

tians or whether adult *H. zapus* range further north.

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Literature Cited

- DINGERKUS, G., AND L. D. UHLER.
1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technol.* 52:229-232.
- GORBUNOVA, N. N.
1964. Razmnozhenie i razvitie polucheshuinykh bychkov (Cottidae, Pisces) (Breeding and development of hemilepidotine sculpins (Cottidae, Pisces)). [In Russ.] *Tr. Inst. Okeanol., Akad. Nauk SSSR* 73:235-251. (Transl. by Isr. Program Sci. Transl., 1966; in T. S. Rass (editor), *Fishes of the Pacific and Indian Oceans, biology and distribution*, p. 249-266; available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT 65-50120.)
- HATTORI, S.
1964. Studies on fish larvae in the Kuroshio and adjacent waters. [In Jpn., Engl. synop.] *Bull. Tokai Reg. Fish. Res. Lab.* 40, 158 p.
- KENDALL, A. W., JR., AND B. VINTER.
1984. Development of hexagrammids (Pisces: Scorpaeniformes) in the Northeastern Pacific Ocean. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 2, 44 p.
- MATARESE, A. C., S. L. RICHARDSON, AND J. R. DUNN.
1981. Larval development of the Pacific tomcod, *Microgadus proximus*, in the Northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae). *Fish. Bull.*, U.S. 78:923-940.
- PEDEN, A. E.
1978. A systematic revision of the hemilepidotine fishes (Cottidae). *Syesis* 11:11-49.
- RICHARDSON, S. L., AND W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomiculatus* (family Scorpaenidae) off Oregon. *Fish. Bull.*, U.S. 77:1-46.
- RICHARDSON, S. L., AND B. B. WASHINGTON.
1980. Guide to identification of some sculpin (Cottidae) larvae from marine and brackish waters off Oregon and adjacent areas in the northeast Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ-430, 56 p.

ANN C. MATARESE
BEVERLY M. VINTER

NOAA, National Marine Fisheries Service
Northwest and Alaska Fisheries Center
2725 Montlake Boulevard East
Seattle, WA 98112-2097

AN APPROACH TO ESTIMATING AN ECOSYSTEM BOX MODEL

Recent trends in ecosystem modeling have produced complex simulation models which are very data intensive (Andersen and Ursin 1977; Laevastu and Larkins 1981). However, in many situations the construction of a biomass budget for a box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982; Polovina 1984).

The ECOPATH model is an analytical procedure to estimate a biomass budget for a box model of an ecosystem given inputs which specify the components of the ecosystem, together with their mortality, diet, and energetics value. A computer program for ECOPATH has been written in BASIC-80, version 5.21, by Microsoft¹ (CP/M version). A listing of the ECOPATH computer program and a user's manual are available from the author.

The ECOPATH model produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the user specified species-groups. The species-groups represent aggregations of species with similar diet and life history characteristics and which have a common physical habitat. The ECOPATH model is not a simulation model with a time component as are some more complex ecosystem models. It estimates a biomass budget for the marine ecosystem in a static situation under the assumption that the ecosystem is at equilibrium conditions.

Equilibrium conditions are defined to exist when the mean annual biomass for each species-group does not change from year to year. This condition results in a system of biomass budget equations which, for species-group *i*, can be expressed as

$$\text{Production of biomass for species } i - \text{all predation on species } i - \text{nonpredatory biomass mortality for species } i - \text{fishery catch for species } i = 0 \text{ for all } i. \quad (1)$$

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i 's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i 's. The mean annual biomass estimates are obtained by solving the system of simultaneous linear equations.

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The formulation of each term of the biomass budget equation will now be presented in detail.

The Model

Biomass Production

Production (P) for a cohort of animals over 1 yr is defined as

$$P = \int_0^1 N_t \frac{d}{dt} (w_t) dt$$

and mean annual biomass (B) for the cohort is defined as

$$B = \int_0^1 N_t w_t dt$$

where N_t is the number of animals and w_t the mean individual weight at time t .

