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## THE ECOPATH II MODEL

by

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### ABSTRACT

The ECOPATH II model is a steady-state model that includes (i) routines for estimating a missing parameter for all groups in an ecosystem and for balancing the flow in the system, (ii) routines for estimating network flow indices, and (iii) miscellaneous routines for deriving further statistics, as selection indices, omnivory indices, and several others.

## THE ECOPATH II MODEL

Since the International Biological Program (IBP) emphasized *ecosystem* research more than two decades ago, ecologists have studied what may be hundreds of systems or parts of systems worldwide. Thanks to the IBP the focus has been on describing the flows and we now have well developed methodologies for measuring trophic interaction between most groups in a system (Vollenweider 1969; Edmondson and Winberg 1971; Holme and McIntyre 1971; Bagenal 1978; Fasham 1984).

While the IBP focused mainly on the lower part of the ecosystem, where the bulk of the flow occurs, developments in the eighties have led to an improved picture of what is happening with the groups on the higher trophic levels of the systems, i.e., usually those that are commercially exploited. Notable here is a number of complex simulation models developed by fisheries biologists (e.g., Andersen and Ursin 1977) some of which are now on the verge of serving as management tools (e.g., Anon. 1989).

The ecosystem analyses of the IBP and follow up studies have led to a large number of excellent scientific papers describing parts of ecosystems. It appears, however, that few of these studies have resulted in presentation of balanced models. We think this is due to the absence of a suitable tool, i.e., a versatile approach for balancing ecosystem models. We hope ECOPATH II will become this tool. The ECOPATH II software system, which we present further below has, we believe, the features needed for this to happen.

### *Programming language*

ECOPATH II is programmed in M.S. Basic 7.0, Professional Developers Version, and is available from the authors in an executable version requiring no commercial software.

## *The architecture of ECOPATH II*

The ECOPATH II model followed on the ECOPATH model of Polovina and Ow (1983), with which it shares its "basic equation" (see below). This equation was originally proposed for the estimation of biomasses in steady-state ecosystems (see also Polovina 1984). However, from its initial version (Pauly et al. 1987), ECOPATH II was conceived as consisting of three interacting structuring elements.

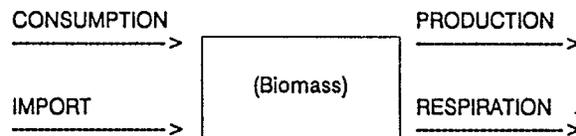
(i) routines for estimating biomasses, or products/biomass ratios, as well as food consumption by the various elements (boxes) of a steady-state trophic model,

(ii) routines based on the theory of Ulanowicz (1986) for analyzing the flows estimated by applying (i) to data, and

(iii) a set of miscellaneous routines for deriving further statistics from the biomasses and flows estimated in (i), and further developing the theory in (ii).

### *ECOPATH. The basic equation*

This routine balances a steady-state model using the 'master equation' of steady-state models,



i.e.,  $\text{Consumption} + \text{Import} = \text{Production} + \text{Respiration}$

where:  $\text{Production} = \text{Export} + \text{Mortality due to Predation} + \text{Flow to Detritus}$

The basic equation of ECOPATH is structured around the feature that, in a balanced system, the consumption of a predator generates the predation mortality of its prey. This can be expressed using a system of simultaneous linear equations which, in ECOPATH II, is solved by the generalized inverse method (Mackay 1981). This method has several advantages over

standard methods for inverting a matrix. Thus it is possible to find a generalized inverse even if the set of equations is overdetermined (more equations than unknowns) and the equations are not consistent, as well as when the system is underdetermined (fewer equations than unknowns), in which case the best possible answer may be obtained.

The main attribute of the basic equation of ECOPATH II is perhaps that by linking the groups it becomes possible to estimate one missing parameter for each of the groups (i.e., biomass, consumption, production rate, or ecotrophic efficiency).

