a long period of time, without "crashing" or "exploding", where populations go either extinct or grow without bound, respectively. This is one reason why most aquatic biologists shy away from constructing such models, or even from interacting with "modellers" (who, often being nonbiologists, may have scant knowledge of the intricate interactions between living organisms). Another reason is that one needs to be able to describe the dynamics of all key biological processes (growth, reproduction, mortality, etc.) to build realistic dynamic models. Obtaining sufficient knowledge to do this is difficult for most ecosystems.

However, "modelling" does not necessarily imply "*simulation* modelling". There are various ways of constructing quantitative models of ecosystems which avoid the intricacies of dynamic simulation modelling, yet still provide many of the benefits of fully-fledged modelling, *viz*:

- requiring the biologist/ecologist to review and standardize all available data on a given ecosystem and identify information gaps;
- requiring the would-be modeller to identify estimates (of states and/or rates) that are mutually incompatible, and which, if true, would prevent the system from maintaining itself (e.g., prey productions that are too low relative to assumed food requirements of predators);

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*Includes extracts from the ECOPATH II manual of Christensen and Pauly (1992a). ICLARM Contribution No. 831.

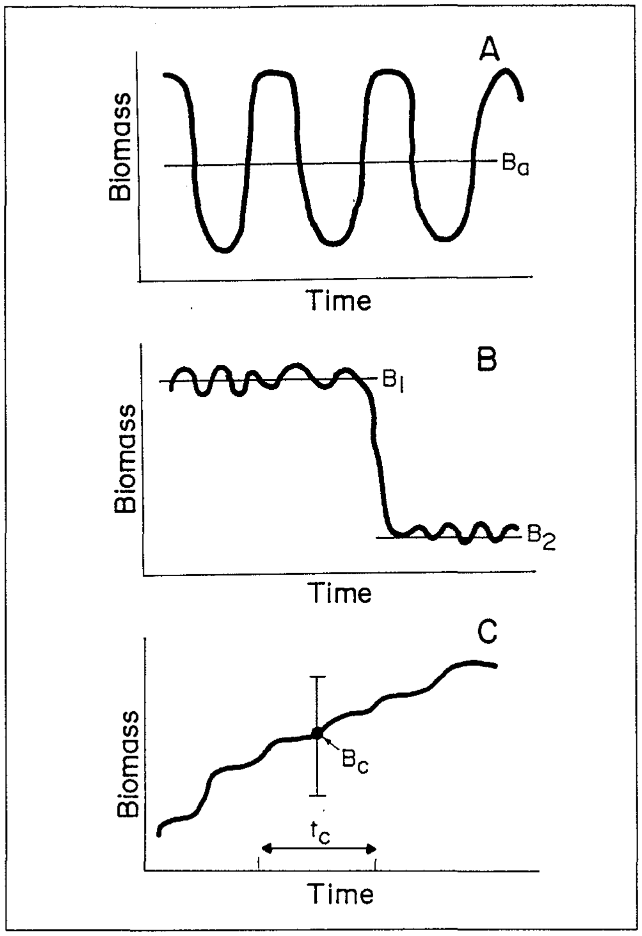

Fig. 1. Schematic representation of possible biomass trends in an ecosystem. (A) Strong, regular changes as, e.g., due to the succession of seasons, not well represented by an annual mean (B_a). (B) Rapid transition between two stable states, of which each is well represented by its own mean (B_1, B_2). (C) Example of a biomass that does not reach equilibrium. During a brief period (t_c), this biomass can be represented by a single value (B_c) whose confidence interval will usually bracket the change of biomass during the interval t_c.

- requiring the same would-be modeller to interact with specialities other than her/his own, e.g., a plankton specialist will have to either cooperate with fish biologists and other colleagues working on various consumer groups, or at least read the literature they produce.

To avail of these and other related advantages without having to get involved in simulation modelling, one's models can be limited to describing "average" (or "steady-state") states and rates. This limitation, as we shall see, is not as constraining as it may appear at first sight. It is consistent with the work of most aquatic biologists, whose state and rate estimates also represent "averages", applying to a certain period (although this generally is neither stated by the authors, nor realized by the readers).

