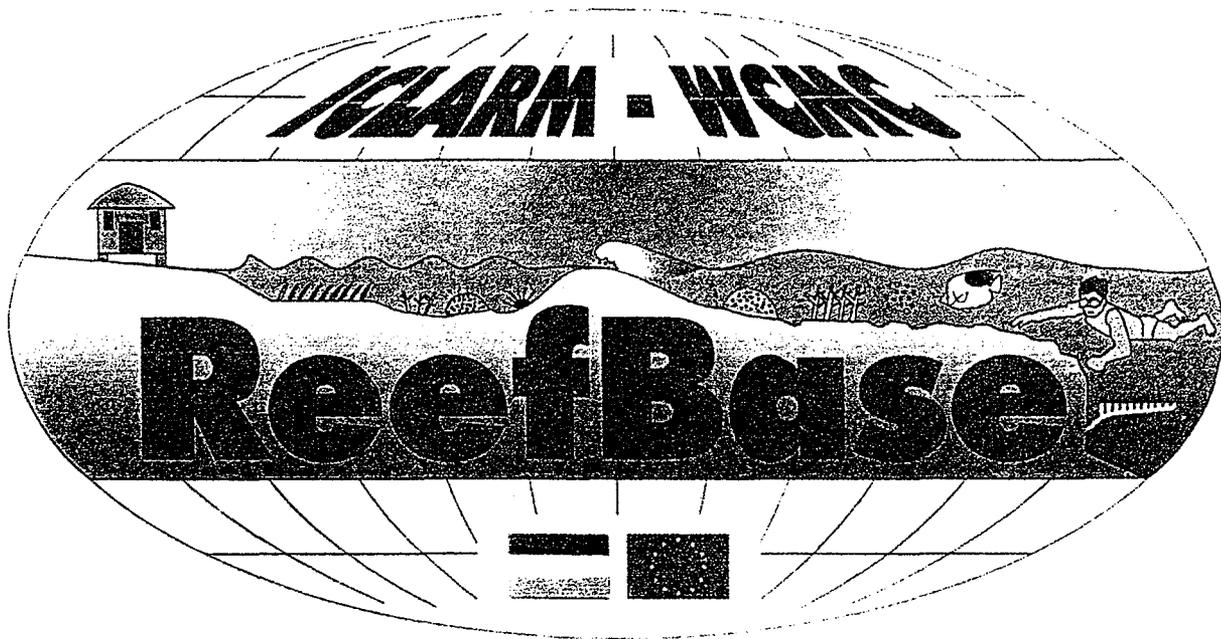


User's Guide



A Global Database on Coral Reefs and Their Resources

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J.W. McManus and M.C. Ablan
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ECOPATH Models of Coral Reef Ecosystems

Pauly, D. and Christiansen, V.

INTRODUCTION

The notion of “modelling coral reef ecosystems” may appear sacrilegious to those who believe that the complexity and variability of coral reefs defy modelling, especially using models of the sort advocated below. Whatever one’s view of modelling, one cannot fail to note, however, that lots of coral reef researchers do fieldwork and publish their results based on the (tacit) assumption that their rate and state estimates (e.g., production of some invertebrate, standing stock of some fish) reflect some aspect of reality, for at least a certain (if generally unstated) period.

This work would greatly improve if one were to apply, to various, well-studied reefs, quantitative approaches through which an assessment can be made of how compatible such published state and rate estimates are, i.e., whether they lead to the balance of mass transfers that must happen in real systems and which can be used to estimate “missing values”.

One such approach is ECOPATH, described in the following sections, with some emphasis on coral reefs. This is preceded, however, by a few clarifications on modelling itself.

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 realistically track the behavior of a system over a long period of time.

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 benefits *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 the assumed food requirements of predators);
- ✦ requiring the same would-be modeller to interact with specialties 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" states and rates. This limitation is not as constraining as it may appear at first sight. It is consistent with the work of most aquatic biologists including coral reef researchers, 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).

Thus, the approach proposed here 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.

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 (e.g., a coral reef before and after the development of a fishery).

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 lack of a time dimension in two such "average" models.

THE ECOPATH MODEL

Trophic models of ecosystems can be constructed most straightforwardly using a set of simultaneous linear equations (one for each group (*i*) in the system), i.e.,
 Production by (*i*) - all predation on (*i*) - non predation losses of (*i*) - export of (*i*) = 0,
 for all (*i*).

This can also be put as

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

where P_i is the production of (*i*), $M2_i$ is the predation mortality of (*i*), EE_i is the Ecotrophic Efficiency of (*i*), $(1 - EE_i)$ is the "other mortality", and EX_i is the Export of (*i*).

Equation (1) can be re-expressed as

$$B_i P/B_i - \sum_{j=1}^n B_j * Q/B_j DC_{ji} - P/B_i * B_i (1-EE_i) - EX_i = 0$$

or

$$B_i P/B_i - EE_i - \sum_{j=1}^n B_j * Q/B_j * DC_{ji} - EX_i = 0 \quad \dots 2)$$

where B_i is the biomass of (i), P/B_i is the production/biomass ratio, Q/B_i is the consumption/biomass ratio and DC_{ji} is the fraction of prey (i) in the average diet of predator (j). This leads to a system of linear equations which can be easily solved using matrix inversion.

