

Graphical Representation of Steady-State Trophic Ecosystem Models*

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Abstract

The traditional method of representing steady-state ecosystem models, usually by scattering interconnected boxes across a page, underutilizes the potential descriptive and explanatory power of graphical representations. Some alternative approaches are proposed: (1) drawing boxes with areas proportional to the logarithms of the biomasses they represent, ordered along the ordinate in terms of their weighted mean trophic levels; (2) plotting boxes as in (1) along the ordinate, but using box-specific particle size for ordering along the abscissa (which leads to "size-shifted" models); and (3) mapping the fluxes between boxes, arranged as in (2), in terms of isolines.

Introduction

Construction and parametrization of steady-state models of aquatic ecosystems have a tradition dating back several decades - see, e.g., Odum and Odum's (1957) model of Eniwetok Reef. Yet, consistently applied rules do not seem to have emerged regarding the graphic representation of such models.

The only approach we have seen used repetitively is the energy circuit language of Odum (1972). In this representation, different symbols are used for producers, consumers, storage groups, etc. We find, however, that the symbols add more complexity than information and would not recommend that language.

We wonder if the absence of usable rules of graphic representation of steady-state models could be caused by the perception that steady-state trophic box models are intrinsically too simple - they consist only of boxes and arrows - for their graphical representation to require much thought about symbols or effort by a graphic artist.

It seems paradoxical to us, however, to devote as much time as is generally done to the construction and parametrization of ecosystem models and so little to the elaboration of the graph representing the model, i.e., the final product.

We believe, indeed, that the same criteria should apply for representations of ecosystem models as for scientific graphs in general, for which Tufte (1983) wrote:

"Excellence in statistical graphics consists of complex ideas communicated with clarity, precision, and efficiency. Graphical displays should

- show the data
- induce the viewer to think about the substance rather than about methodology, graphic design, the technology of graphic production, or something else
- avoid distorting what the data have to say
- present many numbers in a small space
- make large data sets coherent
- encourage the eye to compare different pieces of data
- reveal the data at several levels of detail, from a broad overview to the fine structure
- serve a reasonably clear purpose: description, exploration, tabulation, or decoration
- be closely integrated with the statistical and verbal descriptions of a data set."

As we hope to show below, there are ways to represent box models such as to (1) increase the descriptive and explanatory impact of the graph and (2) facilitate comparisons between ecosystems.

The first of these two points does not need

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elaborating, but the second does: the baroque cacophony of style used by different authors and illustrated in Fig. 1 may be one key reason why few useful generalizations have emerged to date from

the comparisons of models of different ecosystems. We suggest, in the following, some rules for representing trophic models of ecosystems. These rules, if adopted, could help overcome some of the