Allen (1971) investigated the production to biomass (P/B) ratio for a cohort over a range of mortality and growth functions. For a number of growth and mortality functions, including negative exponential mortality and von Bertalanffy growth, the ratio of annual production to mean biomass for a cohort is the annual instantaneous total mortality (Z_i). For a species-group which consists of n cohorts or species, with instantaneous annual total mortality (Z_i) for cohort or species i , where mortality is determined by a negative exponential function and growth by a von Bertalanffy growth function, the total species-group production (P) is the sum of the cohort production (P_i) and can be expressed as

$$P = \sum_{i=1}^n P_i = \sum_{i=1}^n Z_i B_i \quad (2)$$

Under the assumption that the Z_i 's are all equal to say Z , then total species-group production can be expressed as

$$P = Z \cdot B$$

where B is the mean annual species-group biomass.

Allen (1971) has also shown that when growth in weight is linear, the P/B ratio is equal to the reciprocal of the mean age for a range of mortality functions. For a number of other growth and mortality functions the ratio of cohort P/B can be the recipro-

cal of the mean lifespan. Thus, for a range of growth and mortality functions, total species-group production can be expressed as

$$P = C \cdot B$$

where B is the mean annual species-group biomass, and C is a parameter.

In an application of ECOPATH to an ecosystem of French Frigate Shoals where there was very little fishing mortality, the P/B ratio for fishes and crustaceans was taken as the annual instantaneous natural mortality (M); whereas, for primary and secondary producers whose growth is more likely to be linear than the von Bertalanffy, the P/B ratio was estimated as the reciprocal of the mean age (Polovina 1984).

Predation Mortality

The predation mortality is the fraction of the biomass of a species-group which is consumed by all predators excluding fishing mortality. Two types of information are needed. First the food web or predator-prey relationships must be defined. A diet composition matrix DC_{ij} must be specified where an entry DC_{ij} from this matrix refers to the proportion (by weight) of prey j in the diet of predator i . The primary source of this information is the analysis of stomach contents data. At least in one study it has been shown that there is a high correlation between diet indices based on weight, volume, and percentage of occurrence for stomach content data, and thus either index may be used to generate the DC matrix (Macdonald and Green 1983). The second type of information needed to ascertain predation mortality is the food requirements of the predator. The ECOPATH model requires the user to specify FR_i , the ratio of annual consumption to mean annual biomass. The annual food required by the predator is the product of FR_i and B_i .

Some values of daily food required as a fraction of body weight range from 0.005 to 0.02 (Laevastu and Larkins 1981). Based on these daily estimates a range of annual food required as a fraction of mean biomass (FR_i) is 1.8 to 7.3.

Nonpredation Mortality

All mortality attributable to causes other than predation and fishing is termed nonpredatory mortality. The ECOPATH model defines ecotrophic efficiency e_i as the fraction of total production which is removed by fishing and predation mortality. This

was 0.95 in the French Frigate Shoals model. The nonpredator mortality rate is $(1 - e_i) \cdot Z_i$, and the amount of production which goes to nonpredation mortality is

$$(1 - e_i) P_i = (1 - e_i) C_i B_i.$$

For n species-groups the biomass budget Equation (1) becomes a system of n simultaneous equations as follows:

$$C_1 B_1 - \sum_{k=1}^n (FR_k) B_k DC_{k1} - (1 - e_1) C_1 B_1 = \text{catch}_1,$$

$$\begin{matrix} \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

$$C_i B_i - \sum_{k=1}^n (FR_k) B_k DC_{ki} - (1 - e_i) C_i B_i = \text{catch}_i,$$

$$\begin{matrix} \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \end{matrix}$$

$$C_n B_n - \sum_{k=1}^n (FR_k) B_k DC_{kn} - (1 - e_n) C_n B_n = \text{catch}_n.$$

With input estimates for parameters C_i , FR_i , DC_{ij} , and e_i for all i and j , and catches (catch_i) if there is fishing, this system of equations is a system of n simultaneous equations linear in the unknown B_i 's. This system of equations can be expressed in matrix form as $AB = C$, where A is an $n \times n$ matrix of coefficients, B is an n -dimensional vector of mean annual species group biomass, and C is the vector of fishery catch where the i th element is the total catch of the i th species-group.