Generally in ECOPATH, only one of the parameters B_i , P/B_i , Q/B_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. 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 an average, or better "mass-balance" 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 (see below).

PARAMETRIZATION

The data requirements of mass-balance models are very limited. At the same time, these models give a summary of the available data and of the trophic flows in the system. Also, and quite importantly, these models help identify gaps in one's knowledge about an ecosystem.

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.

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- (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 (Jarre et al. 1991; Pauly 1986).
 - (ii) The existing holistic methods for estimation of Q/B are empirical regressions for prediction of Q/B from some easy to quantify characteristics of the animals for which the Q/B values are required (Palomares and Pauly 1989).

Production

Production ($P = B_r \cdot (P/B)_i$) includes all matter elaborated by a group (whether it is ultimately eaten, fished or dies of other causes) over the period considered. Total 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 (Allen 1971).

Predation

In a trophic model such as constructed by ECOPATH, it is predation that links the groups in a system. Thus, what is consumption for one group is mortality 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 which 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 "percent 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 weights or volumes, i.e. as the proportion (weight or volume) each prey constitutes to the overall diet.

Respiration

As mentioned above, respiration is estimated by ECOPATH as a difference, and hence is not a required parameter. If, however, explicit estimation of respiration are available, they 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., P/B, to be unknown.

TROPHIC AGGREGATION

In addition to including a routine for calculating trophic levels, the ECOPATH system includes a routine that aggregates the entire system into discrete trophic levels, i.e., 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).

OTHER FEATURES OF ECOPATH

Trophic models such as constructed by ECOPATH allow a surprisingly large number of inferences to be drawn from their flow structure (see contributions in Christensen and Pauly 1993), and the software itself (ECOPATH 3.0) includes help messages that define the relevant concepts, and describe the routines that implement them.

ECOPATH Applications to Coral Reefs

To date (May 1996) ECOPATH has been applied to six coral reef systems *viz.*:

- ✦ French Frigate Shoals (Polovina 1984);
- ✦ Virgin Islands (Opitz 1991 and in press);
- ✦ Fringing Reefs, French Polynesia (Arias-González 1993);
- ✦ Bareer Reef, French Polynesia (Arias-González 1993);
- ✦ Bolinao Reef Flat, Philippines (Aliño et al. 1993);
- ✦ Looe Key Reef, Florida (J. Venier and D. Pauly, *MS*)

The ReefBase CD-ROM is distributed with ECOPATH files for the first five of these models, representing a wide range of coral reef system types, and which can be easily modified to represent other coral reefs.

Although the ECOPATH approach was initially developed for application to coral reef systems (Polovina 1984), subsequent applications to coral reefs were the results of work by direct collaborators, and or graduate students of V. Christensen and D. Pauly, suggesting that coral reef scientists -- as opposed, e.g., to fisheries scientists in general, or to freshwater biologists - may still have reservations about the ECOPATH approach. Yet it is built around two propositions about which few would be able to argue:

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- ✦ that in a coral reef, as in any other ecosystem, mass-balance must exist, i.e., that the biomass produced by the components of the ecosystem must be either consumed within the ecosystem, exported or otherwise accounted for, and
 - ✦ that the biomass and rates (of production, mortality and consumption) reported in published accounts of single species within ecosystems must be compatible with the biomass and rates reported for their preys AND their predators, for at least the period stated or implied in relevant publications (Pauly and Christensen 1994). One reason for the reservations about the ECOPATH approach may be the initial emphasis, in papers based on this approach, on the *equilibrium* or *steady-state* assumption seemingly implied in the resulting models.

This assumption, in fact, is not really required, as long as mass balance is retained. Thus, the biomass of a species or group at the end of the period covered by a model does not need to be the same as at the beginning. Neither is it necessary for seasonal changes of biomass, production or food consumption to be ignored: they can be explicitly accounted for.

The latest (Windows) version of ECOPATH includes routines which allow for considering such changes, and more will follow, e.g., to facilitate the construction of seasonal models. Also, the Windows version, while capable of reading and analyzing files generated with the earlier, DOS version, incorporates a new Monte Carlo simulation routine, as required, e.g., to evaluate the precision of outputs in a (semi-)Bayesian context (Christensen and Pauly 1995). These routines can be applied to all forthcoming coral reef models, e.g., to the model of Looe Key Reef, Florida presently being constructed by Mr. Judson Venier, a graduate student at the Fisheries Centre, UBC and his advisor (D. Pauly), and, retroactively, to the detailed models constructed e.g., by Opitz (1991) and Arias-Gonzalez (1993).

Future development of ECOPATH will involve incorporation of ECOSIM, a software for constructing simulation models, based on prior parametrization using ECOPATH II, and enabling tracking changes over time of the various interacting components of ecosystems e.g., coral reefs.

Another future development is the use of ECOPATH for tracking the fate within a quantified food web of radio-isotopes or pollutants, of which the former at least should be of interest to coral reef researchers in the Pacific.

Contact V. Christensen (villychr@centrum.dk) or D. Pauly (pauly@fisheries.com) for information on these developments.

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