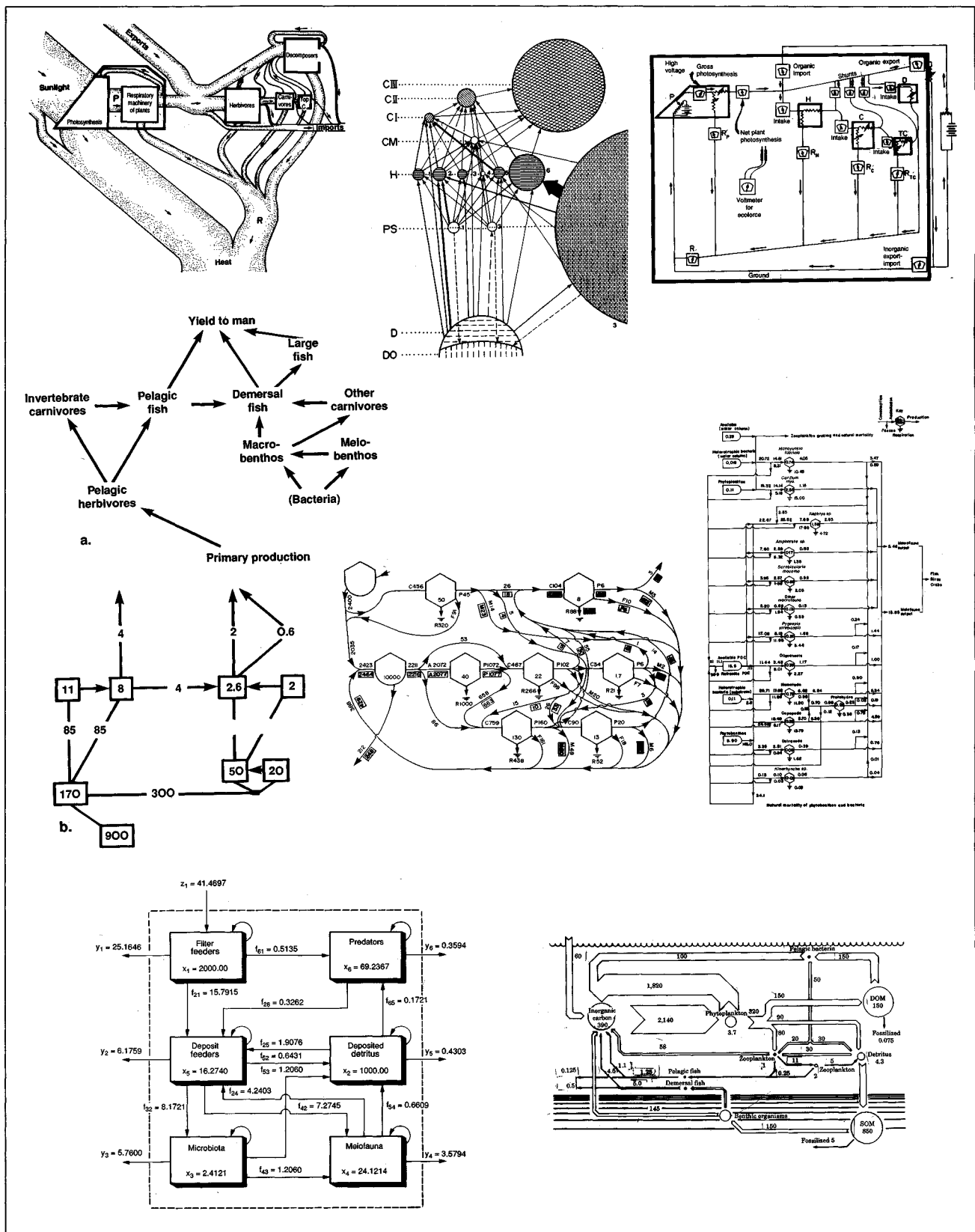


Fig. 1. Selected examples of published representations of steady-state trophic models of aquatic ecosystems.

problems in (1) and (2) above, mainly by making creative use of the ordinate and abscissa implied in each graph, and of the quantitative scale which - since Descartes - comes along with these axes, if only implicitly.

Using the Y-Axis

Often, trophic models are drawn such that the boxes representing organisms low in the food chain (or web) are placed in the lower part of the graph, along with the plants, while the boxes representing organisms high in the food chain (web) are put higher up.

We propose to make explicit use of this mode of graphing, i.e., to plot the boxes representing the organisms of an ecosystem such that the horizontal axis of symmetry of each box is aligned with the trophic level of the box in question (Fig. 2). This implies estimating these trophic levels, as opposed to making *a priori* assumptions about them (as, e.g., some cases included in Fig. 1). The estimation in question can be performed using various methods, notably the ECOPATH II software discussed elsewhere in this volume. Note that the trophic levels so estimated need not be (and generally are not) whole numbers, as assumed in some food chain theories (e.g., Pimm 1982).

Using the X-Axis (I)

Using trophic level as Y-axis is not sufficient to define the relative position of the elements of a model, and two approaches may be considered for ordering the boxes along the X-axis:

1. arranging the boxes such that they do not overlap, and/or with emphasis on some symmetry, i.e., such that the resulting graph is esthetically pleasing, or
2. arranging the boxes such that the arrows linking the boxes cross each other as little as possible, hence, maximizing intelligibility of the graph.

