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THREE NEW APPROACHES FOR THE GRAPHICAL REPRESENTATION OF STEADY-STATE TROPHIC ECOSYSTEM MODELS*

by

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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: (i) 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; (ii) plotting boxes as in (i) along the ordinate, but using box-specific particle size for ordering along the abscissa (which leads to "size-shifted" models), and (iii) mapping the fluxes between boxes, arranged as in (ii), in terms of isolines.

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INTRODUCTION

Although the construction and parametrization of steady-state models of aquatic ecosystems has a tradition dating back several decades - see, e.g., Odum and Odum's (1957) model of Eniwetok Reef 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 have opted not to use the 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 efforts 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 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 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 - go with these axes.

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., in Fig. 1). The estimation in question can be performed using various methods, notably the ECOPATH II software (Christensen and Pauly 1990). Note that the trophic levels so estimated need not (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:

(i) 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

(ii) 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 (i) and (ii) 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.

We have introduced another rule of construction in Fig. 2. Thus, 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 the key attribute. The relevant compilation, (see, e.g, Bonner 1965, Calder 1984, Ulanowicz and Platt 1985) indeed 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 (i) a single-species, steady-state population, including lots of small, young organisms and fewer larger, old organisms, or (ii) several species, each with its own size composition. In the second case, the model builder may have to either construct a cumulated multispecies size distribution, or use the 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) the average size of adults, i.e., mean of 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 W_∞ 0.3, or (c) the size at which the relative food consumption is highest (this generally occurs at the juvenile stage)

In the present approach 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 be a function of the total mortality of the population. This is illustrated in Fig. 3 where the individual mean weight as a function of total mortality on a double logarithmic plot. The growth of individuals in the population is described with the specialized VBGF (Pauly 1984, Eq. 4.11) with parameters, typical of a medium-sized species, i.e., $W_\infty = 10$ kg, K = 0.5, $t_o = -0.1$ years.

The mortalities are within the range that are normally found for organisms of this size (i.e., from unexploited to heavily exploited). As can be seen from the figure, the weight is strongly correlated with the total mortality rates in the observed range. If the population is in steady-state (as all populations considered here are assumed to be), the total mortality rate is the same as the production/biomass ratio (Allen 1971). As the correlation is negative we suggest to use log (1,000/PB) as a measure of (log) size.

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 (1,000/PB) and weight is shown on Fig. 4. As can be seen the two variables are correlated; the correlation coefficient is 0.88. As expected there is considerable variation around the regression line. This variation is undoubtedly influenced by the used measure of size as this measure varies with the exploitation rate (see Fig. 3).

We suggest to expand the dataset and make a generally applicable regression to predict P/B ratios for a group from the average organism size. By including additional readily quantifiable parameters (e.g., net efficiency and temperature) we are confident that the prediction ability can be further increased. It should be noted that a main advantage of the proposed measure of size is that it is based on information already available in the ECOPATH II.

Using this measure of size (or any other previously mentioned) it is straightforward to plot the compartments of a trophic model on a surface defined by trophic level *versus* 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).

In Figs. 6a and 6b, we have shown similar size-shifted graphs of two ecosystems, but here we have indicated flows with straight lines. The figure shows that at least three of the groups in (b) are outliers. A closer examination justifies the position of (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 used P/B ratios are based on rather loose assumptions, and that it seems unrealistic that these groups should have as high P/B ratios as assumed. Due to these and similar observations, we suggest to use a test for 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 non-respiratory and non-detrital flows in a system, and subsequently taking the geometric mean of all positive slopes weighted after the size of the flows. For the two systems on Figs. 6a and 6b, the slopes are 1.00 and 0.98 respectively (disregarding flows from the three outlier groups (1, 2, and 3) on Fig. 6b.)

We propose that the value of $\bar{b}$ of 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 (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 (non-respiratory and non-detrital) 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 $\bar{b}$ (see above) could be used to characterize the size-shifted nature of network of flows used to represent steady-state trophic ecosystem models.

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 raised a discussion and that the rapidly improving software for graphing will not just lead to an increased occurrence of "ducks" or junk-graphs, but that scientists will use their creative abilities to make graphs that are of pleasure for the human eye as well as the mind.

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Table 1. Reported total mortality rats (or production/biomass ratios) and corresponding organism weight gives log of max weight for the smallest organism, and 0.3 * max weight for the larger, as the aim is to produce a measure of the mean weight inthe population.

