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Aspects of the Ecopath approach and software relevant to the PWS model

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The Ecopath model was originally described J. Polovina (1984, 1995) of the U.S. National Marine Fisheries Service (Honolulu Laboratory). V. Christensen and D. Pauly, previously both at the International Center for Living Aquatic Resources Management (ICLARM), carried further the work (see Christensen and Pauly 1992a), and made it widely available in the form of a well-documented software for computers running MS-DOS (Christensen and Pauly 1992b), and later Windows (Christensen and Pauly 1995, 1996). Both versions allow rapid construction and verification of mass-balance models of ecosystems, as is clear from its present (1999) distribution to 1600 registered users in more than 90 countries.

The data requirements of an Ecopath model are expressed by its two 'Master Equations'. These equations are based on an assumption of mass-balance, and formulate that for any given group its production can be described as:

Production = Catches + Predation + Biomass accumulation + Net migration + Other mortality, …1

and further that

Consumption = Production + Unassimilated food + Respiration. …2

The first Master Equation is crucial in linking predator and prey in a system. Re-expressed and -arranged the equation reads,

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i \quad \ldots 3$$

where B_i and B_j are biomasses (the latter pertaining to all consumers of i);

P/B_i is the production/biomass ratio, equivalent to total mortality (Z) under most circumstances (Allen 1971);

EE_i is the ecotrophic efficiency, or the fraction of production (P= B*(P/B)) that is utilized within the system (including net migration and biomass accumulation);

Y_i is equal the fisheries catch per unit area and time (i.e., Y = F*B);

Q/B_j the food consumption per unit biomass of j; and

DC_{ji} the contribution of i to the diet of j (see also Box 1);

BA_i is the biomass accumulation of I (positive or negative, flow rate with units of energy per unit area and time);

NM_i is the net migration of I (emigration less immigration) with unit of energy per unit area and time.

An important aspect facilitating construction of an Ecopath model is that P/B under most circumstances corresponds to total instantaneous mortality rate (Z) in most circumstances (Allen 1971). There are several ways to estimate production (and P/B) directly, however, the combination of cohort-specific abundance and growth data required for many of these methods is usually difficult to assemble. Thus, Allen's formal demonstration of the relationship between P/B with Z is extremely useful, as numerous methods exist, in fisheries science for the estimation of Z from catch-at-age (Ricker 1975), length-frequency (Pauly and Gayanilo 1997), or other data (Pauly 1984).

An attribute of the Ecopath approach is that all of the parameters of its first master equation are amenable to direct estimation, except the ecotrophic efficiency, which is thus often left as the unknown to be estimated when the master equation is solved.

The steps involved in construction of an Ecopath model consist essentially of:

(i) Identification of the area and period for

which a model is to be constructed;
(ii) Definition of the functional groups (i.e., 'boxes') to be included;
(iii) Entry of a diet matrix, expressing the fraction that each 'box' in the model represents in the diet of its consumers;
(iv) Entry of food consumption rate, of production/biomass ratio or of biomass, and of fisheries catches, if any, for each box;
(v) Balance the model, or modify entries (iii and iv) until input = output for each box;
(vi) Analyze model outputs (e.g., system characteristics, estimated trophic levels) including simulations of functional responses to disturbances and other changes;

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

The mass-balance modelling approach documented in this report 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 3.1' (Christensen and Pauly 1995, 1996) and Ecopath with Ecosim (Pauly 1998, Walters et al., in press). 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

$$P_i - M2_i - P_i(1-EE_i) - EX_i = 0 \quad \ldots1)$$

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

$$B_i{*}P/B_i - \Sigma_j B_j{*}Q/B_j{*}DC_{ij} - P/B_i{*}B_i(1-EE_i) - EX_i = 0 \quad \ldots1)$$

or

$$B_i{*}P/B_i{*}EE_i - \Sigma_j B_j{*}Q/B_j{*}DC_{ij} - EX_i = 0 \quad \ldots2)$$

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_{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:

$$B_1P/B_1EE_1 - B_1Q/B_1DC_{11} - B_2Q/B_2DC_{21} - \ldots - B_nQ/B_nDC_{n1} - EX_1 = 0$$

$$B_2P/B_2EE_2 - B_1Q/B_1DC_{12} - B_2Q/B_2DC_{22} - \ldots - B_nQ/B_nDC_{n2} - EX_2 = 0$$

$$B_nP/B_nEE_n - B_1Q/B_1DC_{1n} - B_2Q/B_2DC_{2n} - \ldots - B_nQ/B_nDC_{nn} - EX_n = 0$$

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 over-determined (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_i, or EE_i may be unknown for any group i. In special cases, however, Q/B_i 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. A term for biomass accumulation (Bacc) may be added to equation (1) in cases where biomass is known to have changed over the period considered in the model.

These steps can be easily implemented if basic parameters can be estimated (see also Box 1), especially as numerous well-documented examples exist of Ecopath applications to aquatic ecosystems (see Pauly and Christensen 1993, and contributions in Christensen and Pauly 1993, and Pauly and Christensen 1996). We sometimes refer here to three ecosystems that have much in common with PWS (the Strait of Georgia, the coast of British Columbia, and the Alaska gyre), documented through the contributions in Pauly and Christensen (1996). In the present report, details are provided, by functional group, on how items (ii) to (vi) were implemented, for the period (1994-1996) in a defined PWS (Figure 2).

Construction of an Ecopath model is followed by model balancing. The first law of thermodynamics states that energy is neither created nor destroyed, but changed from one form to another. The total energy in a closed system remains constant, though the form of that energy changes. The PWS Ecopath model is not based on the assumption of a closed system; rather, the working assumption is that the energy flowing into PWS's biotic system (primary production, and imported secondary production) is equal to the energy used within the defined system and flowing out of it.

For the purposes of the model, the assumption of mass-balance (conservation of energy) is also made for every identified component of the ecosystem. However, the Ecopath formulation includes a biomass accumulation factor so that trends in populations, or ecosystem components, can be represented, and hence the model is not necessarily a steady-state model. The assumption of mass-balance is extremely useful for parameterization of ecosystem models, we always have imperfect knowledge, and mass-balance offers a powerful constraint to the parameterization process. An iterative model balancing approach can serve to increase knowledge about ecosystem components as well as the whole ecosystem, especially if conducted within a collaborative synthesis of information (see the following section on collaboration). This is so because energy flows in and out of each component must be reconciled among connected components. The balancing methodology employed for the PWS model is described in the section on 'Constructing and Balancing the Model' following the 'Model Inputs' section below.

Contributed diet compositions and the overall food web produced by the model were compared to the food web elements previously published for PWS by McRoy and Wyllie Echeverria (1990). This procedure for verification was conducted for every component of the model, and comments regarding similarity are included at the end of this report.

The current project also features examples of the uses of Ecosim and Ecospace to simulate spatial and temporal responses of biotic components to various perturbations and scenarios. This is followed by a discussion of the application of the PWS model for future resource planning, and how it may shed light on the effects of EVOS.

Surface areas of PWS depth zones and habitats

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Estimating biomasses on a Sound wide basis requires estimating the areal extent over which organisms are distributed. For example, sampling in the nearshore is often stratified by depth, habitat type, or both. As a result, raising local estimates to the sound as a whole requires estimation of the relative proportions of each depth or habitat type within the ecosystem. Estimates of area covered by different depth strata are given in Table 1. Estimates of areas covered by different subtidal habitats are given in Table 2, and areas covered by different intertidal shoreline types are given in Table 3.