We have tried to incorporate (1) and (2) in the construction of Fig. 2. We note in this context that software for electronic hardware development exist, e.g., SCHEMA II and ORCAD, which can be used to optimize the positioning of elements and to conduct check of energy pathways and that such software is of use for constructing ecosystem flow charts as well.

As the astute reader will have noted, the sizes of the boxes plotted on Fig. 2 themselves contain information: their area is proportional to the logarithm of the biomass in each box.

We found this trick to be particularly useful in helping the reader visualize the relative role and

impact of the organisms in each box - something which boxes of equal sizes do not even attempt, and which boxes with dimensions directly proportional to biomass fail to do well. To avoid the problem of taking logarithms of values less than 1 we have also found it useful to make the box sides equal to the third root of the biomasses, thus assuming the boxes to be three-dimensional.

We have introduced another rule of construction in Fig. 2. All flows entering a box do this on the lower half of the box, while flows exiting a box do it from the upper half. Flows that enter a box can be combined, while flows that leave a box cannot branch, but they can be merged with flows exiting other boxes. This ensures compatibility with shortcut circuit checks in electronic hardware design software, and at the same time it simplifies the flow chart. "Cannibalism" or zero-order flows are shown as circles originating from the top half of a box and entering the lower half.

On the other hand, we abstain here from representing flows through arrows of different sizes (i.e., with thickness proportional to the log of the flow represented) because we found that this cluttered up our models. Indeed, it is often necessary to omit, for clarity's sake, lesser flows from graphs representing highly interconnected systems. Moreover, there appear to be far more effective ways of representing flows, as will be shown below.

Using the X-Axis (II)

Powerful holistic approaches have recently emerged in biology and ecology which demonstrate that the *size* of organisms is their key attribute. The relevant compilations (see, e.g. Bonner 1965; Calder 1984; Ulanowicz and Platt 1985) show that virtually all important characteristics of organisms, ranging from their physiology to their population dynamics and from their gross anatomy to their ecology, can be expressed as tight double logarithmic plots, often ranging in size from bacteria to whales (24 orders of magnitude). This suggests that insights could be gained by using size as the abscissa scale of graphic representation of ecosystems.

Following common usage, we assume a weight-to-volume conversion based on a specific weight equal to unity. This enables comparability between organisms with different shapes. One problem here is the choice of the appropriate "mean weight" for the aggregate of organisms within a box, which may consist of (1) a single-species, steady-state population, including lots of small, young organisms and fewer larger, old organisms, or (2) several species, each with its own size composition. In the second case, the model builder may have to construct either a cumulated multispecies size distribution or use the