Species/ group	Annual P/B	(1,000/ P/B)	Max weight (g)	Log weight	Source
Bacteria	197.00	0.71	1.00E - 12	-12.00	3
Microbial population	21.90	1.66	6.67E - 08	-7.18	1
Eurocercus lamellatus	20.00	1.70	2.00E - 04	-3.70	13
Microbial population	18.25	1.74	3.33E - 09	-8.48	1
Microbial population	12.17	1.91	6.25E - 09	-8.20	1
Nematoda	8.38	2.08	6.85E - 09	-2.16	11
Shrimps	7.57	2.12	6.00E+01	1.26	8
Tantarsini	6.50	2.19	1.00E - 01	-1.00	13
Shrimps	5.38	2.27	6.00E+01	1.26	9
Shrimps	5.38	2.27	6.00E+01	1.26	4
Meiofauna	5.33	2.27	6.40E - 03	-2.19	12
Zooplankton	5.00	2.30	3.31E - 03	-2.48	7
Hyalella	4.50	2.35	1.00E+00	0.00	13
Crabs	2.50	2.60	4.00E+02	2.08	10
Achoveta	2.30	2.64	1.00E+02	1.48	3
Goat fish	1.92	2.72	4.59E+02	2.14	6
Sardine	1.80	2.74	2.00E+02	1.78	3
Loligo spp.	1.50	2.82	1.50E+02	1.65	2
Illex spp.	1.50	2,82	6.00E+02	2.26	2
Mugil spp.	1.20	2.92	5.00E+03	3.18	4
anchovies & sardines	1.13	2.95	2.01E+02	1.78	6
Herrings	1.11	2.96	4.00E+01	1.60	4
Octopus	1.10	2.96	1.09E+04	3.51	4
Mojarra	1.09	2.96	3.00E+02	1.95	4
Bonito.	0.91	3.04	1.50E+04	3.65	3
Horse mackerel	0.85	3.07	3.00E+03	2.95	3
Mackerel	0.85	3.07	8.00E+02	2.38	3
Squids	0.84	3.08	2.07E+02	2.32	6
Mackerel	0.73	3.14	8.00E+02	2.38	5
Cod	0.72	3.14	3.04E+04	3.96	2
Lutjanus spp.	0.70	4.15	1.50E+04	3.65	4
Porgies	0.65	3.19	5.00E+03	3.18	4
King mackerel	0.65	3.19	5.00E+04	4.18	4
Croakers	0.64	3.19	3.14E+03	2.97	6
Yellowtail flounder	0.63	3.20	1.20E+03	2.56	2

Table 1 Cont'd...

Species/ Group	Annual P/B	(1,000/ P/B)	Max weight (g)	Log weight	Source
Catfish	0.62	3.21	6.62E+02	2.30	6
Mackerel	0.62	3.21	4.16E+02	2.10	6
Silver hake	0.59	3.23	9.00E - 02	2.43	2
Scombrids & barracudas	0.57	3.24	9.41E+03	3.45	6
Grunts	0.57	3.24	5.86E+02	2.25	6
Sharks	0.50	3.30	6.26E+05	5.27	5
Red grouper	0.50	3.30	2.30E+04	3.84	4
Snappers & groupers	0.49	3.31	2.98E+03	2.95	6
Other flounders	0.46	3.34	1.20E+03	2.56	2
Red hake	0.46	3.34	8.00E+02	2.38	2
Pollock	0.46	3.34	1.00E+04	3.48	2
Carangids	0.45	3.35	4.78E+02	2.68	6
Snappers	0.44	3.35	1.50E+04	3.65	4
Haddock	0.41	3.39	5.40E+03	3.21	2
Small sharks	0.40	3.40	7.00E+03	3.32	6
Grunts	0.40	3.40	1.00E+04	3.48	4
Mackerel	0.34	3.47	8.00E+02	2.38	2
Sharks	0.32	3.50	6.26E - 05	5.27	4
Hake	0.30	3.52	1.00E+04	3.48	3
Arius spp.	0.29	3.54	2.60E - 03	2.89	4
Herring	0.29	3.54	4.00E+01	1.08	2
Sharks	0.28	3.55	6.26E+05	5.27	5
Redfish	0.24	3.61	2.00E - 03	2.78	2

Source:

1	Sorokin 1981
2	Cohen et al. 1982
3	Lewis 1981
4	Chavez et al., this vol.
5	Sheridan et al., this vol.
6.	Mendoza, this vol.
7	Reyes-Merchant et al., this vol.
8	Abarca-Arenas et al., this vol.
9	Arreguin-Sanchez et al., this vol.
10	de la Cruz-Agüero, this vol.
11	Warwick et al. 1979
12	Elmgren 1984
13	Jørgensen 1979