The approach we propose is to use states and rates estimated for single species in a multispecies context to describe aquatic ecosystems in rigorous, quantitative terms, during the (arbitrary) period to which the state and rate estimates apply (Fig. 1).

In many cases, the period considered will be one (typical) year, with the state and rate estimates used for model construction pertaining to different years. Such models may represent a decade or more, during which little changes have occurred.

When ecosystems have undergone massive changes, two or more models may be needed, representing the ecosystem before, (during) and after the changes (Fig. 1). As an example, three models of the Peruvian upwelling ecosystem were constructed, covering different periods before and after the collapse of the anchoveta fisheries (Jarre et al. 1991). Other examples of this can be found in this volume for Lake Tanganyika, Lake Victoria, and Lake Turkana, all in Africa.

When seasonal changes are to be emphasized, different models may be constructed for each season, or for extreme situations ("summer" *vs*. "winter"). As an example, Baird and Ulanowicz (1989) constructed four models describing the seasons in Chesapeake Bay and one "average" model to represent the whole year. Likewise, Jarre and Pauly (this vol.) describe the dynamics of the annual cycle of the Peruvian upwelling system using 12 steady-state models, each representing a monthly period.

The same idea can be applied to aquaculture situations, where a pond and its producers and consumers can be described for instance at the beginning, midpoint and end of a growing season. Alternatively, a pond can be modelled as the average of such states. Ruddle and Christensen (this vol.) illustrate this approach.

Judicious identification of periods long enough for sufficient data to be available, but short enough for massive changes not to have occurred, will thus solve most problems associated with the lack of a time dimension in "steady-state" models.

The ECOPATH II Model

The ECOPATH II system combines an approach by Polovina (1984a) for estimation of biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem with an approach proposed by Ulanowicz (1986) for analysis of flows between the elements of ecosystems (Christensen and Pauly 1992b).

As described by Pauly et al. (this vol.), the core routine of ECOPATH II is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984b, 1985).

The ecosystem is modelled 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

$$P_i - M2_i - P_i\,(1\text{-}EE_i) - EX_i = 0 \qquad ...1)$$

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

$$B_i{*}PB_i - \sum_{j=1}^{n} B_j{*}QB_j{*}DC_{ji} - PB_i{*}B_i\,(1\text{-}EE_i) - EX_i = 0$$

or

$$B_i{*}PB_i{*}EE_i - \sum_{j=1}^{n} B_j{*}QB_j{*}DC_{ji} - EX_i = 0 \qquad ...2)$$

where B_i is the biomass of *(i)*, PB_i is the production/biomass ratio, QB_i is the consumption/biomass ratio and DC_{ji} 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,

$$B_1PB_1EE_1\text{-}B_1QB_1DC_{11}\text{-}B_2QB_2DC_{21}\text{-}...\text{-}B_nQB_nDC_{n1}\text{-}EX_1 = 0$$
$$B_2PB_2EE_2\text{-}B_1QB_1DC_{12}\text{-}B_2QB_2DC_{22}\text{-}...\text{-}B_nQB_nDC_{n2}\text{-}EX_2 = 0$$

:

:

$$B_nPB_nEE_n\text{-}B_1QB_1DC_{1n}\text{-}B_2QB_2DC_{2n}\text{-}...\text{-}B_nQB_nDC_{nn}\text{-}EX_n = 0$$

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

For example, 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 underdetermined (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, PB_i, QB_i, or EE_i may be unknown for any group i. In special cases, however, QB_i may be unknown in addition to one of the other parameters (Christensen and Pauly 1992a). Exports and diet compositions are always required for all groups.

The Energy Balance of a Box

A box, in an ECOPATH II model, may be a group of (ecologically) related species, a single species, or a single size/age group of a given species.

In a "steady-state" model, the energy input and output of all living groups must be (or are) balanced, by definition.

The basic ECOPATH equation (1) includes only the production of a box. Here production equals predation mortality plus export plus other mortality. When balancing the energy flow of a box, other flows should be included. Thus,

Consumption = production + respiration + unassimilated food

From this the respiration can be estimated as a difference (but see below).