If the matrix A is of full rank and if there are some fishery catches for some species so the vector C is not null, then there typically exists a unique nontrivial solution vector of biomass B . If there are no fishery catches then it is necessary to provide an estimate of at least one of the mean species group biomass B_i before there exists a unique nontrivial biomass vector B which solves the budget equation. In the application of ECOPATH to an ecosystem at French Frigate Shoals where there was no fishing mortality, the biomasses of three apex predators were estimated from field censuses and treated as known inputs. In this application the i th element of C vector was the annual predation by the three apex predators on the i th species-group.

Five years of field work targeting most of the components of the marine ecosystem at French Frigate

Schoals in the Northwestern Hawaiian Islands provided the estimates for many of the input parameters required by the ECOPATH model as well as some estimates of biomass and production to serve to evaluate the estimates produced by the model. The estimates of biomass and production generated by the application of ECOPATH to French Frigate Shoals are given in Figure 1. In general the model's estimates of biomass and production are in good agreement with the available field data (Polovina 1984). In the application of the French Frigate Shoals, the biomasses of the top level carnivores are treated as fixed inputs thus a particularly appropriate validation of the model is the comparison of the estimate of net benthic primary production with an independent estimate from field data. The model estimated net benthic primary production, adjusted to the total 1,200 km² habitat of French Frigate Shoals, at 2.3×10^6 kg · km⁻² · yr⁻¹ while the estimate based on field data was 2.5×10^6 kg · km⁻² · yr⁻¹ (Grigg et al. 1984).

The Computer Program

The ECOPATH model has been implemented via two BASIC language programs. The "dialect" of the language used is BASIC-80, version 5.21, by Microsoft (CP/M version). These programs are designed to be used interactively on a terminal or a hard-copy printer. The first program is the input parameter program which accepts the input parameters and formats them into a BASIC sequential file. The second program is the ECOPATH model itself.

Literature Cited

- ALLEN, K. R.
1971. Relation between production and biomass. *J. Fish. Res. Board Can.* 28:1573-1581.
- ANDERSEN, K. P., AND E. URSIN.
1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Medd. Dan. Fisk. Havunders.*, New Ser., 7:319-435.
- GRIGG, R. W., J. J. POLOVINA, AND M. J. ATKINSON.
1984. Model of a coral reef ecosystem: Part III Resource Limitation, Community Regulation, Fishery Yield, and Resource Management. *Coral Reefs* 3:23-27.
- LAEVASTU T., AND H. A. LARKINS.
1981. Marine fisheries ecosystem: its quantitative evaluation and management. *Fishing News Books*, Farnham, Surrey, Engl., 162 p.
- MACDONALD, J. S., AND R. H. GREEN.
1983. Redundancy of variables used to describe importance of prey species in fish diets. *Can. J. Fish. Aquat. Sci.* 40:635-637.
- PAULY, D.
1982. Notes on tropical multispecies fisheries, with a short