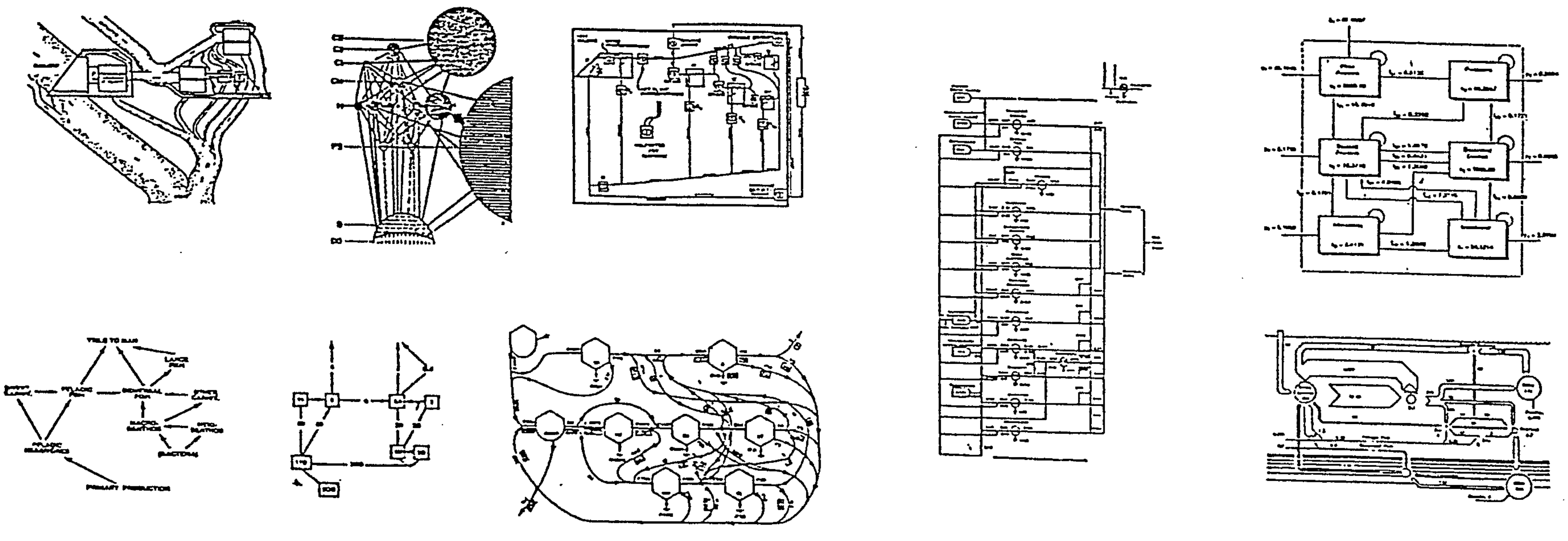

Fig. 1. Selected examples of published representations of steady-state trophic models of aquatic ecosystems.