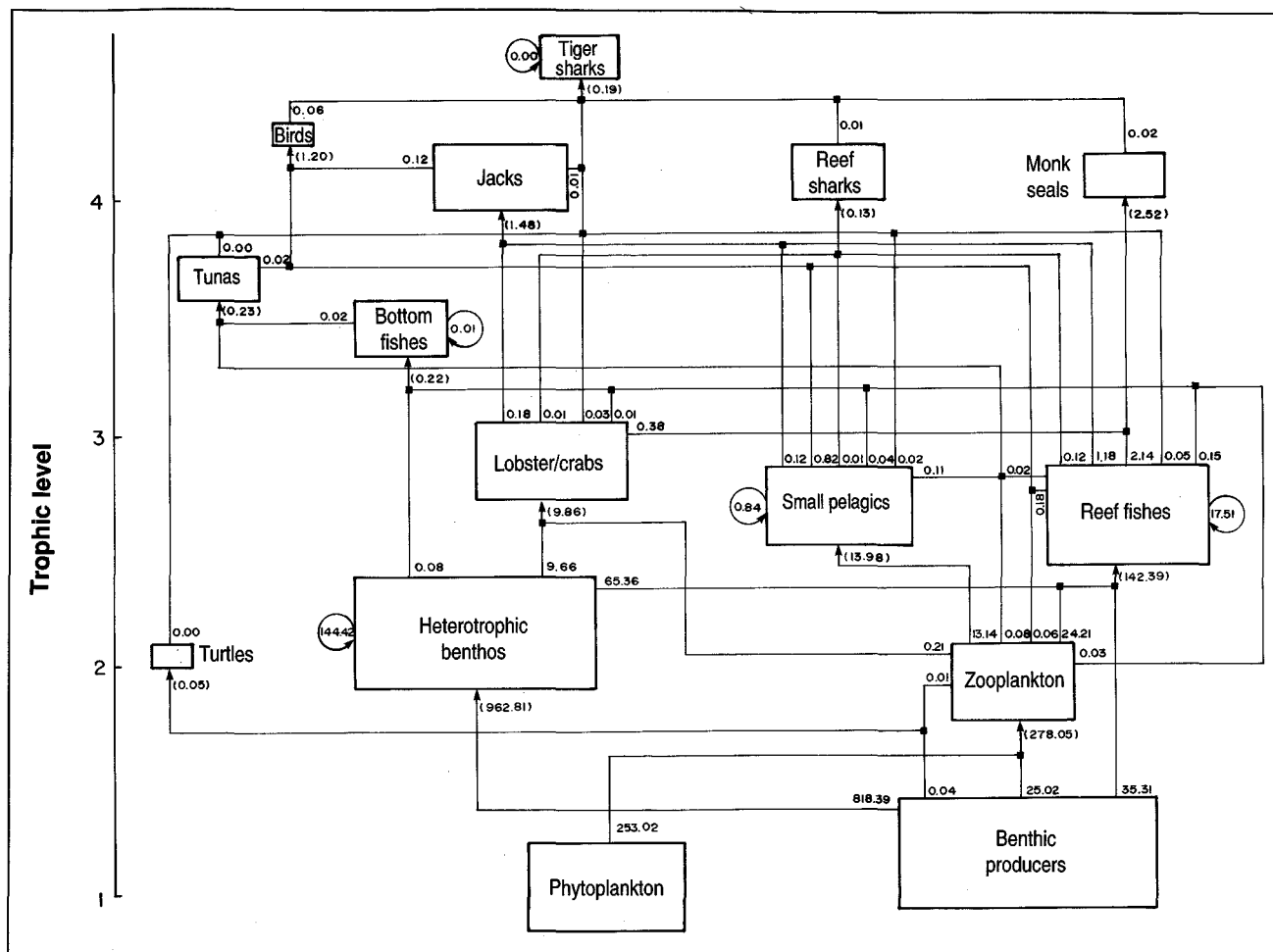


Fig. 2. Representation of the French Frigate Shoals coral reef ecosystem (Polovina 1984). The area of each box is proportional to the logarithm of the biomass of each group. Flows exit the top half of a box and enter the bottom half (see text for further constructional details).

size distribution of a single species representative of the other taxa in the box.

Whatever choice is taken, some measure of central tendency of the size distribution will have to be used, i.e.,

- a statistically based index, e.g., the mean, mode or median, or
- a biologically based index, e.g., (a) a representative size of adults, i.e., the mean size at first maturity (W_m) and of asymptotic (W_∞) or maximum size (W_{max}), as used in Pauly (1982), or (b) W_m itself which, in fishes, roughly corresponds to the peak of the biomass curve, and to $0.3 * W_\infty$, or (c) the size at which relative food consumption is highest (this generally occurs at the juvenile stage, below $0.3 * W_\infty$).

Here, we have chosen a measure of size which, due to its simplicity, needs some explanation. The measure of size should represent the "average" organism in a group. For a given population this size will among others be a function of the total mortality of the population. This is illustrated in Fig. 3, which shows population mean weight as a function of total mortality (within the range of mortality normally