Parametrization

The data requirements of steady-state models are very limited in comparison to those of simulation models. At the same time, steady-state models are very useful for making summaries of available data and trophic flows in a system. Also, and quite importantly, these models help identify gaps in one's knowledge about an ecosystem. Together, this makes steady-state models a good starting point for ecosystem modelling.

Consumption

There are various approaches for obtaining estimates of consumption/biomass ratio (QB); they may be split into (i) analytical methods and (ii) holistic methods.

(i) The analytical methods involve estimation of ration, pertaining to one or several size/age classes, and their subsequent extrapolation to a wide range of size/age classes, representing an age-structured population exposed to a constant or variable mortality.

The required estimates of ration are obtained from laboratory experiments, from studies of the dynamics of stomach contents in nature (Jarre et al. 1991; see Fig. 2), or by combining laboratory and field data (Pauly 1986).

(ii) The existing holistic methods for estimation of QB are empirical regressions for prediction of QB from some easy to quantify characteristics of the animals for which the QB values are required (Palomares and Pauly 1989; Pauly et al. 1990; Palomares 1991; Pauly et al., this vol.).

Production

Production includes all matter elaborated by a group (whether it is ultimately eaten, fished or dies of other causes) over the period considered. Total

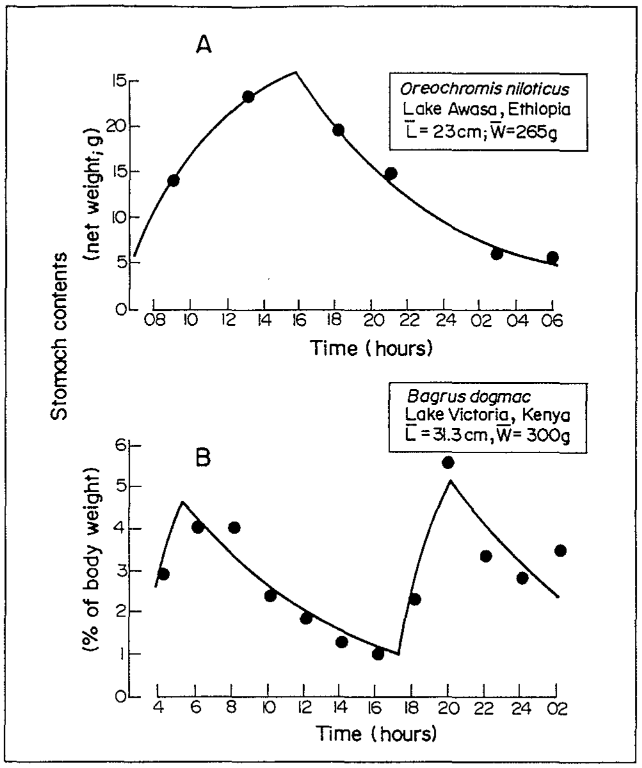

Fig. 2. Two daily cycles of stomach contents of African fishes (from Palomares 1991), fitted by means of the MAXIMS software of Jarre et al. (1990). (A) *Oreochromis niloticus* (Cichlidae), based on data in Getachew (1987). Note single feeding period, from 7 to 16 hours. (B) *Bagrus dogmac* (Bagridae), based on data in Okach and Dadzie (1988). Note two feeding periods per day, at dawn and dusk, as often occurs in piscivores (Hobson et al. 1981).

mortality, when constant, is equal to production over biomass. Therefore, in steady-state models, it is safe to treat estimates of total mortality (Z) as equivalent to the production/biomass ratio (P/B) (Allen 1971).

Predation

In a trophic model such as constructed by ECOPATH II, it is predation that links the groups in a system. Thus, what is consumption for one group is mortality (production) for its prey. Therefore, information on predation is important for understanding the dynamics of ecosystems. Unfortunately, properly presented information on diet composition is sparse - fish population dynamics has traditionally treated fish populations as if they were independent, and a large part of the available information on diet compositions is expressed on a "per cent occurrence" or "point" basis or as "dominance", all of which are of little use for quantification of diets. What are needed are measures based on energy, weight or volume.

For quantified ecosystem models such as ECOPATH II, the diet compositions should be expressed as the proportion (weight, volume or energy) each prey constitutes to the overall diet.