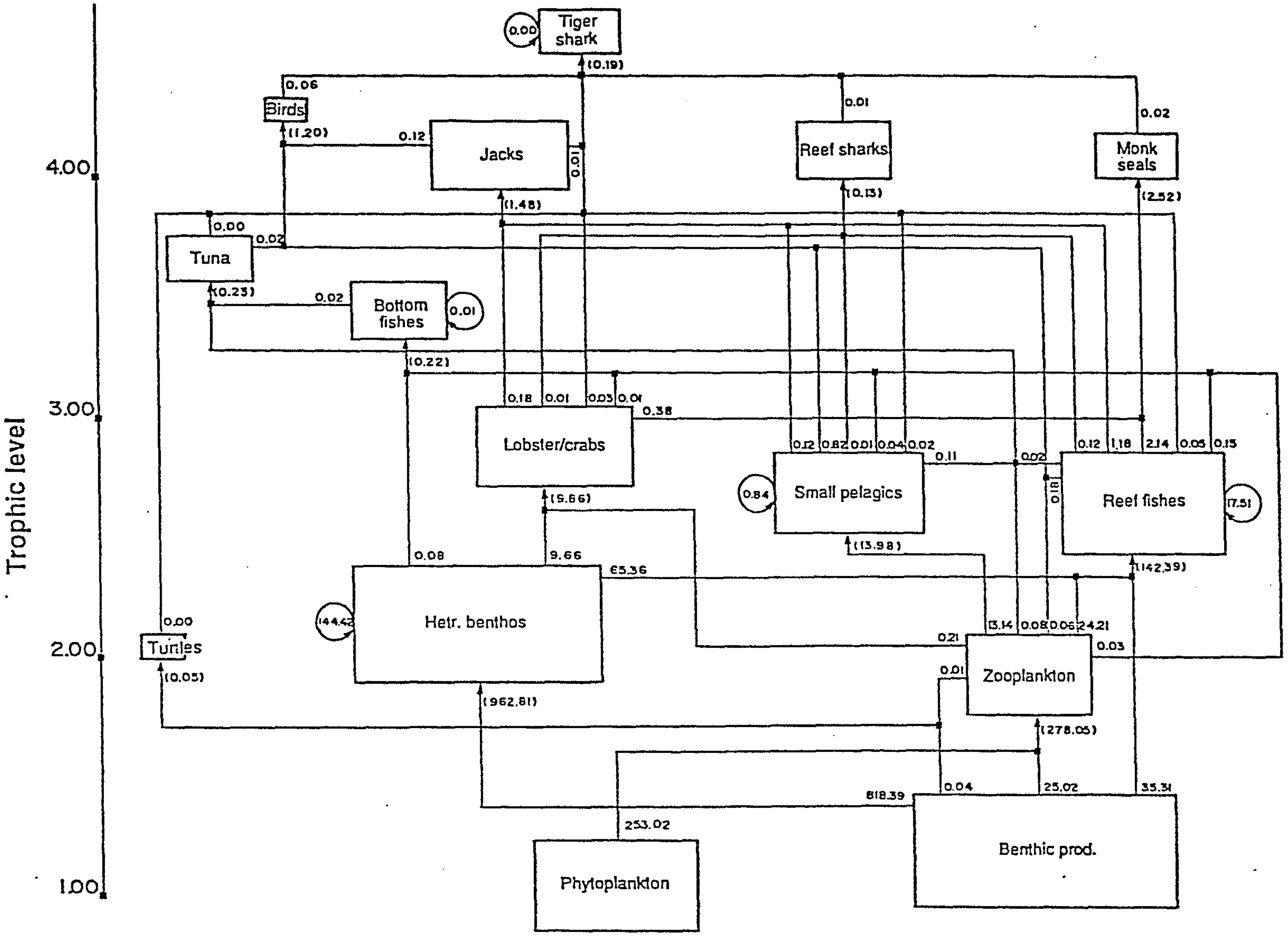

Fig. 2. Representation of the French Frigate ecosystem (Polovina 1984). The area of each box is proportional to the logarithm of the biomass of each group. Flows exit the top half of a box and enter the bottom half.

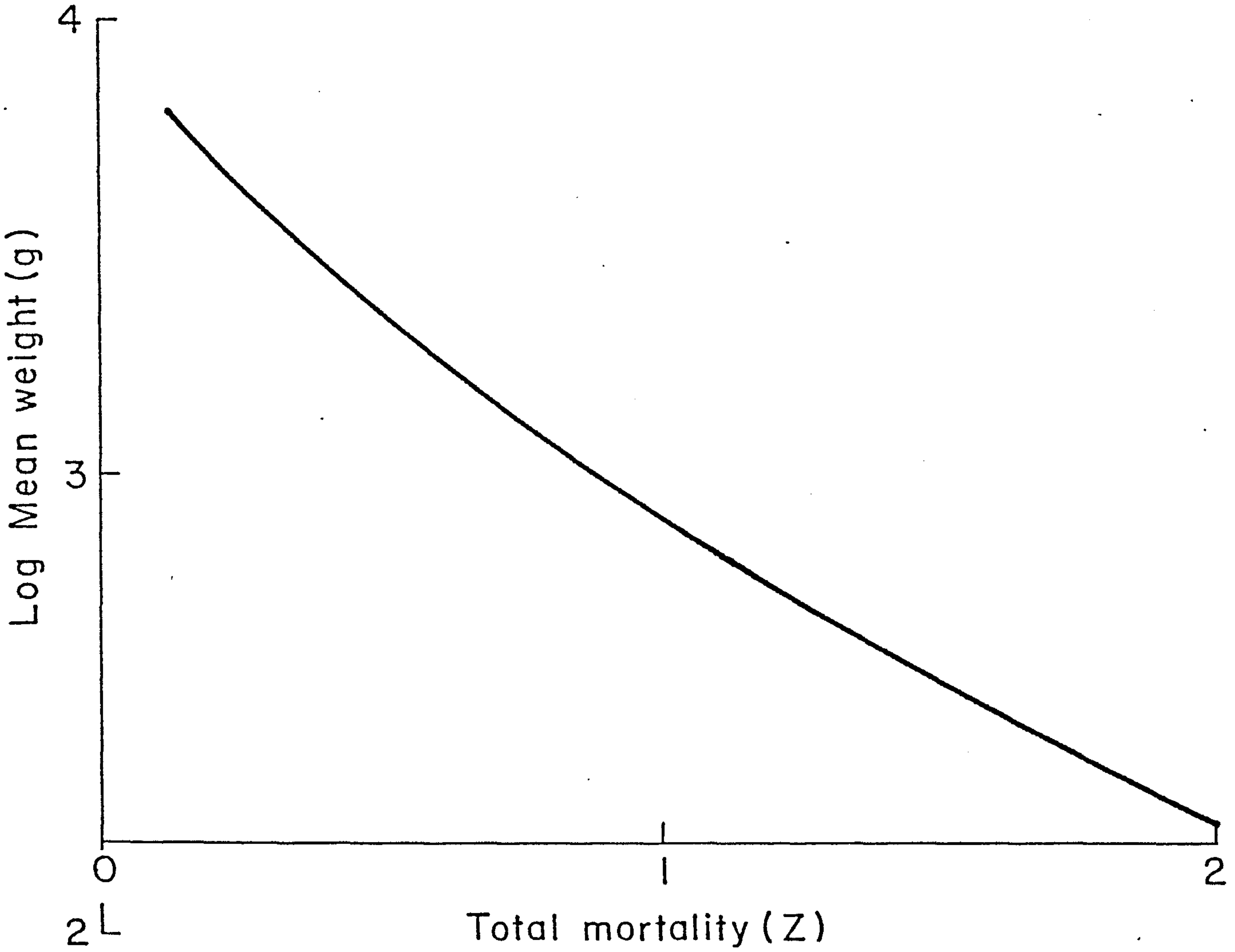

Fig. 3. Spherical radius (cm) for the average fish in a population with growth following the special VBGF with parameters W = 10 kg, t_0 = -0.1 years, K = 0.5, as a function of total mortality, Z (log scale).