#### *Ulanowicz's theory*

The release of the ECOPATH II model can be seen as a marriage. Not because it is an unbreakable unit, far from, but because it links the world of theoretical ecologists with that of biologists in fisheries and aquaculture. We have thus implemented a number of routines suggested by R.E. Ulanowicz and others. Most notable is the inclusion of a routine for calculating "ascendency" as suggested by Ulanowicz and Norden (1990). Ascendency is a measure of average mutual information in a system. It is scaled by system throughput.

Judged from the theoretical foundation of the concept it seems likely that the ascendency "correlates well with most of Odum's (1969) 24 properties of 'mature' ecosystems. It appears that in the absence of major perturbations, systems mature in the direction of increasing maturity" (Ulanowicz and Norden 1990).

It should be mentioned, perhaps, that as yet only very few ecosystems have been analyzed using the Ulanowicz theory and that it remains to be shown how good a correlation exists between ascendency and maturity. A first attempt at investigating this, however, is presented in the "Global Comparisons of Aquatic Ecosystems" poster (this vol.). For a more thorough discussion of the ascendency concept, it is strongly recommended to examine Ulanowicz (1986) in detail.

#### *Trophic level*

Lindeman (1942) introduced the concept of trophic level. By grouping the taxa occurring in an ecosystem into discrete trophic levels, (producers, herbivores, first-order carnivores, second-order carnivores, etc.), he gave, indeed, appealing pictures of ecosystems. Further, by treating the ecosystem as a thermodynamic unit he could describe the efficiencies of transfers between trophic levels.

Many authors have used pyramids to show these groupings at trophic levels (see, e.g., Fig. 1a). These Lindeman pyramids have for a long time been an important part of high-school ecology, but, as can be expected, the pyramids have also been criticized for being too simple. Thus Cousin (1985), noting that "a hawk feeds on five trophic levels", suggested to abandon the trophic level concept.

Alternatively one can accept that only few species can be placed on discrete trophic levels and instead introduce fractional trophic levels, as suggested by, e.g., Odum and Heald (1975).

ECOPATH II includes such fractional trophic levels. The relevant routine assigns trophic levels (TL) of 1 to producers and detritus (as in the IBP studies) and a trophic level of 1+ [the weighted average of the preys' trophic level] to consumers.

Following this approach a consumer eating 40% plants (TL = 1) and 60% herbivores (TL = 2) will be at trophic level  $1 + [0.4 * 1 + 0.6 * 2] = 2.6$ .

In addition to the calculation of fractional trophic levels we have implemented a routine that aggregates the entire system into discrete trophic levels *sensu* Lindeman. This routine is based on an approach suggested by Ulanowicz (unpubl. data); it reverses the routine for calculation of fractional trophic levels. Thus, 40% of the flow through the consumer group mentioned above would be attributed to the herbivore level and 60% to the first-order predator level. The same, incidentally can be done with Cousin's hawk.

This leads to a further development of the pyramid metaphor: one can give them three dimensions, just as they have in Egypt. An example of this is given in Fig. 1b, where the volume of each of the discrete trophic levels is proportional to the total throughput of the trophic level. The pyramid (as well as those in the poster on "Global Comparisons of Aquatic Ecosystems" (this vol.)) has been drawn so that the (smallest) topangle equals  $4/[\text{the geometric mean trophic efficiency of all consumer trophic levels}]$ . A small topangle - and a "thin" pyramid are thus characteristic of a system with efficient transfer of flow up through the pyramid; and a wide topangle - and a "fat" pyramid are, correspondingly, characteristic of an inefficient system. For the sake of intersystem comparability, we have only included the consumer trophic levels in these pyramids.

The main advantages of using three-dimensional pyramids to show throughput are (1) this obviates the need for using logarithms for scaling and (2) that intersystem comparisons on the same relative scale becomes feasible. (See the poster "Global Comparisons of Aquatic Ecosystems", this vol.) We hope that our solid modified Lindeman pyramids will be perceived as a useful approach for improving the quality of graphics used in representing ecosystems (see also the poster "Three New Approaches for the Graphical Representation of Box Models of Ecosystems", this vol.).