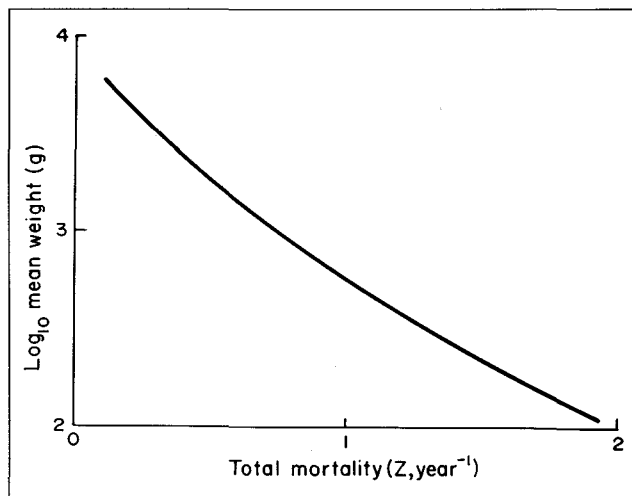


Fig. 3. Weight (g, log scale) for the average fish in a population with growth following the von Bertalanffy growth function, with parameters $W_\infty = 10^4$ g, $t_0 = -0.1$ year, $K = 0.5$ year⁻¹, as a function of total mortality, Z (year⁻¹).

found for organisms of this size [i.e., from unexploited to heavily exploited]).

As can be seen from the figure, weight is strongly correlated with total mortality rates in the observed range. If the population is in steady state (as all populations considered here are assumed to be), total mortality rate is equivalent to production/biomass ratio (P/B; Allen 1971). As the correlation is negative, we suggest to use the inverse log (B/P) as a measure of (log) size. The unit for biomass/production is time, e.g., year.

To further explore the proportionality between P/B and size, we have extracted 58 cases of reported total mortality rates (or production/biomass ratios) and corresponding organism weights from published data (Table 1).

The correlation between the measure of size, i.e., log (B/P) and weight is shown on Fig. 4. As can be seen, the two variables are highly correlated ($r = 0.88$). However, there is considerable variation around the regression line. This is partly due to the measure of size we used, which varies with the exploitation rate (c.f. Fig. 3).

Using log (biomass/production) as an indirect measure of size (or any of the other above-mentioned direct measures of size), it is straightforward to plot the compartments of a trophic model on a surface defined by trophic level *vs.* organism size. This leads to what we shall call here *size-shifted models*. This name was selected because in aquatic ecosystems, predators are usually much larger than their preys, which induces a rightward shift in the resulting graphs (Fig. 5).

Figs. 6a and 6b show size-shifted graphs of two ecosystems, in which the flows are represented by

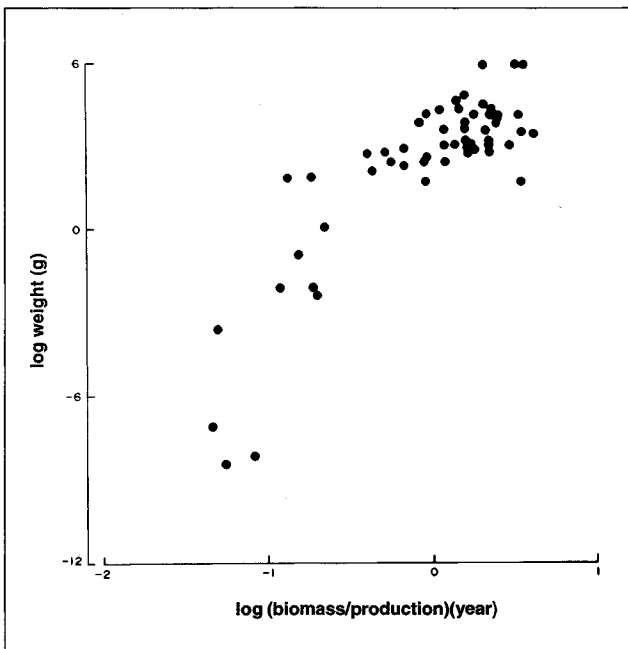


Fig. 4. Average weight (log) as a function of inverse mortality (or B/P) rate for 58 groups (see Table 1).

straight lines. Fig. 6a illustrates a case in which size and trophic level correlate rather well, for all groups. On the other hand, at least three of the groups in Fig. 6b are outliers. A closer examination justifies the position of group (5), i.e., of turtles. These are large organisms feeding on small plants. For the other groups that seem misplaced, i.e., (2) monk seals, (3) birds, and perhaps (1) tiger sharks, it should be noted that the P/B ratios used were preliminary estimates, and it might be that these groups do not have the high P/B ratios that were assumed. These and similar observations suggest the general usefulness of this approach, and of outliers to pinpoint questionable P/B ratios.