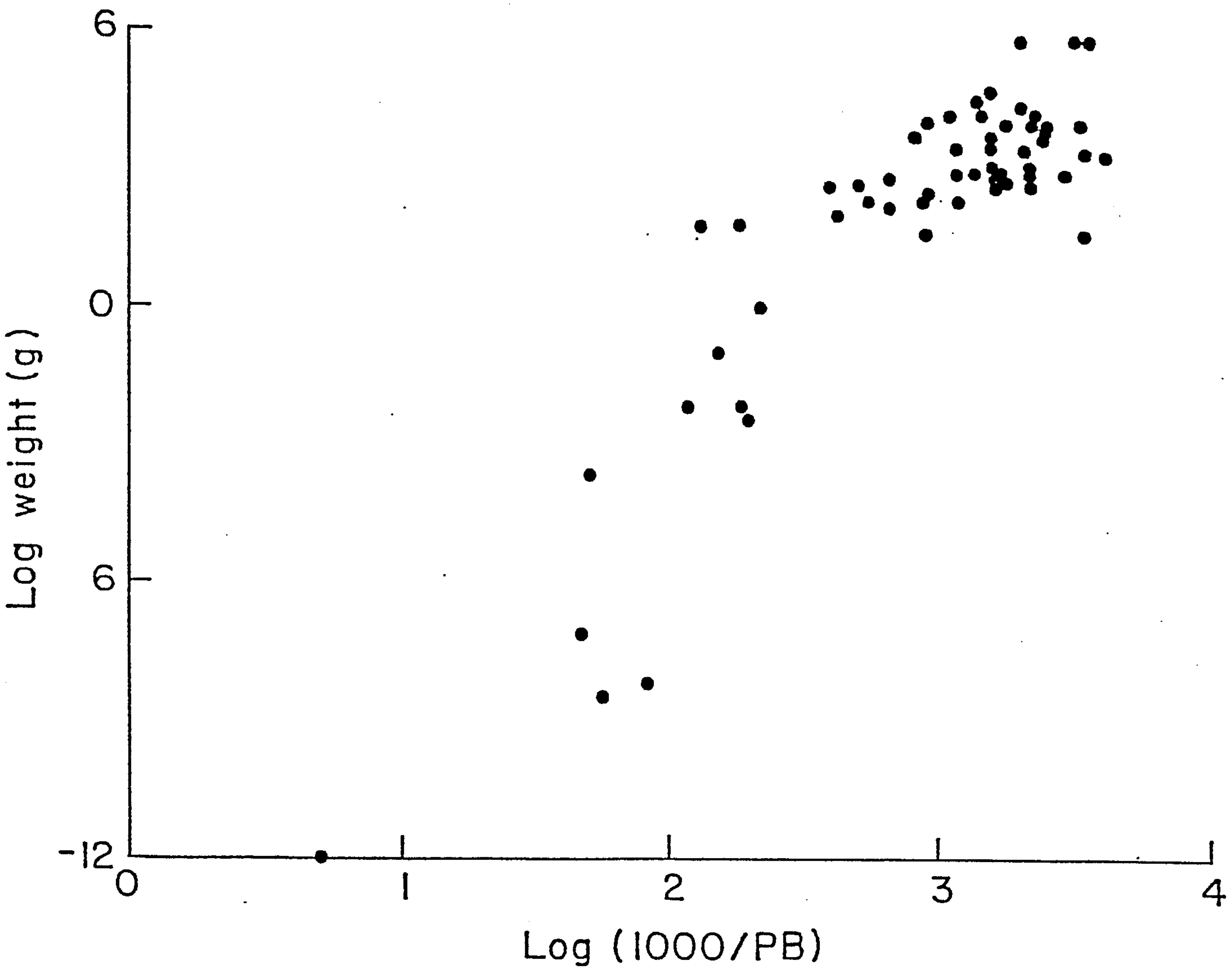

Fig. 4. Average weight (log) as a function of mortality (or P/B) rate for 58 groups (see Table 1).