#### *Omnivory index*

Pauly et al. (1987) introduced the concept of 'omnivory index' in which they included the ECOPATH II model. This index is calculated as the variance of the trophic level of a consumer's prey groups. It can be seen indicating how a consumer feeds on the steps of the Lindeman pyramid. When the value of the omnivory index is zero the consumer in question operates on a single discrete trophic level. Cousin's hawk on the other hand would have a high omnivory index.

#### *Selection indices*

One of the most widely used indices for selection is the Ivlev electivity index,  $E_i$  (Ivlev 1961) defined as,

$$E_i = (r_i - P_i)/(r_i + P_i)$$

where  $r_i$  is the relative abundance of a prey in a predator's diet and  $P_i$  is the prey's relative abundance in the ecosystem. Note that within ECOPATH II, the  $r_i$  and  $P_i$  refer to biomass, not numbers.  $E_i$  is scaled so that  $E_i = -1$  corresponds to total avoidance,  $E_i = 0$  represents non-selective feeding, and  $E_i = 1$  shows exclusive feeding.

We have included the Ivlev index because it is often used in the literature. Ivlev's electivity index has however a major shortcoming, seriously limiting its usefulness as a selection index; as shown by, e.g., Jacobs (1974), the Ivlev index is not independent of prey density.

A better approach may be to use a standardized forage ratio ( $S_i$ ) as suggested by Chesson (1983). This latter index is independent of prey availability and it is given by

$$S_i = (r_i/P_i)/(\sum_n r_n/P_n)$$

where  $r_i$  and  $P_i$  are defined as above and  $n$  is the number of groups in the system. The standardized forage ratio takes values between 0 and 1, with  $S_i = 0$  representing avoidance and  $S_i = 1$  exclusive feeding.

As implemented in ECOPATH II, the forage ratio has been reformatted such to vary between -1 and 1 where -1, 0 and 1 can be interpreted as with the Ivlev index.

#### *Cycling index*

An index for how much of the flow that is recycled has been included in ECOPATH II. The cycling index which was developed by Finn (1976) is expressed as percentage of total throughput. It was originally intended to quantify one of

Odum's (1969) 24 properties of a mature system. However, its interpretation is apparently not as simple as Odum conceived, with cycling increasing as a system matures. Findings by Wulff and Ulanowicz (1989) suggest, indeed, that the opposite can be the case.

#### *Fishery efficiency*

The gross efficiency of a fishery or another form of human exploitation can be calculated as total catch over total primary production. If total primary production is not input, a calculated total primary production is used instead. This index is obviously zero in unexploited systems.

#### MIXED TROPHIC IMPACTS

Leontief (1951) developed a method to reveal the direct and indirect interactions in the economy of the USA, using what has since been called the Leontief matrix. Such matrix was introduced to ecology by Hannon (1973) and Hannon and Joiris (1989). The latter developed the method further so that it becomes possible to give qualitative statements of the effect which changes in a group will have on the other groups in a system.

Ulanowicz and Puccia (unpubl. data) developed a similar approach, and a routine based on their method has been implemented in the ECOPATH II model. An example of the use of mixed trophic impact is given in Fig. 2 for the Sierra Leone River Estuary ecosystem (based mainly on data in Longhurst 1983).

#### *Cycles and pathways*

A routine based on an approach suggested by Ulanowicz (1986) has been implemented to describe the numerous cycles and pathways that are implied in an ecosystem.

#### *Aggregation of boxes*

The ascendancy and other features of an ecosystem is affected by the number of groups included in the description. Therefore it seems necessary to standardize

the number of boxes that are included in each system to be able to compare the ascendancy between the systems. Pongase ("Efficient Aggregation of Boxes in Trophic Ecosystem Models", this vol.) has investigated how the ascendancy changes with the number of boxes. He showed that if the systems comprise ten boxes or more, the ascendancy was not markedly affected by a further increase in the number of boxes.