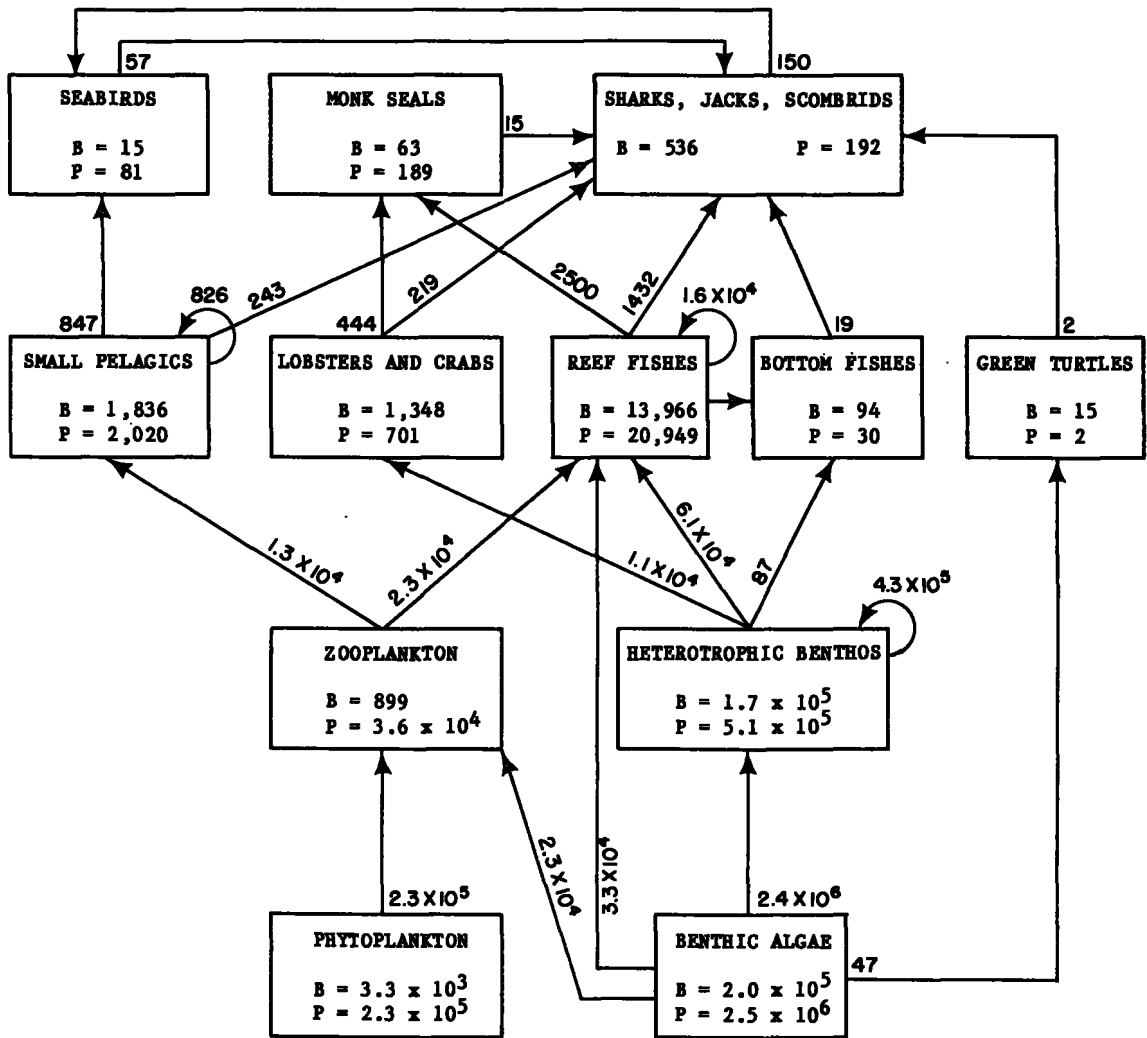


FIGURE 1. - Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of (kg/km^2) based on a habitat area of $1,200 \text{ km}^2$. The values associated with the arrows represent the production from the lower trophic level consumed by the higher trophic level (Polovina in press).

bibliography of the food and feeding habits of tropical fish. In Report on the regional training course on fishery stock assessment, 1 September-9 October 1981, Samutprakarn, Thailand, p. 30-35 and 92-98. Tech. Rep. 1, Part II, SCS/GEN/82/41, Manila.

POLOVINA, J. J.

1984. Model of a coral reef ecosystem, Part I: ECOPATH and

its application to French Frigate Shoals. Coral Reefs 3:1-11. WALSH, J. J.

1981. A carbon budget for overfishing off Peru. Nature 290: 300-304.

JEFFREY J. POLOVINA

MARK D. OW

Southwest Fisheries Center Honolulu Laboratory
 National Marine Fisheries Service, NOAA
 P.O. Box 3830
 Honolulu, HI 96812