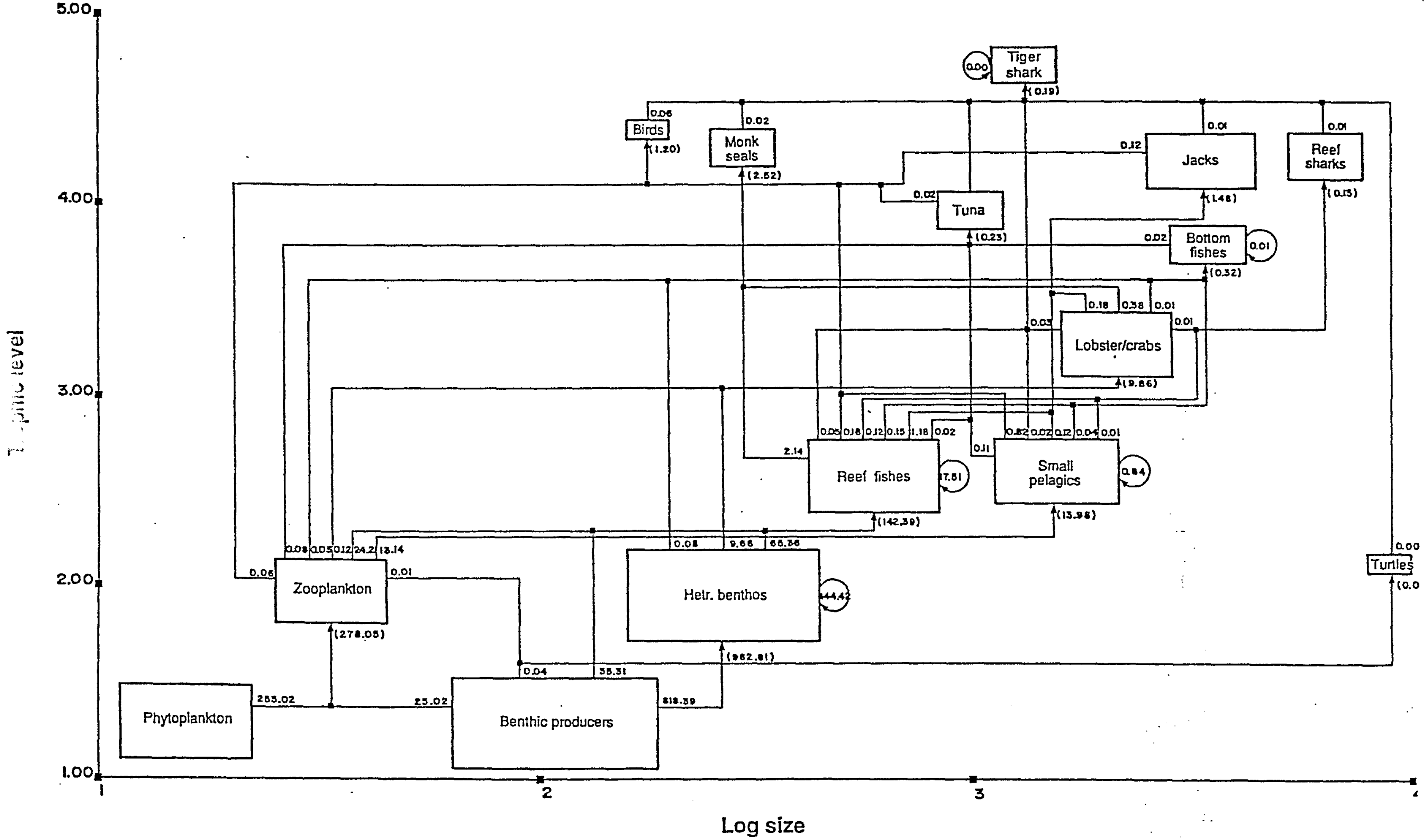

Fig. 5. Size-shifted representation of the French Frigate Shoals. The boxes are positioned after average size and trophic level.