The shift that is observed on Figs. 6a and 6b can be quantified by calculating the slopes of all nonrespiratory and nondetrital flows in a system, then taking the geometric mean of all positive slopes weighted by the size of the flows. For the two systems on Figs. 6a and 6b, the slopes are almost the same, 1.00 and 0.98, respectively (disregarding flows from the three outlier groups on Fig. 6b).

We propose that the value of this slope for a given ecosystem be used to characterize the way trophic levels and size interact in the ecosystem in question.

Using the Z-Axis - Flow Intensity

The size-shifted models described above and in Figs. 5 and 6 have two dimensions: trophic level and organism size. However, since the publication of Fasham (1984), awareness of the importance of flows has considerably increased and new approaches for deriving indices of ecosystem structure exclusively from network of flows have been developed (e.g., Ulanowicz 1986).

Similar developments have not occurred at the graphical level, however, i.e., no approach appears to have been proposed to date to graphically express the "signature" of an ecosystem's network of flows.

We propose that such a signature be obtained by adding a third dimension to graphs such as Fig. 6, i.e., by expressing the (nonrespiratory and nondetrital) flows as arrows with a width proportional to the log of their intensity, adding up overlapping flows (by grid squares) then drawing isolines of the log flow intensity for the whole system (Fig. 7).

As might be seen, this approach leads to complete obliteration of the boxes of a system, and of the individual flows between them, leaving only an isopleth diagram to characterize the system as a whole.

We suggest that such graphs, perhaps even better than the index b (see above) could be used to characterize the size-shifted nature of the network of flows used to represent steady-state trophic ecosystem models.

Table 1. Reported total mortality rates (Z) (or production/biomass ratios [P/B]) and the organism weights for 58 groups of organisms.