The routine that was used for this investigation is a part of ECOPATH II. It is based on an approach suggested by Ulanowicz (1986).

In addition to the aggregation algorithm suggested by Ulanowicz, we have made it possible in the ECOPATH II to aggregate specific groups or groups that differ by no more than an arbitrary difference in trophic level. The resulting dataset can be used for further analysis with the ECOPATH II model.

#### CONCLUSION

The ECOPATH II model as it is briefly documented here represents an attempt to present an approach and a software that should be useful to any fishery biologist or aquatic ecologist. We have seen it used for systems as diverse as, e.g., rice-fish culture systems, Chinese carp polyculture systems, estuaries, upwelling systems and the open oceans. We see the interest for the approach as an indication of the need for a model that made the transition from readily available population characteristics to balanced ecosystem models a feasible and even easy step. We intend to carry the development of ECOPATH II further, and encourage researchers with interest in using or help developing the model to contact us.

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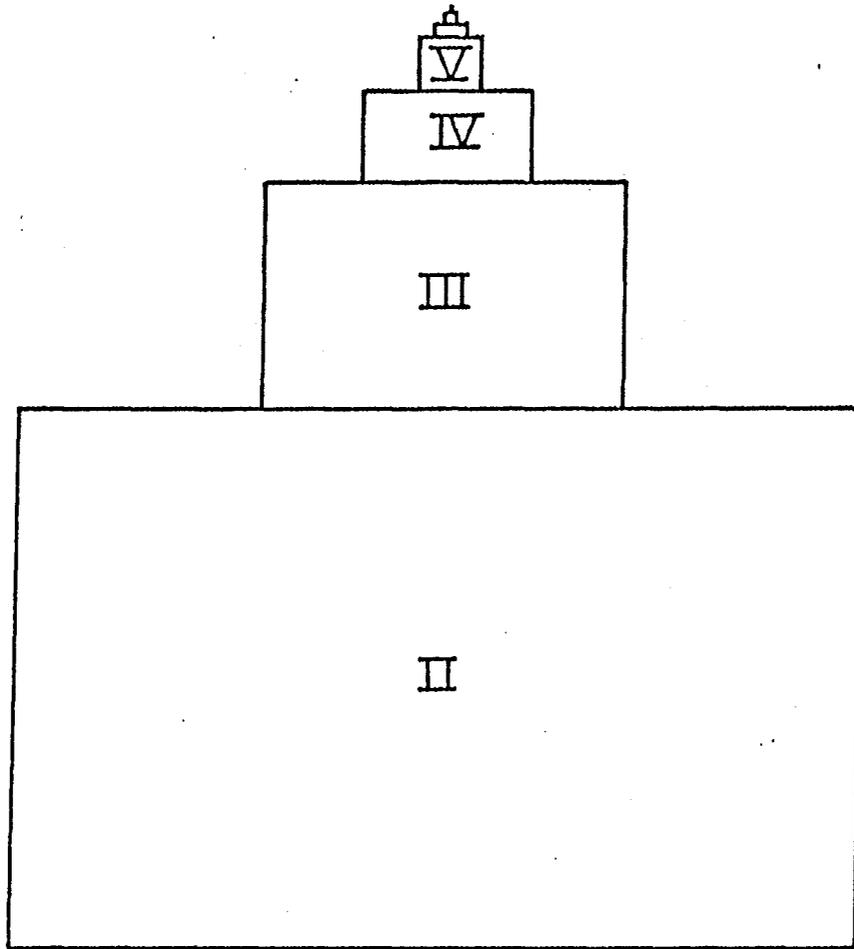


Fig. 1a. The traditional Lindeman pyramid as depicted in numerous ecology textbooks, e.g., Krebs (1972). The system shown here is the Sierra Leone River Estuary ecosystem. The area of each box is proportional to the throughput on each trophic level.