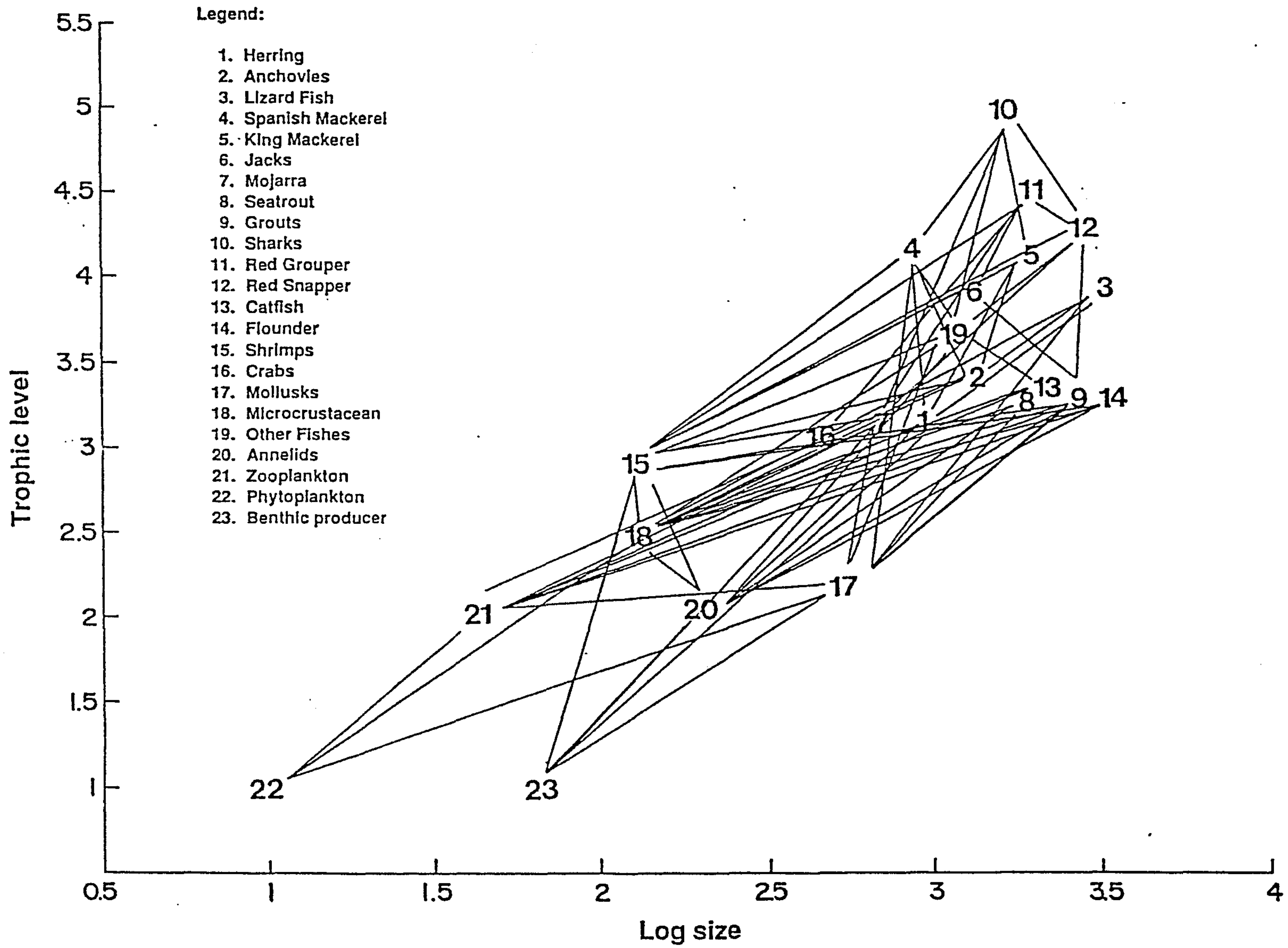

Fig. 6a. Size-shifted representation of the Western Gulf of Mexico ecosystem (Chavez and Arreguin-Sanchez this vol.). Lines indicate presence of flow (5%) between boxes.