Species/group	P/B or Z (year ⁻¹)	Weight (g) ^a	References
Bacteria	197.00	1.00·10 ⁻¹²	Lewis (1981)
Microbial population	21.90	6.67·10 ⁻⁸	Sorokin (1981)
<i>Eurocerus lamellatus</i>	20.00	2.00·10 ⁻⁴	Jørgensen (1979)
Microbial population	18.25	3.33·10 ⁻⁹	Sorokin (1981)
Microbial population	12.17	6.25·10 ⁻⁹	Sorokin (1981)
Nematoda	8.38	6.85·10 ⁻⁹	Warwick et al. (1979)
Shrimps	7.57	6.00·10 ¹	Abarca-Arenas and Valero-Pacheco (this vol.)
<i>Tantarsini</i>	6.50	1.00·10 ⁻¹	Jørgensen (1979)
Shrimps	5.38	6.00·10 ¹	Arreguín-Sánchez et al. (this vol.)
Shrimps	5.38	6.00·10 ¹	Chávez et al. (this vol.)
Meiofauna	5.33	6.40·10 ⁻³	Elmgren (1984)
Zooplankton	5.00	3.31·10 ⁻³	Reyes-Marchant et al. (this vol.)
<i>Hyalella</i>	4.50	1.00	Jørgensen (1979)
Crabs	2.50	4.00·10 ²	de la Cruz-Aguero (this vol.)
Anchoveta	2.30	1.00·10 ²	Lewis (1981)
Goat fish	1.92	4.59·10 ²	Mendoza (this vol.)
Sardine	1.80	2.00·10 ²	Lewis (1981)
<i>Loligo</i> spp.	1.50	1.50·10 ²	Cohen et al. (1982)
<i>Illex</i> spp.	1.50	6.00·10 ²	Cohen et al. (1982)
<i>Mugil</i> spp.	1.20	5.00·10 ³	Chávez et al. (this vol.)
Anchovies and sardines	1.13	2.01·10 ²	Mendoza (this vol.)
Herrings	1.11	4.00·10 ¹	Chávez et al. (this vol.)
Octopus	1.10	1.09·10 ⁴	Chávez et al. (this vol.)
Mojarra	1.09	3.00·10 ²	Chávez et al. (this vol.)
Bonito	0.91	1.50·10 ⁴	Lewis (1981)
Horse mackerel	0.85	3.00·10 ³	Lewis (1981)
Mackerel	0.85	8.00·10 ²	Lewis (1981)
Squids	0.84	2.07·10 ²	Mendoza (this vol.)
Mackerel	0.73	8.00·10 ²	Sheridan et al. (1984)
Cod	0.72	3.04·10 ⁴	Cohen et al. (1982)
<i>Lutjanus</i> spp.	0.70	1.50·10 ⁴	Chávez et al. (this vol.)
Porgies	0.65	5.00·10 ³	Chávez et al. (this vol.)
King mackerel	0.65	5.00·10 ⁴	Chávez et al. (this vol.)
Croakers	0.64	3.14·10 ³	Mendoza (this vol.)
Yellowtail flounder	0.63	1.20·10 ³	Cohen et al. (1982)
Catfish	0.62	6.62·10 ²	Mendoza (this vol.)
Mackerel	0.62	4.16·10 ²	Mendoza (this vol.)
Silver hake	0.59	9.00·10 ²	Cohen et al. (1982)
Scombrids and barracudas	0.57	9.41·10 ³	Mendoza (this vol.)
Grunts	0.57	5.86·10 ²	Mendoza (this vol.)
Sharks	0.50	6.26·10 ⁵	Browder (this vol.)
Red grouper	0.50	2.30·10 ⁴	Chávez et al. (this vol.)
Snappers and groupers	0.49	2.98·10 ³	Mendoza (this vol.)
Other flounders	0.46	1.20·10 ³	Cohen et al. (1982)
Red hake	0.46	8.00·10 ²	Cohen et al. (1982)
Pollock	0.46	1.00·10 ⁴	Cohen et al. (1982)
Carangids	0.45	4.78·10 ²	Mendoza (this vol.)
Snappers	0.44	0.50·10 ⁴	Chávez et al. (this vol.)
Haddock	0.41	5.40·10 ³	Cohen et al. (1982)
Small sharks	0.40	7.00·10 ³	Mendoza (this vol.)
Grunts	0.40	1.00·10 ⁴	Chávez et al. (this vol.)
Mackerel	0.34	8.00·10 ²	Cohen et al. (1982)
Sharks	0.32	6.26·10 ⁵	Chávez et al. (this vol.)
Hake	0.30	1.00·10 ⁴	Lewis (1981)
<i>Arius</i> spp.	0.29	2.60·10 ³	Chávez et al. (this vol.)
Herring	0.29	4.00·10 ¹	Cohen et al. (1982)
Sharks	0.28	6.26·10 ⁵	Sheridan et al. (1984)
Redfish	0.24	2.00·10 ³	Cohen et al. (1982)

^aReported mean weights or maximum reported weight * 0.3, to approximate mean weight in population.

Fig. 6b. Size-shifted representation of the French Frigate Shoals ecosystem (Polovina 1984). All flows are included. (Cf. with Fig.2)