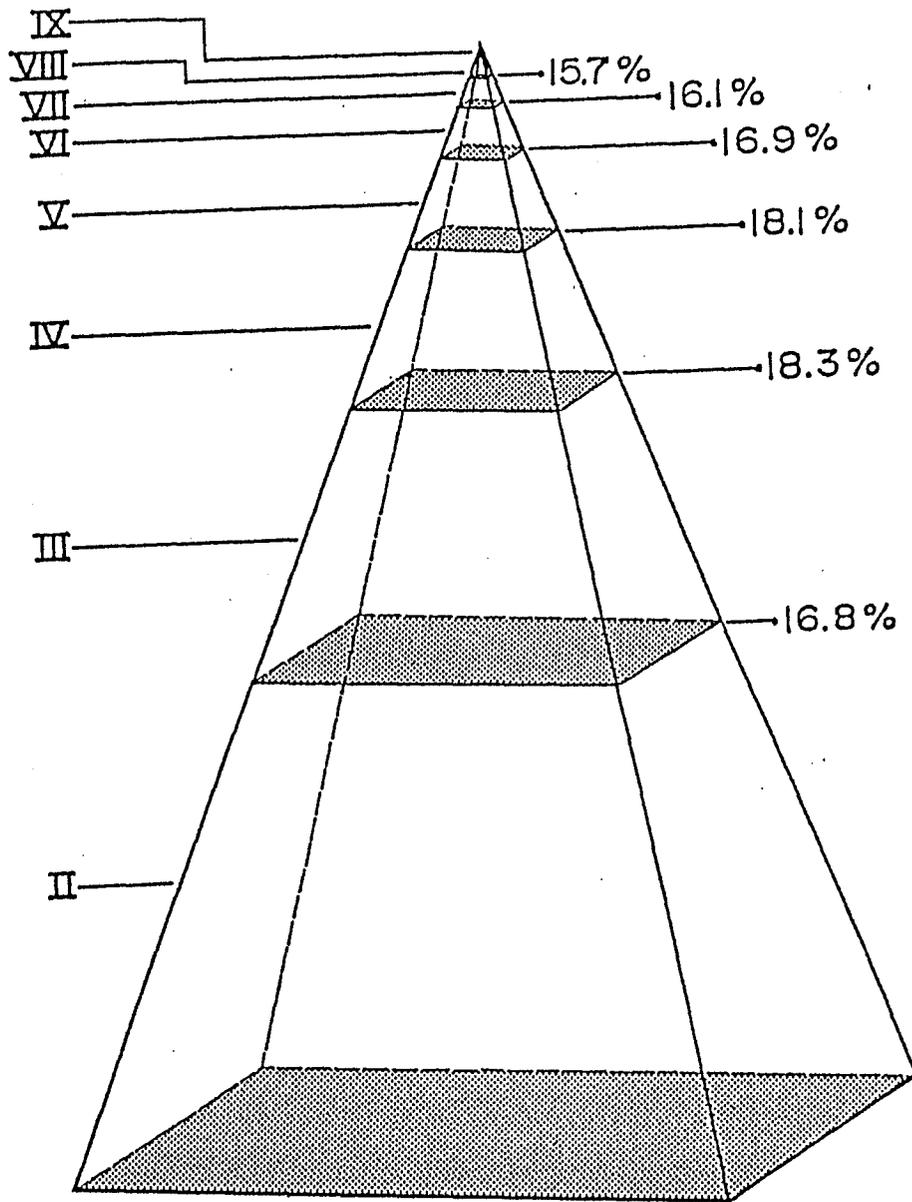


Fig. 1b. The Lindeman pyramid as a solid pyramid. The system is the same as in (a). The volume of each trophic level is proportional to the throughput at that level. The right side of the pyramid gives the transfer efficiencies for each discrete trophic level (Roman letters to the left) The smallest topangle is  $4/[\text{geometric mean efficiency of all consumer trophic levels}]$ .