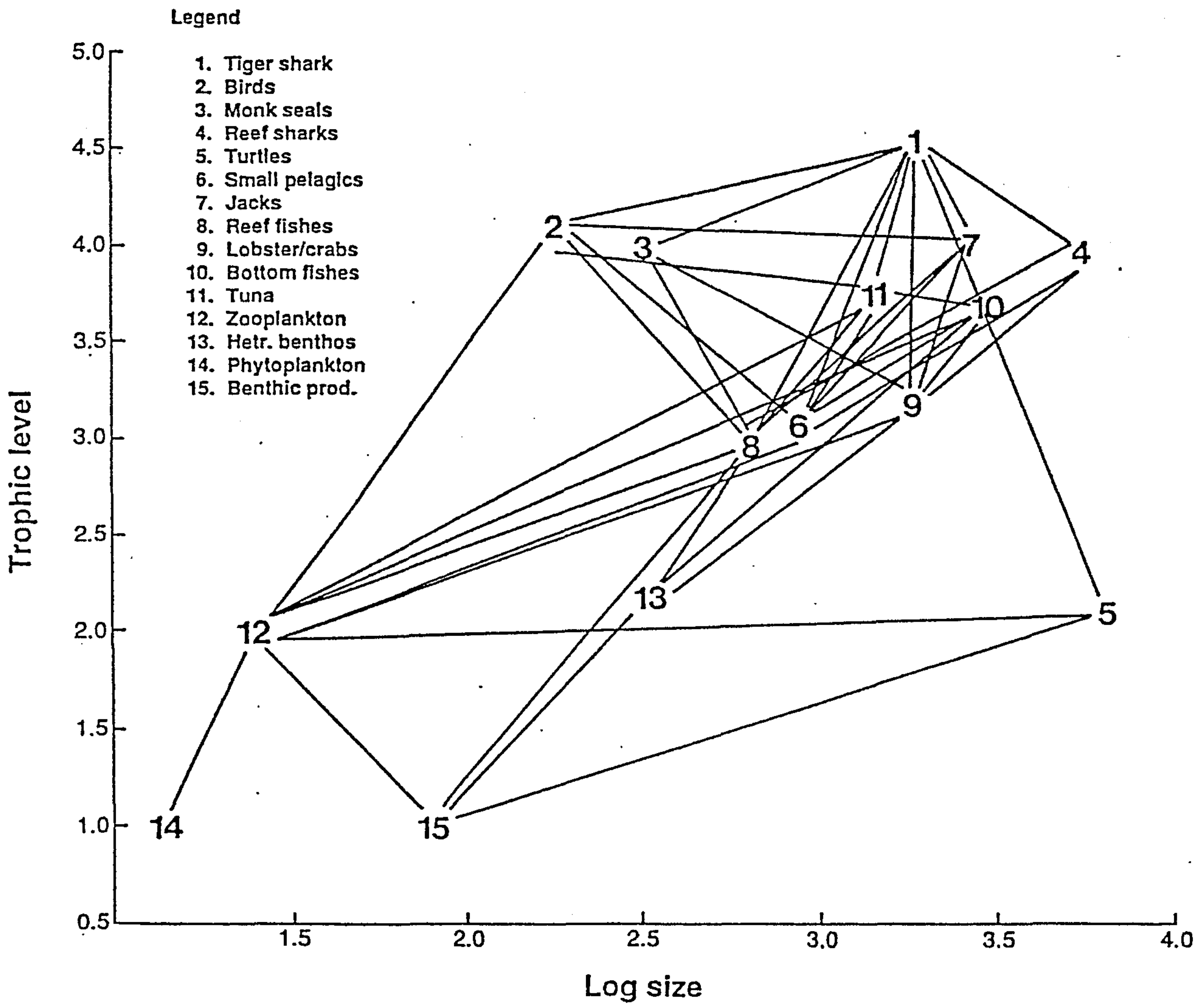

Fig. 6b. As 6a, but for the French Frigate Shoals (Polovina 1984). All flows are included.

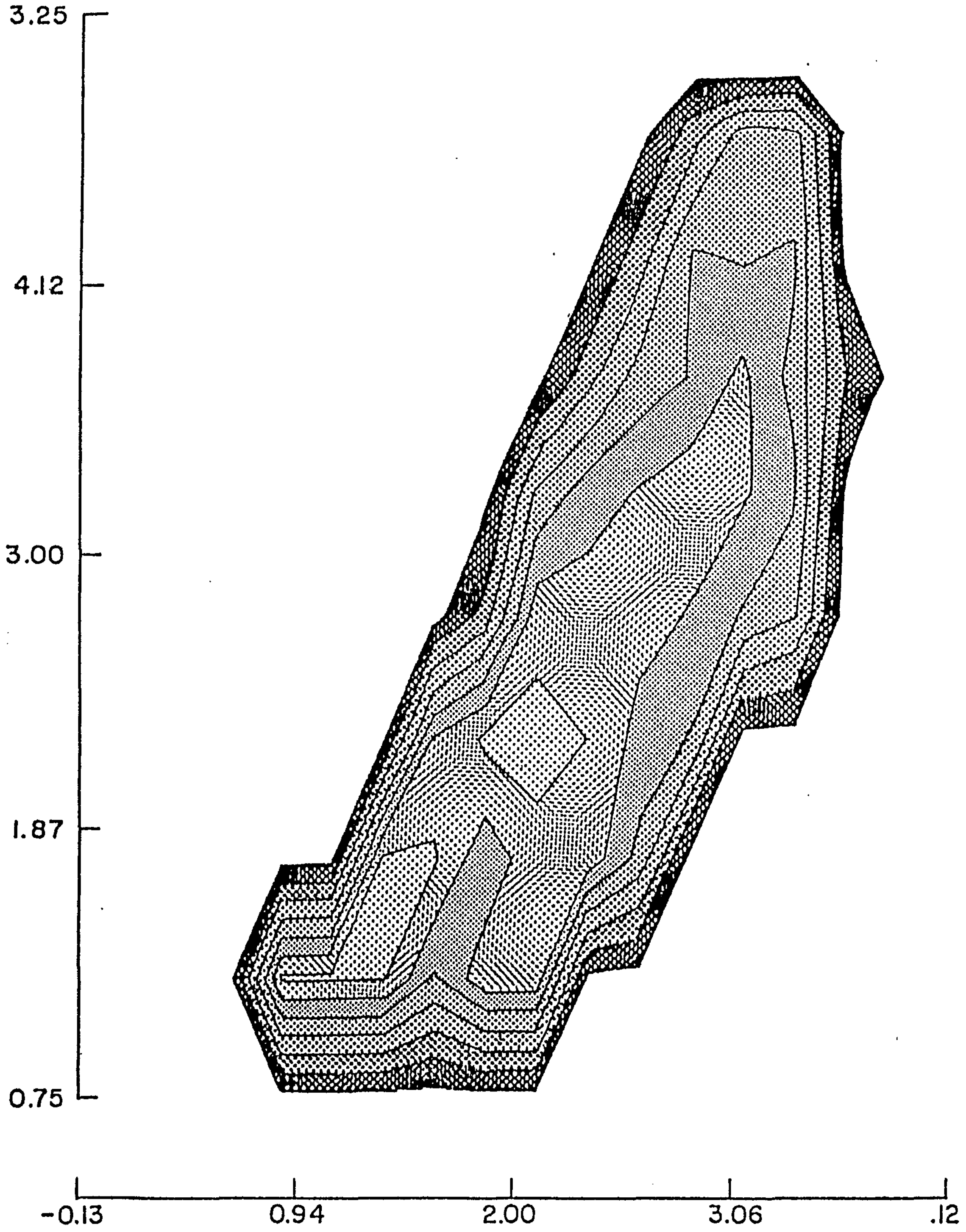

Fig. 7. "Signature" of a steady-state trophic ecosystem model (Western Gulf of Mexico, Chavez and Arreguin-Sanchez, this vol.) as an isopleth of flow intensity (log scale).