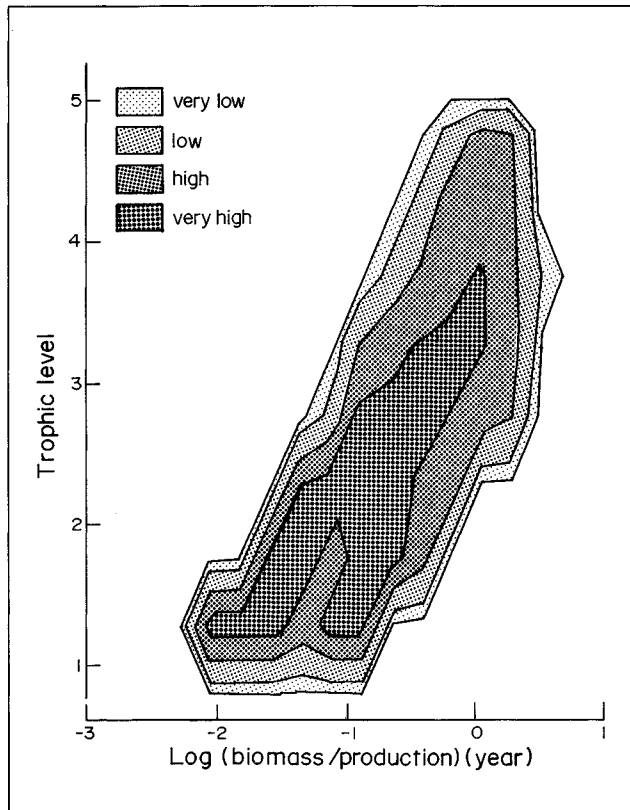
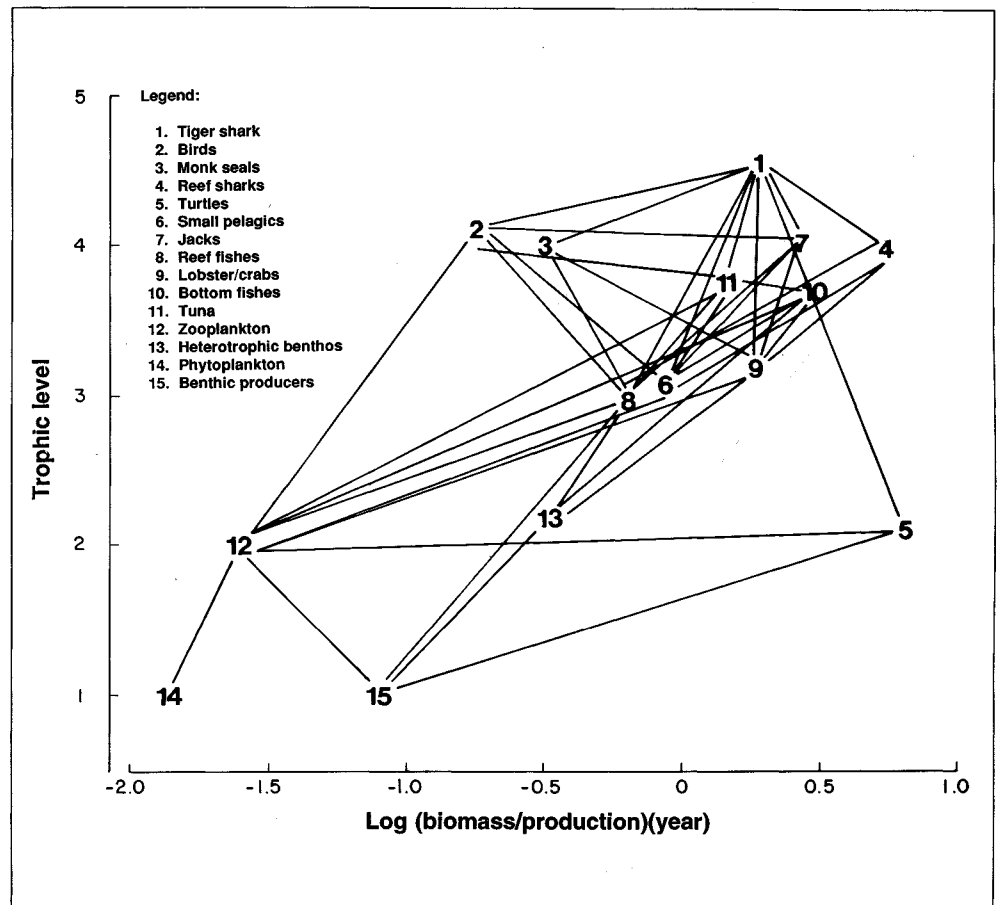


Fig. 7. "Signature" of a steady-state trophic ecosystem model (Western Gulf of Mexico, Chávez and Arreguín-Sánchez, this vol.) as an isopleth of flow intensity.

Conclusion

Time will tell whether any of the suggested new approaches for graphical representation of steady-state trophic models will become widely accepted. We hope, however, to have initiated a discussion and that the rapidly improving software for graphing will not just lead to an increased occurrence of the "ducks" or junk-graphs justifiably criticized by Tufte (1983), but that the constructors of ecosystem models will use their creative abilities to make graphs that are of pleasure for the eye as well as for the mind.

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