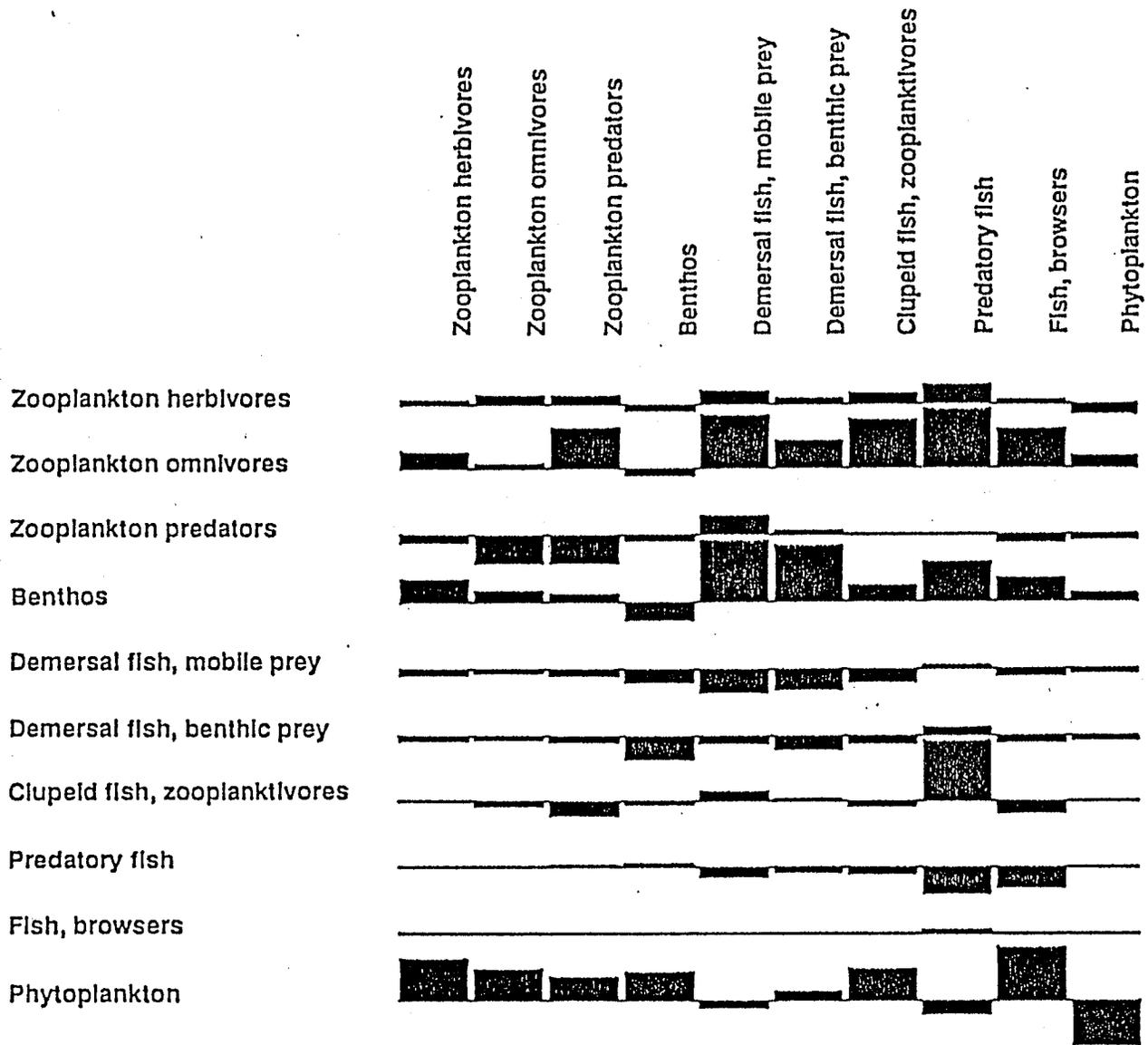


Fig. 2a. Mixed trophic impacts in the Sierra Leone River Estuary ecosystem. The figure shows the direct and indirect impacts on all groups in the system from an increase in the biomass of the group given to the left of each histogram. The impacts are relative and comparable between histograms.