Respiration

As mentioned above, respiration is estimated by ECOPATH II as a difference, and hence is not a required parameter. If, however, explicit estimates of respiration are available, these can be used for "calibration", i.e., a model's inputs can be modified until, for any given box, the computed respiration matches the available estimate; this approach makes it possible for another parameter of that box, e.g., PB, to be unknown.

Network Flow Indices

The ECOPATH II software links concepts developed by theoretical ecologists, especially the theory of Ulanowicz (1986), with those used by biologists involved with fisheries and aquaculture management. The following section gives a brief account of some of the concepts from theoretical ecology that are included in ECOPATH II.

Ascendency is a measure of the average mutual information in a system, scaled by system throughput. These quantities are derived from information theory (Ulanowicz 1986; Ulanowicz and Norden 1990). If one knows the location of a unit of energy, the uncertainty of where it will go next is reduced by an amount known as the "average mutual information",

$$I = \Sigma_{ij}\ f_{ij}\ Q_i\ \ \log(f_{ij}/\Sigma_k(f_{kj}\ Q_k)),$$

where, if T_{ij} is a measure of the energy flow from j to i, f_{ij} is the fraction of the total flow from j that is represented by T_{ij}, or

$$f_{ij} = T_{ij}/\Sigma_k\ T_{kj}.$$

Q_i is the probability that a unit of energy passes through i, or

$$Q_i = \Sigma_k\ T_{ki}\ /\ \Sigma_{lm}\ T_{lm}.$$

I is a probability and is scaled by multiplication with the total throughput of the system, T, where

$$T = \ \Sigma_{ij}T_{ij}.$$

Thus,

$$A = T * I,$$

where A is called "ascendency". There is an upper limit for the size of the ascendency, estimated from

$$C = H * T,$$

where C is called "development capacity" and H is called "statistical entropy" and is estimated from

$$H = - \Sigma_i Q_i \log Q_i.$$

The difference between capacity and ascendency is called "system overhead". This provides a limit for the increase of ascendency and reflects the system's "strength in reserve" from which it can draw to meet unexpected perturbations (Ulanowicz 1986).

Ascendency, overheads and capacity can all be split into contributions from imports, internal flow, exports and dissipations (respiration). These contributions are additive; examples can be found in several of the contributions in this volume.

The unit for these measures is "flowbits", or the product of flow (e.g., $t \cdot km^{-2} \cdot year^{-1}$) and bits, an information unit corresponding to the amount of uncertainty associated with a single binary decision.

Trophic Aggregation

In addition to including a routine for calculating group-specific fractional trophic levels, as suggested by Odum and Heald (1975), we have included a routine in the ECOPATH II system that aggregates the entire system into discrete trophic levels *sensu* Lindeman (1942). This routine is used by a number of the authors in this volume, and is based on an approach suggested by Ulanowicz (in press) which reverses the routine for calculation of fractional trophic levels. For example, if a group obtains 40% of its food as a herbivore and 60% as a first-order carnivore, 40% and 60% of the flow through the group are attributed to the herbivore level and the first consumer level, respectively.

Based on these computations, the efficiency of transfer between discrete trophic levels can be calculated as the ratio of the flow that is transferred from one trophic level to the next (or to the fishery) and the throughput at the trophic level.

Mixed Trophic Impacts

Leontief (1951) developed a method to quantify the direct and indirect interactions of various sectors of the economy of the USA, using what has since been called the Leontief matrix. This was first used in ecology by Hannon (1973) and Hannon and Joiris (1989) to assess the impact of any group in a system on all other groups.

Ulanowicz and Puccia (1990) developed a similar approach, and a routine based on their method has been incorporated in the ECOPATH II system. Examples of the use and interpretation of mixed trophic impacts are given in a number of the contributions in this volume.

Conclusion

We hope that the rationale presented in this paper, together with the other contributions in this volume, will help establish the potential of steady-state modelling as a tool to improve our understanding of ecosystems, especially for data-sparse areas.

ECOPATH II, and forthcoming new developments (Christensen 1991), will, we hope, build a bridge between methodologies commonly used by fisheries biologists and by theoretical ecologists.

Acknowledgement

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