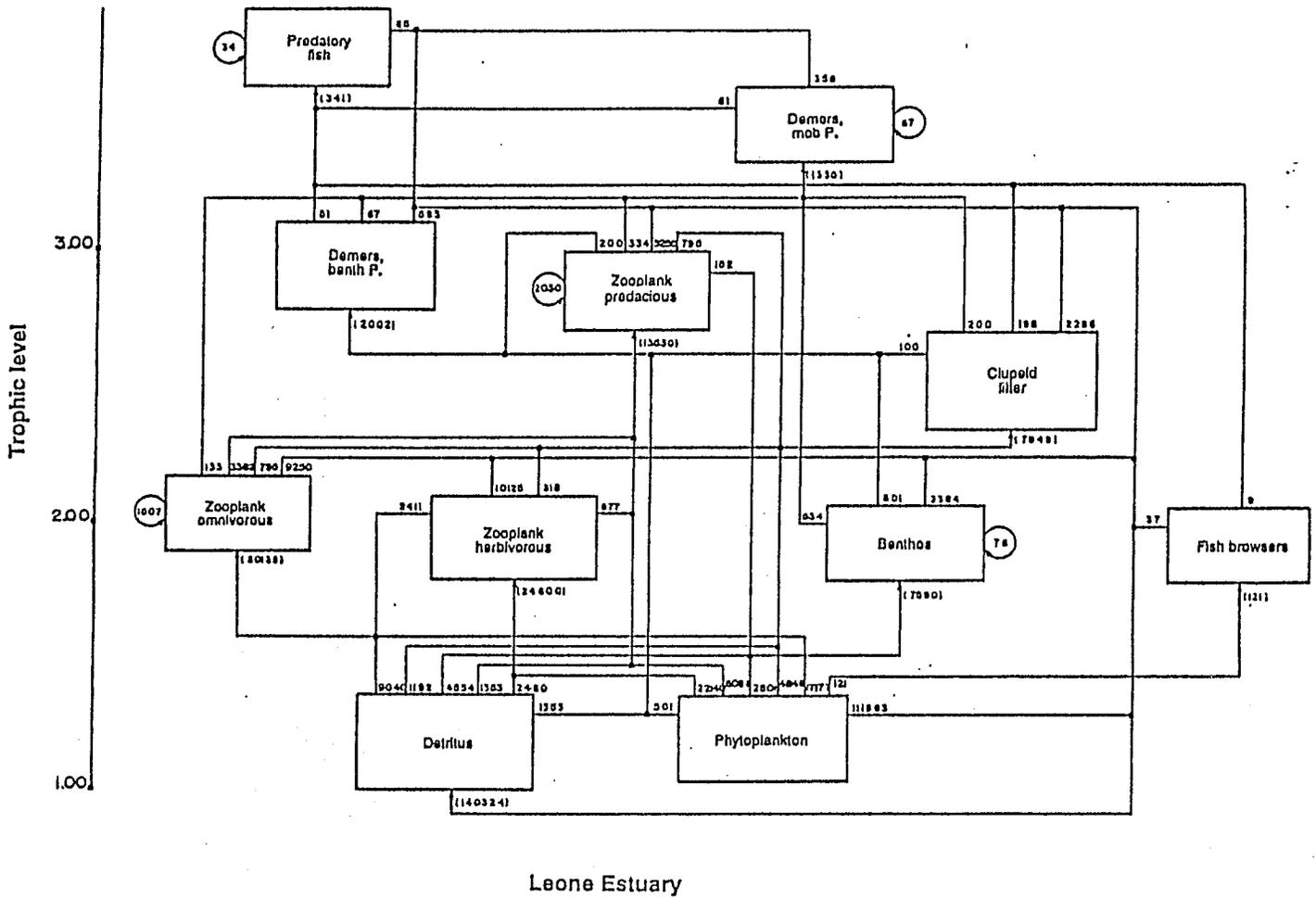


Fig. 2b. The flow diagram of the Sierra Leone River Estuary.